The systematic anatomy of Grevilleeae and Persooniinae (proteaceae)

Dorothy Margaret Catling

The Systematic Anatomy of Grevilleeae and Persooniinae (Proteaceae)

Dorothy Margaret Catling

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Declaration

I declare that the work within this thesis submitted by me for the degree of Doctor of Philosophy is my own original work and has not been submitted for a degree at this or any other University.

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ABSTRACT

The anatomy of leaves was described for 91 species in the Grevilleeae and 15 species in the Persooniinae. The anatomy of the stem-node-leaf continuum was described for 57 species in the Grevilleeae and 6 species in the Persooniinae.

Anatomical features were discussed in the context of taxonomic relationships in genera and, briefly, at higher levels.

In *Hakea*, anatomical data supported the groupings proposed by taxonomists. In *Grevillea*, recognised natural groups were supported and anatomical features were useful in demonstrating homologies in the leaves of some Groups. In *Persoonia* anatomy supported some proposed groupings but, in others, anatomical characteristics showed considerable diversity.

The variability of character states, homologies and homoplasies and the suitability of anatomical data for cladistic analyses was considered.

A preliminary cladistic analysis was made and discussed.

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INTRODUCTION

The purpose of this study

The purpose of this study was to provide descriptions of the anatomy of stems, nodes, leaf bases and leaves of genera in the tribe Grevilleeae and the subtribe Persooniinae of the Proteaceae. The Grevilleeae comprises 3 genera, *Grevillea*, *Hakea* and *Finschia* and the Persooniinae 2, *Garnieria* and *Persoonia*.

Anatomical descriptions will be contributed to the revised edition of Anatomy of the Dicotyledons (Metcalfe and Chalk, 1950).

A close collaboration with Australian taxonomists has developed. Anatomical characteristics will be added to those from other disciplines in revisions of genera which began with the preparation of the new Flora of Australia.

The limitations of this study

The Proteaceae is a large family comprising 75 genera (Johnson and Briggs, 1975), most of which occur in Australia or South Africa. A few representatives are found in the West Pacific and East Asia and in Southern and Central America.

Although the programme was extended to include a few taxa when it seemed relevant to this study, in a limited time, it was not feasible to undertake an overview of the family. It would have been possible to examine very few representatives of each genus and, so, conclusions would have been unreliable.

Plant Taxonomy

The purpose of taxonomy

Davis and Heywood (1963) prefaced their work with a quotation from A. Tindell Hopwood (1959), "The urge to classify is a fundamental human instinct". For botanists, taxonomy is the search for an hierarchical system which will file information and reflect relationships among taxa. Information can be extracted and used to identify plants. "A plant's name is the key to its literature" (van Steenis, 1957). Identification is necessary to many disciplines in biology. If the identity is dubious, the value of work might be diminished, results might not be repeatable. Biologists work with species and their findings might be heavily influenced by the choice of species (Mayr, 1957). Davis and Heywood (1963) reminded us that taxonomy was basic to other disciplines and dependent upon them. The subject has evolved over many years and has not been independent of the social and political environment in which it has developed. For some years there has been a decline in the teaching of taxonomy but, recently, its importance has been acknowledged, especially in conservation and biodiversity (House of Lords Committee Report, 1991).

Early taxonomy

Often, the origins of taxonomy are traced to ancient Greece, to the Peripatetic School in Athens and, especially, to the work of Aristotle and Theophrastus (Davis and Heywood, 1963; Morton, 1981). Aristotelian philosophy has been said to have had a direct influence on the *a priori* reasoning of European taxonomists and, particularly, of Linnaeus (Davis and Heywood, 1963).

Tredenick (1975) has suggested that, in Athens, an increasing interest in rhetoric and dialectic led men to think in abstract terms. This author gave the following explanation of Plato's ideal Theory.

"To each class of objects which have a common nature or definition there corresponds a permanent entity, independent of the members of the class, which is that absolute characteristic which is imperfectly imitated or shared by the several members."

It was against this background that Aristotle and Theophrastus studied animals and plants. Even so, according to Peck (1965), a thorough study of observable differentiae was preferred to an arbitrary selection of features. Aristotle has written:

"But the facts have not yet been sufficiently ascertained; and if at any future time they are ascertained, then credence must be given to the direct evidence of the senses rather than to theories - and to theories too provided that the results which they show agree with what is observed" (Aristotle: *Generation of Animals*, trans. A. L. Peck, 1943).

Although both Aristotle and Theophrastus compared living things and carefully observed their characteristics, they did not attempt to organise them in an hierarchical system. Much of their work was associated with agriculture and horticulture.

The Platonic Academy valued the principles of Logical Division, particularly the rules of Dichotomy or the "Excluded Middle", illustrated by the search for a definition of the angler at the beginning of *The Sophist* (Plato: *The Sophist*. Trans. A. E. Taylor, 1961).

In some but not all of Aristotle's work, dichotomy seems to have been accepted but in '*Parts of Animals*, Book 1', dichotomy is criticised because it splits natural groups.

Meyer (1855) was of the opinion that most of the differentiae which some biologists considered as characteristics distinguishing genera were not used in this way of Aristotle. He said that group names were not meant to mark systematic divisions but were intended only as descriptions. Balme (1962) has said that it is wrong to assume that Aristotle "Put systematics first

in zoology and morphology first in systematics" and Peck (1965) has suggested that whilst Aristotle recognised a definite *scala naturae*, the rungs of the ladder were not the stages of a taxonomic scheme and there is no evidence that Aristotle felt they should be.

For Theophrastus, the study of medicinal herbs was only a part, and probably not an important part, of his work. The writings of Diocles, a physician and contemporary of Theophrastus, dealt particularly with food and drug plants. Only fragments of Diocles' work have survived but they formed the basis of later studies, for example, those of Pliny and Dioscorides, whose *Materia Medica* was completed in A.D.60. Morton (1981) has said that the work of Theophrastus was a culmination not a beginning.

During the Middle Ages, the study of science declined. Medicine was one of the few disciplines which had a continuous history from Hellenistic times until the Renaissance. The work of Dioscorides was constantly copied. Botanical studies were associated with the knowledge of medicinal plants.

The Renaissance

The Renaissance began in the great commercial cities of Northern Italy. Important universities were established in Padua, Bologna and Pisa. In medical schools, the works of Dioscorides were critically studied and many Italian physicians wrote commentaries on them. Attempts to identify plants described by Dioscorides and Pliny led to a study of local species and, eventually, to the publication of Italian manuscripts. Gradually, interest in plants extended beyond the limits of *Materia Medica*. To help in identification and to fulfil the need for greater accuracy, illustrations were made from life. The appreciation of the wealth of botanical life was enlarged by the voyages of exploration of the fifteenth and sixteenth centuries. In Europe, gardens became fashionable and there was increased enthusiasm for the cultivation of exotic species. The first Chairs of Botany were endowed in

Padua in 1533 and in Bologna in 1534, both in association with medical schools, and the first botanic gardens were established in Pisa in 1543 and in Padua in 1545. Consideration of the classification of plants and the choice of characters used in classification gained in importance. It was necessary to question whether plants should be classified for general usefulness or because they were related to one another.

From the middle of the sixteenth century until the influence of Darwin in the nineteenth century, problems in taxonomy were centred around a degree of conflict between *a priori* reasoning and empiricism. The choice of method still concerns taxonomists.

Linnaeus

In his *Genera Plantarum* (1737) Linnaeus described all the genera which he knew and accepted, often basing his description on one species which was familiar to him. In his generic descriptions only floral characters were cited. In *Species Plantarum* (1753) he keyed out nearly 6,000 species in 1,000 genera. Especially during his early studies, Linnaeus attached particular importance to the number and, to a lesser degree, the arrangement of the stamens. Genera were grouped in 24 classes which were subdivided into orders by the numbers of their pistils. Linnaeus was not the first to observe sexuality in plants. This had been proved experimentally by Camerarius in 1694 and, as early as 1718, Boerhaave was teaching the doctrine to his students in Leiden (Morton, 1981).

Linnaeus' work had great impact in most of the Western World where his taxonomic system and terminology were adopted.

Davis and Heywood (1963) thought that, to some extent, the wide adoption of Linnaeus' earlier work, based on logical division supported by a *priori* judgement, led to a neglect of vegetative characters and delayed the

development of a natural system in the Adansonian sense. They suggested that Ray's understanding of the species was perhaps more complete.

Ray believed that all parts of the plant should be studied in classification. He recognised genotypic and phenotypic variation but realised that only the former was of taxonomic significance. Like Cesalpino before him and Linnaeus after him, Ray thought that forms should breed true within the limits of their variation. Following Bauhin (1623), Ray recognised monocotyledons and dicotyledons although he did not use them as his primary divisions, for which he retained habit, subsequently using the categories Monocotyledons and Dicotyledons and then characters of the fruits to further divide groups. Later subdivisions considered characters of the leaf and flower (Ray, 1657, 1660, 1662).

Post Linnaean taxonomy

Adanson, a student of Bernard de Jussieu's published *Familles des Plantes* in 1763. Cain (1959) has suggested that Adanson was ahead of his time. He rejected artificial systems believing that all the characters used should be given equal consideration. Cain felt that Adanson's approach was correct because all organs of the plant should be taken into account to evaluate natural affinity and, also, because the *a priori* principles which were more popular in the early part of the eighteenth century were either superfluous or wrong. Nevertheless, Adanson was not successful. Stearn (1961) has suggested that, probably, Adanson used too few characters and that some of the structures compared were not homologous. Although Adanson's method was not accepted by his contemporaries, Davis and Heywood (1963) have suggested that it helped to establish the natural system as a goal for taxonomy.

From the times of the de Jussieu family until Darwin, botanical thinking was dominated by three generations of the de Candolle family

(Cain, 1959). Auguste de Candolle continued in the approach of Antoine-Laurent de Jussieu. In 1813, he published *Theorie Elementaire de Botanique* "an exposition of the principles of natural classification and the art of studying and describing plants". He believed that all the organs of the plant should be studied and he felt that truly natural classes were necessarily the same whether established on one set of functional characters or another.

Robert Brown was a contemporary of de Candolle. Although he studied floral morphology, he did not devise a system of classification but Humboldt considered him to be *Botanicorum facile princeps*. It was Brown (1810a) who first made a detailed taxonomic treatment of the Proteaceae.

Gradually, more consideration was given to the idea that organisms had not reproduced themselves unchanged since some moment of divine creation but had undergone a development in time. In France, these changes in biological thinking occurred against the background of the Enlightenment. The growth of evolutionary ideas was stimulated by developments in geology and comparative morphology.

Morton (1981) has suggested that the first scientist to publish an overt evolutionary hypothesis was Buffon who, in 1753, cited natural and still continuing processes to support his theory of the evolution of the earth. He gave a clear evaluation of changes and developments in organisms, including the suggestion that 'Ape is of the family of man'. These ideas spread in the intellectual climate of the Enlightenment and, in a few years, in scientific circles, it was generally accepted that animals and plants had changed in the past and would change in the future. Even before this, in 1750, Offray de la Mettrie outlined a theory of evolution in his short essay *Systeme d'Epicure*. La Mettrie excluded any sense of purpose or teleology. He declared "Nature had no more idea of making an eye to see with than has water of acting as a mirror for a shepherdess" (Morton, 1981).

In the middle of the seventeenth century in Germany, Koelreuter repeated Camerarius' work which showed sexuality in plants and continued to conduct his own experiments in which he succeeded in producing plant hybrids and made many careful observations about pollination and fertilization.

The study of affinities practised by biologists devising natural systems of classification was discussed by Lamarck in his *Philosophie Zoologique* and used as one of his leading and most convincing arguments in favour of evolution. Lamarck has been criticised for his assumptions that use or disuse brought about changes in the organs of animals but, in discussing plants, he was less precise, only suggesting that the environment could stimulate change.

Darwin

Darwin's persuasion of evolution and natural selection was not a sudden conversion. The possibility of change in living organisms had been discussed since the middle of the eighteenth century. In 1825, when Darwin went to Edinburgh, at the age of sixteen, to begin his medical studies, the University was already open to many of the new ideas. Darwin met many reformers in science and politics. One of the most notable was Robert Grant who had given up medicine preferring to study marine life. He was a Francophile who was totally committed to sweeping changes in science and society. He followed the teachings of Lamarck. According to Desmond and Moore (1991), "Darwin was coming under the wing of an uncompromising evolutionist". However, in spite of growing support for the new ideas in some quarters, many evolutionists were careful in talking about them. For the Church and the Scientific Establishment they were anathema.

In 1831, Darwin was offered the chance to join the *Beagle* on a two year survey of the coast of South America. The voyage became a journey

around the world. Specimens from the voyage were distributed amongst specialists. Richard Owen examined animals preserved in spirit and some fossils, whilst other fossils were sent to the Geological Society and the British Museum and to Oxford and Cambridge. Thomas Bell, newly appointed Professor of Zoology at King's College London, accepted the reptiles. Birds were studied at the Laboratory of the Zoological Society where John Gould gave his opinion on the finches describing them as an entirely new group containing twelve species. The results of this work and an account of the journey were to be published in a Journal of several volumes. As Darwin worked, he became even more convinced of evolution and the process of natural selection but he still delayed publication of his theory. There can be no doubt that both the opinion of his devout wife and his fear of offending the Scientific Establishment influenced him strongly in this decision.

In 1858, Darwin received a copy of a manuscript from Alfred Russel Wallace. The paper had been written in three days after Wallace had read Malthus' *Essay on Population* (1826). The first edition of this work, published in 1798, had had a great effect on Darwin when he read it during his journey in the *Beagle*. Darwin was unwilling to detract from the interest in Wallace's paper, although colleagues urged him to make his own work known, but, eventually, he agreed that it should be communicated to the Linnaean Society together with his letter to Asa Gray, dated 1857, and an abstract written in 1844. This happened on 1st July 1858. *The Origin of the Species* was published in 1859.

Desmond (1989) has said that Darwin's book came as a bombshell and that, as the metaphor suggests, it was attacked by the dons and devines as an act of terrorism against the old, wealthy elite.

Post Darwinian taxonomy

Although Davis and Heywood (1963) have told us that "The whole course of biological thought was radically changed by the publication of *The Origin of the Species*, there was no revolution in taxonomic thinking. At the end of the preevolutionary era, Bentham and Hooker published *Genera Plantarum* (1862-83). The classification was pre Darwinian in concept. It was largely natural in content and in the delimitation of its groups and owed much to de Jussieu and de Candolle. Hooker was a friend of Darwin and an enthusiastic supporter of natural selection but Bentham persuaded him to continue the work according to the original plan. In an introductory essay to his *Flora Tasmaniae*, published a few months after *The Origin of the Species*, Hooker discussed the natural relationships of plants which could be interpreted as evolution by selection and considered the problems surrounding Darwin's ideas. His balanced debate and final approval of Darwin's work gave weight to the new theory.

Stevens (1984) has told us that although there was now an explanation for classifying together similar individuals, a theory of evolution by means of natural selection did not alter the process of classification but Stuessy (1990) has suggested that taxonomists began to look at their finished classifications in a different light. In the view of Davis and Heywood (1963) "A characteristic of post Darwinian taxonomy has been the construction of phylogenetic trees on extremely dubious evidence. The evolution of organs has been mistaken for the evolution of taxonomic groups and a vast amount of time has been spent in constructing hypothetical trees that might have been better spent in building up a natural system based on overall resemblances".

Table 1.

Examples of Twentieth Century Publications in Plant Taxonomy

Year	Author	Title
1937	Dobzhansky, J.	Genetics and the Origin of Species
1940	Huxley, J.S. (Ed.)	The New Systematics
1942	Huxley, J.S.	Evolution: The Modern Synthesis
1942	Mayr, E.	Systematics and the Origin of Species
1950	Stebbins, G.L.	Variation and Evolution in Plants
1951	Clausen, J.	Stages in the Evolution of Plant Species
1953	Simpson, G.G.	The Major Features of Evolution
1953	Heslop-Harrison, J.	New Concepts in Flowering plant Taxonomy

Population studies

Davis and Heywood (1963) have suggested that one important effect of the publication of *The Origin of the Species* (1859) was the development of the idea that species are not represented by types but by populations. Population studies particularly concerned classification at and below the specific level. Although Darwin had become aware of the significance of population systematics, a more complete understanding of variations was not gained until the re discovery of Mendel's principles of heredity in 1900. Taxonomy extended into cytology, cytogenetics, genetics, experimental and comparative cultivation and similar studies, many of which were grouped under the general title Biosystematics. By the middle of the twentieth century, approaches to taxonomy were revised and discussed in many books (Table 1).

Numerical taxonomy

The term "phenetic" was introduced by Cain and Harrison (1960) to mean a relationship "By overall similarity, based on all available characters without any weighting". Sokal and Sneath (1963) used phenetic to refer to a relationship between taxa "Evaluated purely on the basis of the resemblance existing now in the material at hand" and "To their overall similarity as judged by the characters of the organisms without any implication as to their relationship by ancestry". Later, this was modified to read "Similarity based on a set of phenotypic characteristics of the objects under study" (Sneath and Sokal, 1973). As far as possible, these techniques reduced the influence of any *a priori* evolutionary bias.

"Numerical taxonomy" was a term defined by Sokal and Sneath (1963) as "The numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities. In 1973, they revised the definition to read "The grouping by

numerical methods of taxonomic units into taxa on the basis of their character states".

It was the original intention that methods of numerical taxonomy would be used to determine phenetic relationships but, for some workers, it has come to mean only the use of some quantitative assessments of relationships in classification (e.g. Duncan and Baum, 1981).

Originally, the phenetic approach laid stress on the analysis of large numbers of characters. It was often necessary to use algorithms with computer programs to handle the large amounts of data and calculate taxonomic distance. Numerical taxonomy, as defined by Sneath and Sokal (1973) was a development from the phenetic method. Some workers have used the two expressions as synonyms but, strictly, this is incorrect. More recently, the meaning of "phenetic" has become less precise. It has been adopted by taxonomists who take a traditional view of classification *albeit* with a belief that an Adansonian approach is to be preferred. Often, few characters are studied and methodology is less rigorous.

Cladistic Methodology

In 1981, daily newspapers brought to the notice of the public a controversy which had been continuing in the pages of *Nature* for some two and a half years. Headlines announced Marxist indoctrination by the British Museum (Natural History).

The argument had begun at a symposium on *Vertebrate Palaeontology and Comparative Anatomy* in Reading in 1978 when Dr R.S. Miles, Head of the Public Services Department, explained the Museum's policy towards its public exhibitions. A summary of his talk was published in *Nature* (1978, vol. 275) and, in the same volume, Dr Halstead of Reading University published an opposing view. In these early discussions, there was no mention of Marxism or cladistic methodology.

In November 1980, Halstead wrote to *Nature*. He recalled his earlier criticisms of the Museum's policies and complained that the two new exhibits, dinosaurs, staged in 1979 and fossil man in 1980, were simply vehicles for the promotion of a system of working out relationships known as cladistics. Halstead asked "What is this all about, what actually is going on and what is behind it all?". He answered that the decrying of Mayr and Simpson and, indeed, of Darwin was an attempt to establish the Marxist-Leninist view of development that qualitative changes occur not gradually but rapidly and abruptly, taking the form of a leap from one state to another. The controversy continued in the pages of *Nature* for some months (e.g. Rosen, 1981; Halstead, 1981).

Some cladists could be aggressive in defending their methodology and many, but not all, were left wing. The ideas of Karl Popper (1959) were adopted by many cladists who hoped to set taxonomy on a sound scientific footing (e.g. Gaffney, 1979; Cartmill, 1981). In Europe, political parties of the left were reconsidering their philosophy (Singer, 1988). Popperian ideas were playing a role in politics and science. "And those works which take notice of my ideas usually ascribe views to me which I have never held." (Popper, 1972).

Even at the time of the correspondence in *Nature*, cladistic thinking was being revised (Patterson, 1980). Today some of the most marked controversies are amongst cladists. Generally, cladistic methodology is accepted as one of several useful approaches to problems of classification. Ten years after the battles in *Nature*, one of the "Young Turks of Cladism" (Johnson and Briggs, 1975) is Botanical Secretary of the Linnaean Society of London.

Cladistic Analysis

Rensch (1954, 1959) contrasted two modes of evolution, cladogenesis, the branching events of phylogeny, and anagenesis, the progressive change within the same evolutionary line over time.

Stuessy (1986) defined cladistics as the concepts and methods for the determination of branching patterns in evolution. Cladistic methodology excludes consideration of anagenesis.

Duncan and Stuessy (1985) have said that the earliest cladistic methods developed from needs to determine the shortest routes between points, e.g. to calculate the smallest amount of cable which could be used between telephone stations (Kruskal, 1956; Prim, 1957). The methods were adopted by phenetic workers. The networks of relationships which were derived were phenetic in the sense of being based on unweighted characters. In later applications, the ideas of patterns of branching relationships led to cladistic analysis. In the next ten years there was a rapid increase in the use of cladistic methodology (e.g. Edwards and Cavalli-Sforza, 1964; Camin and Sokal, 1965; Throckmorton, 1965). In 1965, Hennig published an English summary of his *Grundzuge einer Theorie der phylogenetischen Systematik* (1950). An English translation which gave a full account of his philosophy and methods was published in 1966. Meanwhile, in the United States, Wagner developed a teaching manual of cladistic techniques which was published by his student, Hardin, in 1957 and, later, by Wagner himself (1961, 1962). Most cladistic analyses in botany were based on Wagner's work. In 1967, Fitch published a method of tree construction using amino acid sequences of cytochrome c. Similar work, using parsimony methodology, was carried out, in Durham, by Boulter (1972, 1974, 1980). The first generalised method for quantitative phyletics, based on Manhattan distance, originally from Kruskal (1956), was published by Kluge and Farris (1969).

Depending on the type of data and algorithms used, the procedure for cladistic analysis will vary. Stuessy (1990) has given the following general procedures which are used by most workers with conventional data, especially morphological data:-

1. Make evolutionary assumptions (select evolutionary units, determine monophyletic groupings, etc.).
2. Select characters of evolutionary interest.
3. Describe and/or measure character states.
4. Ascertain homologies of characters and character states.
5. Construct character state networks.
6. Determine polarity of character state networks (primitive vs. derived conditions), i.e. "root" the character state networks to form character state trees.
7. Construct basic data matrix.
8. Select algorithm and generate trees (cladograms).
9. Construct classification based upon cladograms.

In giving examples of the use of this method, Stuessy has said that, having checked the homologies of the characters and character states, the character states should be put in a logical sequence based primarily on parsimony of state changes. He suggested that this will be obvious when only two states occur but will become more complicated when there are three or more. The character state network is then rooted to form a character state tree by deciding which state is the most primitive. The states are placed in a basic data matrix, coded to reflect their primitive or derived status.

The most common algorithm used to construct a cladogram is by shared derived character states.

According to Stuessy (1990), fundamentally, shared primitive features are not considered significant in the generation of cladograms because they

are shared by many distantly related taxa but can be used in comparisons within the group under investigation and with closely related groups in an attempt to evaluate primitive or derived character states.

In cladistic methodology, algorithms for tree construction can be grouped depending on whether they use similarities or differences of character states. Some methods depend on Manhattan distance and group specimens using the minimum amount of distance between specimens. Other methods are based on shared derived character states and the maximum number of shared states between specimens is used to construct the tree. Another view of grouping the algorithms considers parsimony, character compatibility and maximum likelihood. Parsimony methods look for trees of minimum evolution among specimens. Character compatibility looks for trees based on the maximum number of characters which have evolved in the same direction. Maximum likelihood leads to the construction of trees which have the highest probability of giving the observed data.

The methods described rely upon assigning characters to a primitive or derived state before analysis. It is also possible to construct a network of relationships among the specimens and then root the network.

The Taxonomy of the Proteaceae

Early history

In 1735, Linnaeus first published the name *Protea*. The group comprised a few species of *Protea, sensu stricto, Leucospermum* and *Leucadendron*. In 1809, Robert Brown used the name to typify the family when he presented his paper *On the natural order of plants called Proteaceae* to the Linnaean Society of London. The paper was later published under the title *On the Proteaceae of Jussieu* (Brown, 1810a).

Table 2.
The Taxonomic Position of the Proteaceae from the Discussion of Venkata-Rao (1971)

Author	Date	Series/Orders	Associated taxa
Bentham & Hooker.	1862-83	Series V. Daphnales.	Thymelaeceae, Penacaceae, Lauraceae, Elaeagnaceae. Santalaceae, Loranthaceae and Balanophoraceae are in the next series the Achlamydosporae.
Engler.	1894.	Proteaceae alone in the Proteales in the class Archichlamydeae.	Between the Urticales and the Santalales.
Hallier.	1912.	Sub-division 3. Rosales and Sapindales.	Santalales with the Myrtales, Tubiflorales and Rubiales in sub-division 4.
Bessey.	1915.	Sapindales.	Santalaceae and Loranthaceae in Celastrales.
Pulle.	1950.	Series IV. Associated with the Myrtales and Rosales, Aristolocheales.	Santalales and Balanophorales in Series II.
Lawrence.	1954.	Proteaceae alone in Proteales.	Next to the Santalales.
Hutchinson.	1959.	Singly in order 22 of the Lignosae.	Next to the Thymelaeales which comprise Gonystylaceae, Thymelaeaceae, Penaeaceae and Nyctagineaceae*.
Rendle.	1959.	Proteaceae alone in the Proteales.	"Undoubtedly, the Proteales and the Santalales are allied to each other and it is difficult to associate the orders with other groups."
Eames. 1961.		Influenced by the interpretation of the nectary as a reduced corolla (Haber, 1961). Therefore cannot be placed in the supposedly primitive Apetalae.	

*Hutchinson regards the Proteaceae as a completely climax group with affinities with Thymelaeaceae.

Later, Brown published two works on Australian members of the family, *Prodromus Florae Novae Hollandiae* (Brown, 1810b) and the *Supplementum Primum* to this work (Brown, 1830).

Brown (1810a) accepted 38 genera in the Proteaceae, sixteen of which were established by him. He divided the family into two groups one of which had indehiscent fruits and the other dehiscent. Venkata-Rao (1971) has said that Brown divided the Proteaceae into two sub families, the Nucamentacea (= Proteoidae) and Folliculares (= Grevilleoideae) in which there were further subdivisions but Johnson and Briggs (1975) have said that subfamilies or tribes were not named by Brown but were set up by Reichenbach (1828), Endlicher (1837) and Engler (1888-9). For the genera known by Brown, his divisions showed excellent correspondence with the two largest families in the most recent taxonomic revision of the family (Johnson and Briggs, 1975).

The origins and affinities of the Proteaceae

The Proteaceae have been given very different positions in various systems of classification (Table 2). Affinities with taxa such as Rosales, Sapindales, Thymelaeaceae, Santalaceae and Loranthaceae, have been suggested. Lawrence (1954) suggested that these differing views were probably the result of a lack of knowledge of the family. By 1971, Venkata-Rao suggested that there was enough information to discuss the affinities of the Proteaceae in a more realistic manner. In shaping his arguments, he used the results of his work on the morphology, cytology, embryology, palynology and floral anatomy of the Proteaceae published between 1957 and 1969 (e.g. Venkata-Rao, 1957, 1959, 1961, 1962, 1963, 1964a and b, 1965a, 1965b, 1966a, etc.) and summarised in his monograph (1971). Because of their importance in his discussions, the position of the Santalales is also recorded in Table 2.

In spite of some floral similarities and a similar geographical distribution, Venkata-Rao rejected Hutchinson's (1946a) suggestion that the Proteaceae were the advanced derivatives of Thymelaeaceae. He said that whilst the flower in the Proteaceae was uniformly simple, the Thymelaeaceae showed greater variety. Venkata-Rao has suggested that both Proteaceae and Thymelaeaceae were probably derived from a common ancestral stock and that, while Proteaceae remained at a low level of organization, Thymelaeaceae evolved and diversified to a greater extent with coincident reductions.

Commenting on the proximity of the Proteaceae, Santalaceae, Loranthaceae and Balanophoraceae in the systems of Engler and Prantl (1887-1915), Rendle (1959) and Lawrence (1954), Venkata-Rao (1971) pointed to the many resemblances in morphological, histological, floral anatomical and embryological features among Proteaceae, Santalaceae, Loranthaceae and Balanophoracae to show that they were derived from common ancestors. He suggested that these families formed a closely knit group in which Proteaceae seemed to be the most primitive and Loranthaceae the most advanced. He felt that there was no evidence to support Hutchinson's (1959) idea that the Proteaceae is a completely climax group.

In the major paper by Johnson and Briggs (1975) the authors cited three systems of classification which were more recent than those considered by Venkata-Rao (1971), Cronquist (1968) included Elaeagnaceae with Proteaceae in the Proteales, one of the orders in the subclass Rosidae. Takhtajan (1969, 1970) recognised a super order Proteanae, within the Rosidae, which included the unifamilial Elaeagnales as well as the Proteales. Thorne (1968) had placed the Elaeagnaceae in the Malviflorae-Rhamnales. Johnson and Briggs said that apart from one or two widely occurring features, the similarities between the Elaeagnaceae and the Proteaceae were only

convergent and secondary. They also rejected any affinities between the Thymelaeaceae and Proteaceae and cited the differences in pollen morphology described by Erdtman (1952) to support this view. Johnson and Briggs (1975) suggested that many of the characters used by Venkata-Rao (1971) in the comparison of the Thymelaeaceae and Proteaceae were "Advanced characters in the respective families and hence scarcely relevant".

Johnson and Briggs (1975) suggested that, to compare families phylogenetically, it was useful to construct summaries of the characteristics of the most recent common ancestors of their living members. In the absence of reliable fossil evidence, they relied on the comparative approach in making a phylogenetic analysis of the Proteaceae. Beginning at the level of the genus, character states were recorded in each taxon. "On the basis of morphological and adaptational principles", the primitive state was established in each character. These data were analysed to prepare a description of Proto-Proteacea. Johnson and Briggs (1975) felt that this description would have applied to a population from which all the Proteaceae known from later periods could have descended. In their opinion, it was unlikely that any modern families were descended from close relatives of Proto Proteacea and so they postulated an early evolutionary history of the Proto Proteacean line after its early divergence. Reasoning in this way, Johnson and Briggs (1975) supported not only a unifamilial order Proteales but, also, its segregation in a uniordinal taxon of higher rank. They cited Novak (1954) as another author who had suggested a long history of isolation for the Proteales.

Proposed changes in the taxonomy of the Proteaceae

Johnson and Briggs (1975) suggested numerous changes in the taxonomic arrangement of the Proteaceae. Only those which affect taxa to be studied in the course of this work are given here.

Genera

75 genera were recognised amongst which were 37 of Brown's (1810) original 38. Of the remaining 38, 31 contained no species known to Brown. It was suggested that *Persoonia*, sensu lato, should be divided into four genera. Three new genera were created. *P. toru* A. Cunn. from New Zealand became *Toronia, P. sect. Acranthera* Benth., endemic to S.W. Australia, became *Acidonia, P. sect. Pycnostylis* Meissn. became *Pycnonia*. These genera have not been formally established and it seems likely that there will be second thoughts about splitting *Persoonia* (Weston, 1991, pers. comm.). Weston (1994) later published the suggestion to include 4 genera, Garnieria, Toronia, Acidonia and Persoonia in the subtride Persooniinae.

Subfamilies, tribes and subtribes

In their earlier work (Johnson and Briggs, 1963), Johnson and Briggs recognised only two subfamilies, Proteoideae and Grevilleoideae. It was thought that *Placospermum* C.T. White and Francis was not appropriately placed in either subfamily.

In 1975, the same authors felt that undue emphasis had been given to fruit characteristics and that *Placospermum* really had much in common with the *Garnieria-Persoonia* group, both in its very large chromosomes and in morphological features. It was decided to establish a subfamily Persoonioideae with two tribes; Persoonieae

and Bellendeneae. The Persoonieae was subdivided into two subtribes, the Persooniinae and the unigeneric Placosperminae.

Venkata-Rao (1971) had suggested that the tribe Placospermeae should be moved from the Grevilleoideae where it had been assigned by Robert Brown (1810) and by those who based their classifications on his groupings, and placed in the Proteoideae next to the Persoonieae. This showed a basic agreement between Venkata-Rao (1971) and Johnson and Briggs (1975) although different rankings were used by the authors.

Within the Grevilleoideae, Johnson and Briggs (1975) grouped 40 genera in seven tribes, five of which were subdivided into subtribes. The subtribe Heliciinae of the tribe Helicieae contained two genera *Helicia* and *Xylomelum*. The tribe Grevilleeae contained *Hakea, Finschia* and *Grevillea.*

In revising Brown's Grevilleeae, Venkata-Rao (1971) transferred *Buckinghamia* and *Darlingia* to the tribe Telopeeae and split the remaining genera into four independent tribes: Oriteae, Macadamieae, Lambertieae and Grevilleeae. *Helicia* and *Xylomelum* were included in the Macadamieae together with *Hicksbeachia, Carnarvonia, Panopsis, Macadamia, Brabeium* and *Heliciopsis.* He suggested that this was the most primitive tribe of the Grevilleoideae being closely related to the Persoonieae of the Proteoideae which, according to his classification, contained 8 genera: *Persoonia, Cenarrhenes, Beauprea, Dilobeia, Bellendenna, Symphyonema, Agastachys* and *Beaupreopsis*. According to the Venkata-Rao's (1971) classification, Grevilleeae contained 7 genera: *Grevillea, Hakea, Finschia, Euplassa, Gevuina, Kermadecia* and *Strangea*. Johnson and Briggs (1975) called this an incongruous mixture apparently based on floral zygomorphy and possession of two ovules. They accused

Venkata-Rao of ignoring the argument that antero-posterior and diagonal zygomorphy must have separate origins and the occurrence of other advanced morphological characters as well as evidence from chromosome numbers. They were adamant that Venkata-Rao's grouping could "On no account be sustained".

This controversy must lead to further disagreement on the grouping of *Helicia* and *Xylomelum* with *Hicksbeachia, Carnarvonia, Panopsis, Macadamia, Brabeium* and *Heliciopsis*. In the classification of Johnson and Briggs (1975) *Carnarvonia* is in the Persoonioideae, not the Grevilleoideae. Both Venkata-Rao (1971) and Johnson and Briggs (1975) agree that this genus has unusual features.

The classification of Johnson and Briggs (1975) is generally acknowledged as the system on which most more recent work on the Proteaceae has been based. There have been no major taxonomic revisions at the family level since that time.

Infrageneric classifications in the Grevilleeae

Grevillea

The first major collection of Australian *Grevillea* was made by Banks and Solander in 1770. In 'On the Proteaceae of Jussieu' (Brown, 1810a) and Prodromus Florae Novae Hollandia (Brown, 1810b), Robert Brown described 38 species of *Grevillea* and, in the Supplementum Primum to the Prodromus, he described 20 new species.

Meisner (1856) published a whole genus treatment and, in 1870, Bentham described 156 species of *Grevillea* in *Flora Australiensis*. Like many other genera in the Proteaceae, after Bentham's publication, *Grevillea* received little attention except for some limited treatment in regional floras (e.g. Willis, 1973; Costermans, 1981). In preparation for a new Flora of New South Wales, McGillivray began his revision of the genus in 1975. His

major work *Grevillea* (McGillivray, 1993) described more than 250 species, 246 of which were endemic to Australia; three were endemic to New Caledonia, one to Indonesia and one to Papua New Guinea. McGillivray arranged the species in 21 Groups based mostly on features of floral morphology. Within larger Groups, there were Subgroups; some suggestions of affinities were indicated. The classification of McGillivray (1993) was used for this project. A later revision of the genus was published by Olde and Marriott (1995). Differences of opinion with McGillivray were mostly at the species level.

Hakea

Like many genera in the Proteaceae, except for some limited development of taxonomic concepts in regional floras (e.g. Black, 1948; Costermans, 1981), *Hakea* had not been revised during this century until work began for the new *Flora of Australia*. A major revision of the genus has been undertaken by Drs W.R. Barker, R.M. Barker and L. Haegi at the Botanic Gardens of Adelaide and State Herbarium. Their preliminary classification, discussed by Barker (1990), was used for this project.

Infrageneric classifications in the Persooniinae

Persoonia

Meisner (1856) divided *Persoonia* into 2 sections, *Leptoslylis* and *Pycnostylis*. He further divided each section into 2 series on the basis of the presence or absence of anther appendages. Bentham (1870) grouped the species in 3 sections which exactly corresponded to 3 of Meisner's series; the fourth was *P. toru*, the New Zealand species. Weston (1983) proposed a new classification of the genus. A summary of this unpublished work was received in Durham in 1988 (Weston, pers. comm.). Although Groups were not clearly defined and the categories might well be revised, the list was a useful guide when the anatomy of the genus was studied.

Systematic Anatomy

The history of plant anatomy is closely associated with the history of the microscope. In the Netherlands, in the seventeenth century, van Leeuwenhoek made and used very small lenses to examine minute objects. Although its inventor is unknown, the compound microscope followed the designing of the first telescope by Lipperhey in Middleburg. In London, Robert Hooke was appointed Curator of Experiments to the Royal Society and, in 1665, he published *Migrographia*.

Like Robert Hooke, Nehemiah Grew was supported by the Royal Society. In 1672, subscriptions totalling fifty pounds were collected from Fellows. This enabled him to become Curator for the anatomy of plants and he was given permission to use the microscope of the Royal Society. The results of his work were published in three books in London (Grew, 1672, 1675, 1679, 1682) and a fourth in Paris.

In Italy, at almost exactly the time that Grew published *Anatomy of Plants Begun*, Malpighi's first work, *Anatome Plantarum Idea* was published in Bologna. His later works were published in London by the Royal Society. Grew and Malpighi had no students and, for some hundred years after their deaths, there were no advances in plant anatomy. When, towards the end of the nineteenth century there was a revival of interest in the subject, botanists from England travelled to the continent to study. Metcalfe (1979) had suggested that Radlkofer, Professor of Botany in Berlin, was one of the first systematic anatomists. He was particularly interested in the Sapindaceae and his work on *Serjania* used anatomical characters in classifying the genus. His anatomical data on the Sapindaceae were summarized in the works of Engler and Prantl (1896). Among the students from England who studied with von Sachs at Wurzberg was D.H. Scott who, shortly after his return to this country, accepted the honorary Keepership of the Jodrell Laboratory at Kew.

Although Scott was primarily a palaeobotanist, it was at his instigation that a major textbook, written by Solereder, a pupil of Radlkofer, was translated and published in English (Solereder, 1899, 1908). Some forty years after the publication of this work *Anatomy of the Dicotyledons* (Metcalfe and Chalk, 1950) was prepared by the Kew Laboratory and The Imperial Forestry Institute at Oxford.

At the Jodrell Laboratory, systematic anatomists worked closely with taxonomists in the Kew Herbarium. In Germany, anatomy was often studied in parallel with physiology (Sachs, 1906).

The history of plant anatomy in France is detailed by Hocquette (1954) and in the United States by Carlquist (1969).

Dr Metcalfe retired from the post of Keeper of the Jodrell Laboratory in 1969. From that time until his death in 1989, he devoted himself to revising the 1950 publication (Metcalfe and Chalk, 1979, 1983, 1985). The work is continuing at Kew and the fourth volume of the revised edition is in press. It is a tribute to Dr Metcalfe's determination to remain up to date in his subject that he enlisted the help of collaborators to write chapters concerning, for example, leaf architecture (Hickey, 1979), the petiole (Howard, 1979), trichome description and classification (Theobald *et al.*, 1979) and the plant surface (Wilkinson, 1979) and to consider techniques such as electron microscopy (Cutler, 1979) and the applications of statistics and computing (Burley and Miller, 1983).

Anatomy, phylogeny and taxonomy

Metcalfe (1983) has said that histological data are not specially significant in taxonomy except as additional characters. He suggested that anatomical characters differ from those that are normally used in herbarium studies only in requiring the relatively high magnification of a microscope to observe them. Systematic anatomy is only one of many lines of investigation

which are included in modern taxonomy. Anatomy can be particularly useful in studying fragments of plants or plant materials and in the complementary exercise, identification.

The taxonomic significance of anatomical characteristics varies amongst taxa. It is necessary to choose useful characters for individual groups (Metcalfe, 1983). This is also true of the phylogenetic significance of characters. Thorne (1963) has pointed out that evolution often tends towards reduction or loss of parts as well as towards greater complexity and elaboration of parts.

It is important to evaluate characters carefully before using them in phenetic or phylogenetic classifications.

The Anatomy of the Proteaceae

Two of the earliest papers which described leaves of the Proteaceae were written by Tassi (1898) and Jönsson (1878-79). Tassi wrote brief notes on fourteen species which included some comments on anatomical features although no detailed descriptions were given. Jönsson recognised paired subsidiary cells associated with stomata in *H. gibbosa* and discussed the occurrence of T shaped hairs. Both authors made beautiful drawings but, in many cases, they were not accurate and interpretations of tissues and cell types were very different from those of later writers. The works of Jönsson and Solereder (1899) were cited in *Anatomy of the Dicotyledons* (Metcalfe and Chalk, 1950) and some of their drawings were reproduced.

Metcalfe and Chalk (1950) summarized what was known about the vegetative anatomy of the Proteaceae based on published works and their own observations. Twenty five genera were described of which twelve were represented in the slide collection of the Jodrell Laboratory. The wood anatomy of twenty eight genera was discussed and, of these, slides of twenty three genera were examined by the authors. The relatively few references

showed how little the anatomy of the Proteaceae had been studied before this time. For leaf anatomy, Renner (1910) and Hamilton (1914, 1927) were reported. For wood, references included Francis (1922), Janssonius (1906-36), Record (1936) and Record and Hess (1943) but all these were general works and there was no publication which dealt particularly with the Proteaceae. Renner (1910) was concerned with features of the epidermis in *Hakea*. Hamilton (1914, 1927) described the sceraphytic (sic.) structures of the leaf in the Australian Proteaceae. He discussed leaf shape in *Hakea* and *Grevillea* and the conditions on hair types and features of the epidermis, as well as the amount and form of sclerenchyma although fibres and sclereids were not always distinguished. Some significance was attributed to the number of rows of abaxial and adaxial palisade and the dimensions of their cells.

Venkata-Rao (1971) supported his views on the taxonomy of the family with information from his own studies of floral anatomy, embryology and seed anatomy (e.g. Venkata-Rao, 1967b, 1969) and compared his interpretations with those of Haber (1961, 1966). When considering the leaves, he discussed their gross morphology and drew conclusions about reduction and structural modification to support a theory of the migration of the family from the rain forests to open spaces and waste lands.

Venkata-Rao (loc. cit.) cited Hare (1944) in suggesting that variations in petiole structure might be shown to have taxonomic interest if a more complete study were made. He quoted Hare's opinion that generally there were three broad types in the arrangement of the vascular and sclerenchymatous tissues of the petiole, the U shaped, the O shaped and the I shaped of his own work. Venkata-Rao reported "In his extensive studies of the petiolar anatomy in Proteaceae, the author has not come across any example of the I type of arrangement. The U and O types merge into one another by intergrading series". He reported that the simplest type of petiolar

structure was one in which there were three widely spaced vascular bundles each of which was associated with some sclerenchyma. He proposed a sequence of increasing complexity but thought that, probably, evolution in the petiole was retrogressive and that more complex types represented the primitive condition and the simpler the advanced.

In discussing leaf anatomy, Venkata-Rao (loc. cit.) suggested that, based on the results of his own studies, the majority of taxa showed xeromorphic features which, he said, indicated that the family "Arose under hygrophytic (rain forest) conditions and spread into the open arid spaces by an evolutionary modification of the leaf". The hygrophytic leaf type was described in *Agastachys odorata* and *Beauprea paniculata*, species included in Persoonieae in the author's revised taxonomy. It was characterised by a uniseriate, poorly cutinised epidermis in which stomata, flush with the surface, were found on both the abaxial and adaxial sides of the leaf and by thick, homogeneous mesophyll composed of spongy mesophyll only. Leaves in other taxa were categorised as dorsiventral, isolateral or centric. Although the characteristics of the leaf were described with reference to taxa studied by the author, there was no discussion of their taxonomic or phylogenetic significance.

Venkata-Rao (1971) briefly mentions the wood anatomical studies of Chattaway (1948) and studies of stem anatomy in *Protea repens* L. and *Leucadendron adscendens* R.Br. (Visser, 1965), as well as the description of root anatomy (Purnell, 1960).

Johnson and Briggs (1975) based most of their conclusions about the taxonomy of the Proteaceae on the study of characters of the flowers and fruit but they also considered some vegetative anatomical characteristics. They commented on vegetative features associated with different habitats, including sclerophylly and nanophylly. In an earlier paper (Johnson and

Table 3.

Hair types used in the Taxonomic Revision of the Proteaceae (Johnson and Briggs, 1975)

Character	Primitive	Derived
Terminal cells of trichomes.	Unbranched	-
"Glandular" hairs (more than 3-celled).	Absent	Present

Table 4.

Wood Anatomical Characters used in the Taxonomic Revision of the Proteaceae (After Johnson & Briggs, 1975)

Character	Primitive Condition	Derived Condition
Vessels	Solitary or in small clusters.	In narrow or broad tangential bands.
Parenchyma	Scanty, paratracheal only.	Broad bands associated with vessels only. Additional bands as well as those associated with vessels.
Rays	(a) Uniseriate only, or variable in size but not divided into different types.	Uniseriate and multiseriate rays both present.
	(b) Rays small (1-2 mm high).	Larger rays present (to 5-10 mm or more).
	(c) Without vascular tissue.	Including strands of vessels and tracheids.
	(d) Without stone-cell clusters.	With stone-cell clusters.

Briggs, 1963) the authors had said that truly compound leaves with distinct leaflets were uncommon in the family and there seemed no reason to accept them as necessarily primitive. They suggested that large flat leaves with a tendency to be pinnatifid, at least in juvenile stages, were common in apparently tropical Proteaceae and that traces of such conditions were frequent in juvenile stages of advanced genera. It was thought that this might well be the ancestral condition, giving rise to simple toothed or entire leaves on the one hand, and the various fully compound leaves on the other. In their later work (Johnson and Briggs, 1975) they gave a table of character states in the Proteaceae in which they detailed adult leaf types. Johnson and Briggs (1975) described the generalized and, in their opinion, primitive venation in the family as pinnate reticulate and more or less brochidodromous, as defined by Hickey (1979). In making their taxonomic revision of the family, the authors used hair types and wood anatomical features as character states (Tables 3 and 4).

Chattaway (1948) considered only very few taxa in evaluating the wood anatomy of the Proteaceae. Mennega (1966) studied *Euplassa* and its relationship with other Proteaceae of the Guianas and Brazil and Lanyon (1979) described the anatomy of three proteaceous timbers: *Placospermum coriaceum, Dilobeia thovarsii* and *Garnieria spathulaefolia*. There are some descriptions of proteaceous woods, mostly commercial timbers, in more general, geographical, works (e.g. Detienne *et al.*, 1982). There is no comprehensive account of the wood anatomy of the Proteaceae.

Following the major taxonomic revisions of the family by Venkata-Rao (1971) and Johnson and Briggs (1975), there have been few publications on the anatomy of the Proteaceae.

Heide-Jorgensen (1978a and b) published three papers on features in the scleromorphic leaves of *Hakea suaveolens*. The occurrence of foliar sclereids in leaves has been discussed by, amongst others, Das (1977), Rao

(1979, 1991) and Rao *et al.* (1985). In 1976, Lamont wrote about the *Hakea sulcata* group. The same author has written on the anatomy of proteoid roots in *Hakea* (e.g. Lamont, 1972, 1973) and has collaborated with others to publish papers on the *Hakea fulcata* group (Lamont *et al.*, 1987) and on *H. trifurcata* (Groom *et al.*, 1994).

To a limited extent, anatomical characters have been used by taxonomists in revising some taxa (e.g. Weston, 1983, 1994; Lee, 1984; Haegi and Barker, 1985; Foreman, 1983).

More has been written about the anatomy of *Hakea* than about *Grevillea*. Most of the papers which treated the larger genus were of general interest (e.g. Medina *et al.*, 1990; Dell, 1977; Sundberg, 1986; Wilson, 1924). Schumucker included some details of leaf anatomy in a study of transpiration in the Proteaceae and Lamont (1982) wrote about the glandular hairs in *Grevillea leucopteris* in a paper which discussed the reproductive biology of the species. Recent papers have described cuticular morphology in North Queensland rainforest Proteaceae (Carpenter, 1994), and the vascularisation of seedlings and cotyledons in the family (Neubauer, 1991).

There has been no comprehensive anatomical study of the family. The first results of the work which has been done in Durham were published in 1995 (Catling and Gates, 1995a and b).

For the Persooniinae, even less has been written about the anatomy than for the Grevilleeae. Some papers have described the wood anatomy, particularly in New Zealand taxa (e.g. Butterfield and Meylan, 1974, 1976 and Patel 1992). The structure of pollen grains has been studied by Fever (1986, 1990). Seed anatomy has been examined by Filla (1925-26). No papers have contained detailed descriptions of the anatomy of leaves or of the stem-leaf continuum.

Ecology and phytogeography

Many Australian Proteaceae are highly xeromorphic. The anatomy of the family cannot be discussed without some consideration of the environment, particularly temperature and water and nutrient availability.

From a study of characteristics of the various taxa, it is possible to construct hypotheses about their centres of origin and their spread to colonise new areas and different climatic regions.

Many authors (e.g. Venkata-Rao, 1957, 1971; Levyns, 1958, 1964; Keast, 1973; Good, 1974) have discussed the past and present distribution of the Proteaceae and several different views about the spread of the family have been expressed. Raven and Axelrod (1972, 1974) particularly discussed the growing acceptance of the theory of continental drift and the significance of the distribution of plants from the former land mass of Gondwanaland.

Johnson and Briggs (1975) divided Australia into several ecogeographic regions to be considered together with a table which showed the distribution of tribes and sub tribes throughout the continent. In an earlier publication (Johnson and Briggs, 1963) the authors had suggested that the Australian Proteaceae had spread from some northern, or at least tropical, source into the southern lands. By 1975, they had modified this hypothesis in the light of developments in the theory of continental drift. Basing their revised ideas on their morphological analyses and biogeographical evidence, Johnson and Briggs suggested that, at the time of their early diversification into sub families, tribes and sub tribes and their spread amongst the southern land masses, the Proteaceae were trees or at least fairly large woody plants, growing in closed forests.

MATERIALS AND METHODS

MATERIALS

Specimens examined are listed in Appendix I

Grevillea

In descriptions and discussions, the infrageneric arrangement of McGillivray (1993) was used. the genus was sampled before this work was available. Species were chosen using Flora Australiensis (Bentham, 1870). Those selected did not represent all the Groups described by McGillivray.

The specimen of *G. repens* was from the collections of Dr D.B. Foreman, Royal Botanic Gardens and National Herbarium, Melbourne, Victoria. Samples and herbarium specimens, together with details of the location and surrounding vegetation were retained in Melbourne.

Hakea

Numbers with the prefix WRB refer to the spirit collection of Dr W.R. Barker. Samples and herbarium specimens, together with details of locations and surrounding vegetation were retained at Adelaide Botanic Gardens and State Herbarium. *Hakea* "Pingelly" L. Haegi, Haegi 4041 and *H. ferruginea* B. Moore, B. Moore 191, were also from the Adelaide collections.

Plants of *H. leucoptera*, *H. nodosa* and *H. muelleriana* were carefully sampled by Mrs Helen Lee. Details were retained by her at La Trobe University. *H. undulata*, R.B.G. Sydney 853783, *H. eriantha*, R.B.G. Sydney 13385 and *H. neurophylla* from Cranbourne Botanic Gardens were collected and fixed on site.

Persoonia

The specimen of *P. mollis* (Weston 1267) was from the collections of Dr Peter Weston, Royal Botanic Gardens, Sydney. Samples and herbarium

specimens, together with details of the location and surrounding vegetation were retained in Sydney.

METHODS

Recipes for reagents are given in Appendix III.

Fixation

Fresh material was fixed in Formalin Acetic Alcohol (FAA) for two to three months, washed thoroughly and stored in 70% methanol. Herbarium material was boiled in water for 10 minutes and treated as fresh material.

Plants were not divided into small pieces but kept intact for study of the three dimensional structure.

X-ray photography

To show venation patterns, leaves were X-rayed using adaptations of the method of Simola (1968). Apparatus comprised a Solus Schell Type F 1947 generator and a Machlett Type AEG X-ray tube. Voltage was maintained at 7 kV and current at 10 ma. Flattened, dried leaves were positioned 300 mm from the tube on Du Pont 'Cranex' X-ray film. Exposure times varied from 18-25 minutes according to the thickness and density of the specimen.

Sectioning

Stem-node-leafbase-leaf continuum

Where sufficient material was available, the whole stem-node-leaf continuum was sectioned. Nodes with mature leaves were chosen.

Above the node, the leaf and stem were pulled together and tied so that they were parallel. The specimen was inverted and held between a split cork in the Naples clamp of a Reichert OME microtome. From below the node to within the leaf, sections 20 μm thick were cut continuously and collected in numbered dishes. Microscope slides were numbered to correspond with dishes and, therefore, with levels within the plant. By sequential examination, it was possible to trace the three dimensional structure.

Centre leaf

Wherever possible, mature leaves from four shoots of decreasing age were sectioned. Leaves were held between a split cork in the Naples clamp of a Reichert OME microtome. Transverse and longitudinal sections 20 μm thick were cut midway between the leaf tip and leaf base.

Staining

To make permanent microscope slides

Sections were cleared and stained with Alcian Blue and Safranin.

Sections were treated in the following ways:

Cleared until they were colourless using commercial sodium hypochlorite solution (Parozone) diluted with an equal amount of distilled water.

Washed in distilled water.

Transferred to Alcian Blue and stained for 5 minutes.

Washed in distilled water.

Transferred to 25% methanol for 2 minutes.

Transferred to Safranin and stained for 2 minutes.

Dehydrated in a graded methanol series (50%, 70%, 90%) and 2 changes of absolute methanol, leaving sections in each solution for 2-3 minutes.

Cleared in Histoclear for 2 minutes.

Mounted in DEPEX or Canada Balsam.

To stain tannin

Freshly cut, uncleared sections were stained in a one percent solution of ferric chloride in 0.1 N hydrochloric acid (Gahan, 1984). Sections were reacted for 15 minutes. Tannin sites showed blue-black.

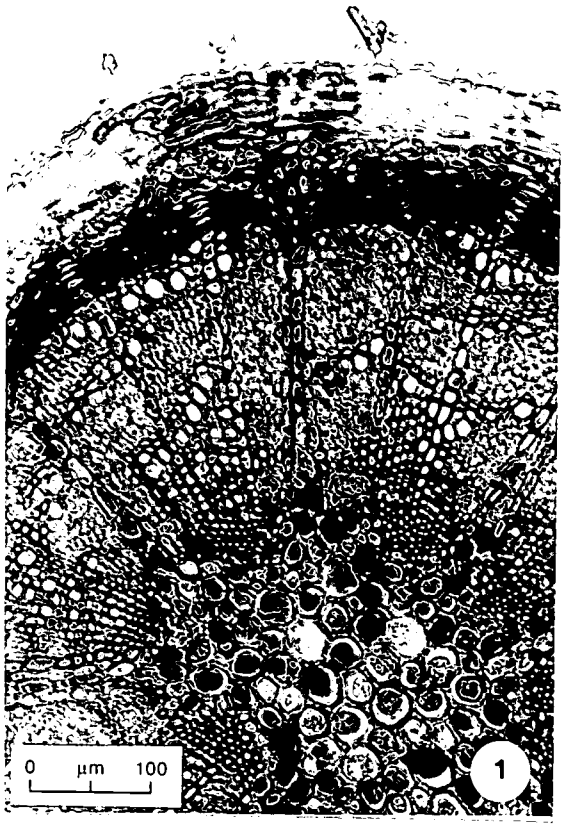
To stain for lignin

Freshly cut, uncleared sections were soaked in a one per cent solution of phloroglucinol in 95 percent alcohol. Sections were drained and put into concentrated hydrochloric acid. Lignified tissues stained red.

Photomicrography

Photomicrographs were taken using a Nikon Optiphot-2 and Kodak Technical Pan film.

Figs. 1-6. - 1, *G. australis* var. *montana* (T.E. Burns 5302/9013). Stem, transverse section. - 2, *G. acuaria* (Melville & George 71.442). Cortex, transverse section. - 3, *G. insignis* (George 343). Cortex, transverse section. - 4, *G. saccata* (D.J. McGillivray & George 3277). Cortex, transverse section. - 5, *G. sericea* (N.S.W. 17828). Pith, transverse section. - 6, *G. sericea* (N.S.W. 18628). Pith, transverse section.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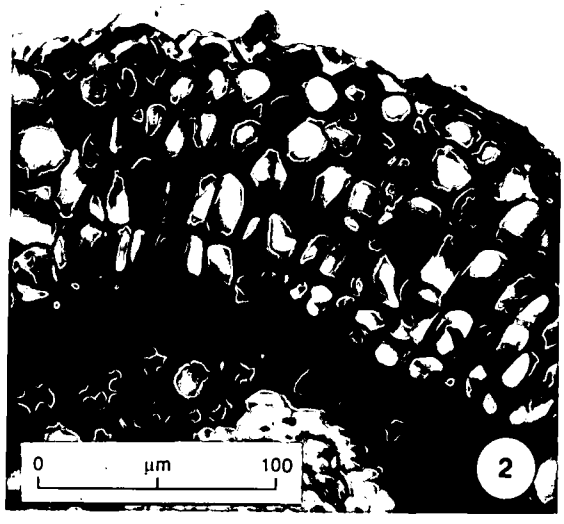
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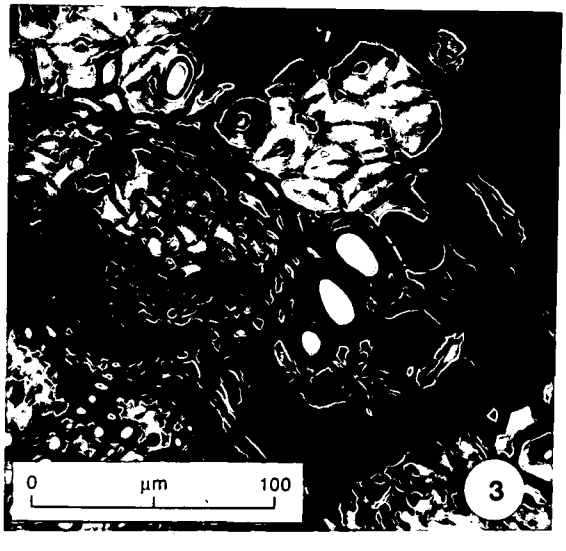
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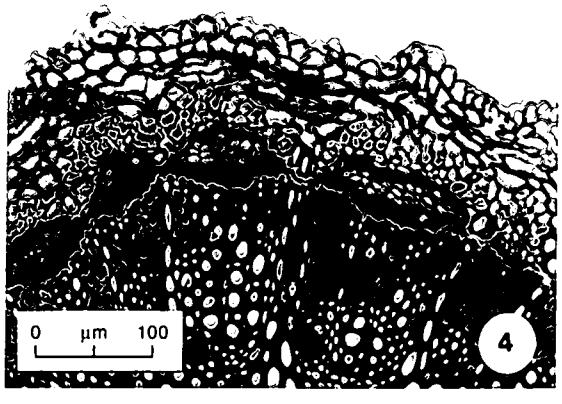
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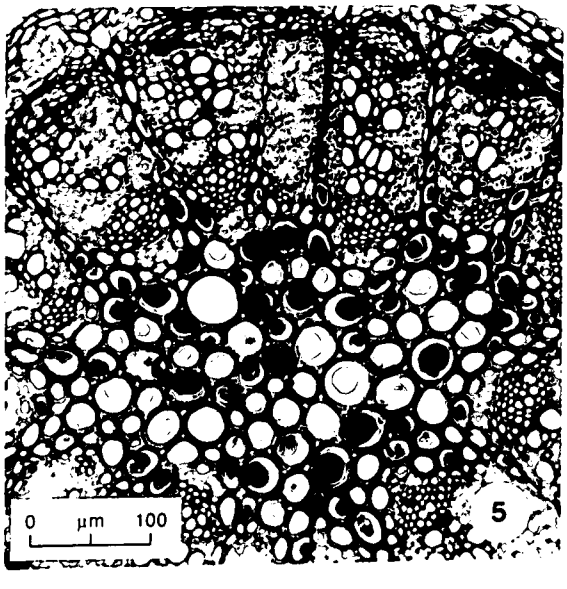
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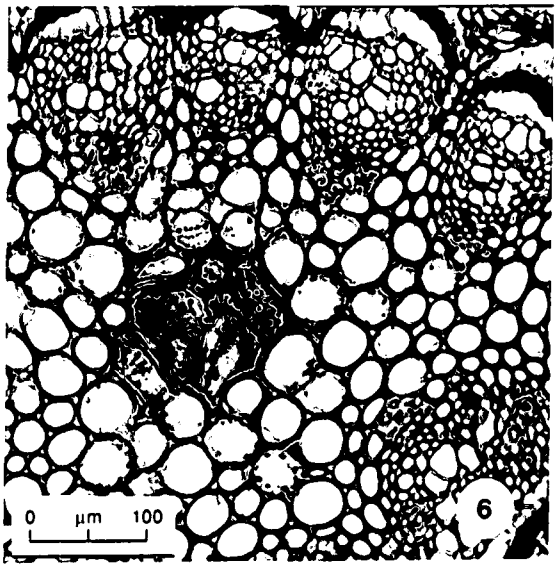
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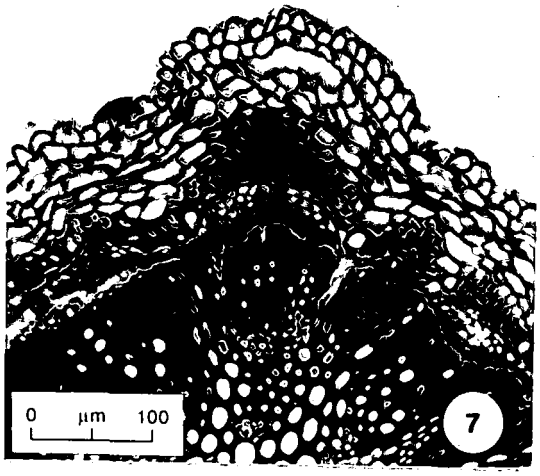
Figs. 7-13. - 7, *G. saccata* (Kew neg. 223b). Median leaf trace, transverse section. - 8, *G. acuaria* (Tindale 3756). Node, transverse section. -9, *G. polybotrya* (Kew no. H973/80 243). Leaf base, transverse section. - 10, *G. polybotrya* (Kew no. H973/80 243). Leaf base with abscission layer, transverse section. - 11, *G. papuana* (NGF 38967). Leaf base, transverse section. - 12-13, *G. occidentalis* (Drummond 270). Leaf base, transverse section.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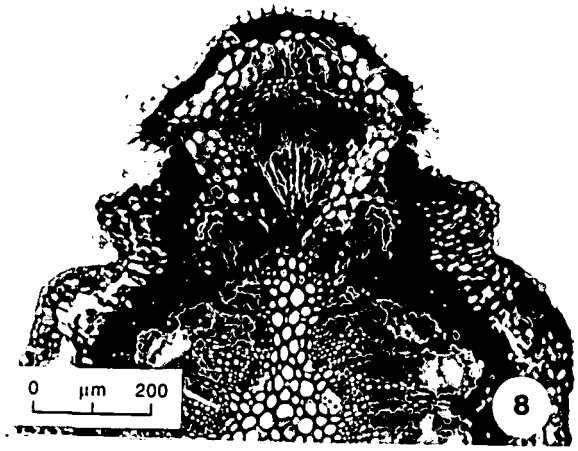
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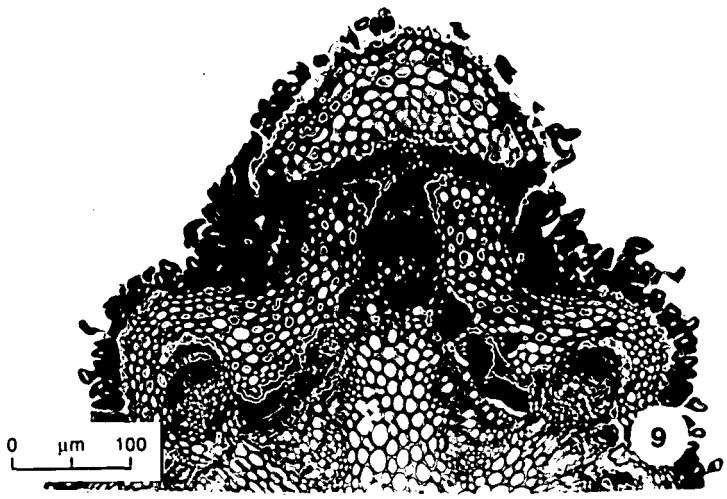
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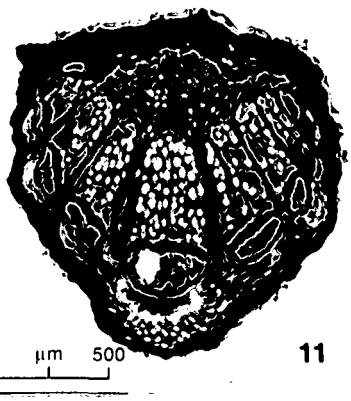
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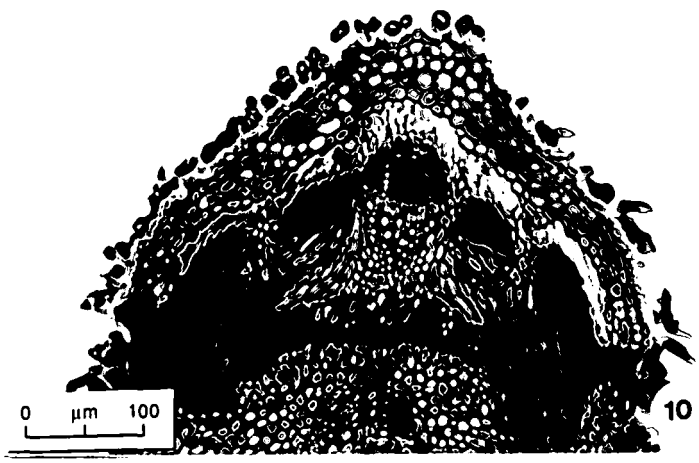
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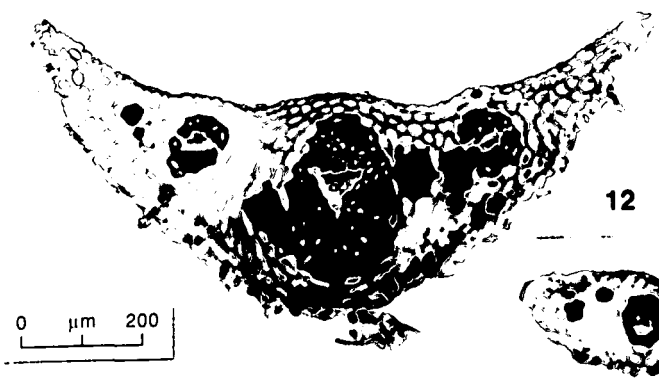
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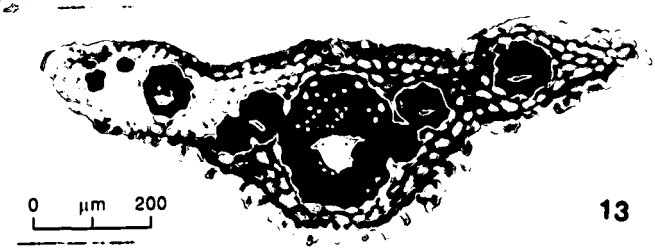
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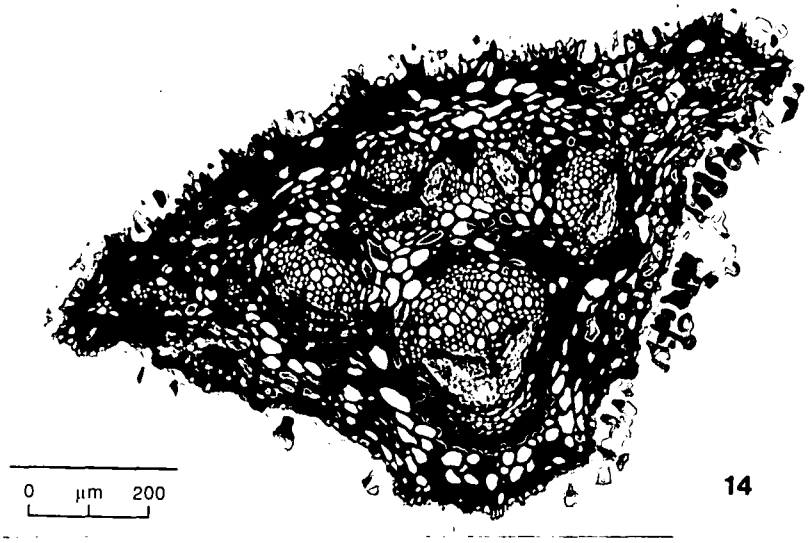
Figs. 14-18. - 14, *G. meisneri* (Vieillard 3092). Leaf base, transverse section. - 15-18, *G. biformis* (Strid 20757). Leaf base, transverse section.



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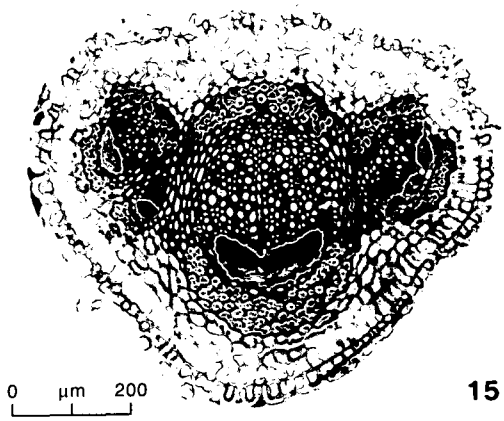

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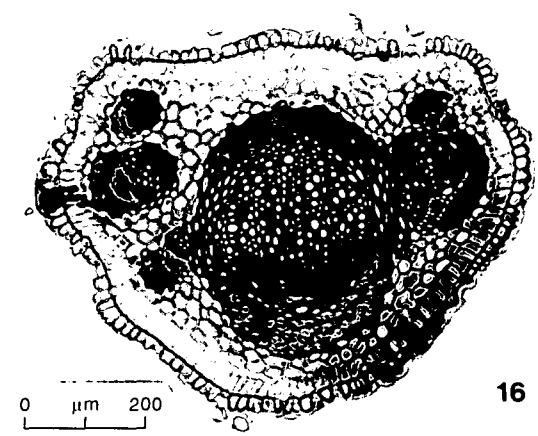

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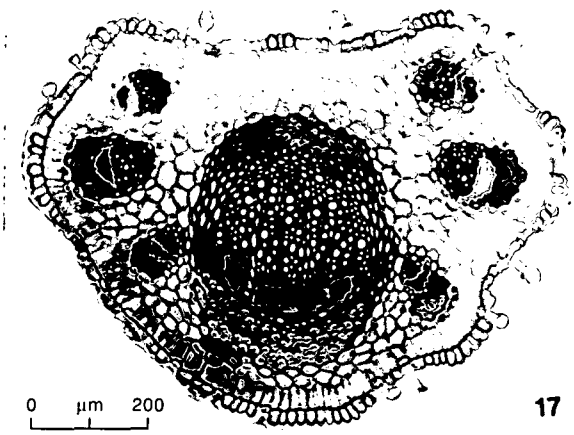

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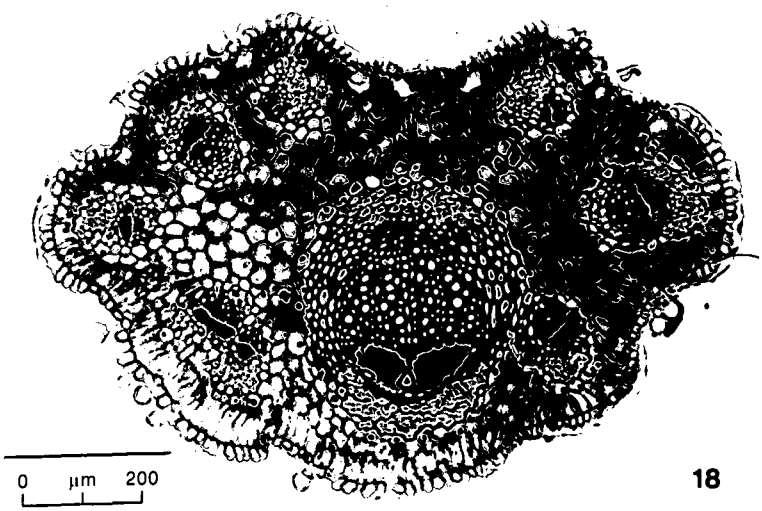
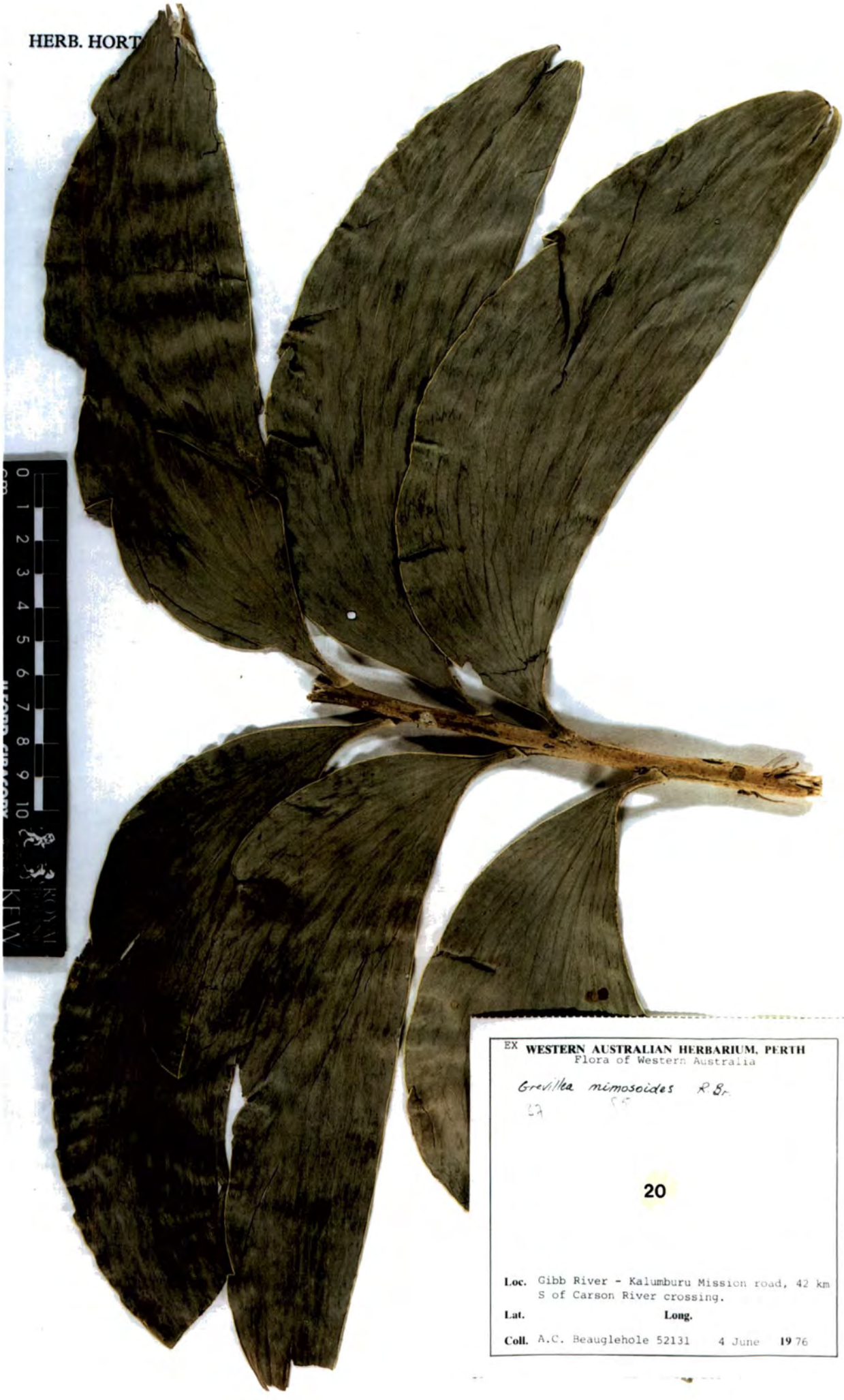


18

Fig. 20. *Grevillea mimosoides*, photograph of herbarium sheet.

Figs. 20A. *Grevillea mimosoides*. Detail of leaf base to show the course of the median leaf trace.



EX **WESTERN AUSTRALIAN HERBARIUM, PERTH**
Flora of Western Australia

Grevillea mimosoides R.Br.

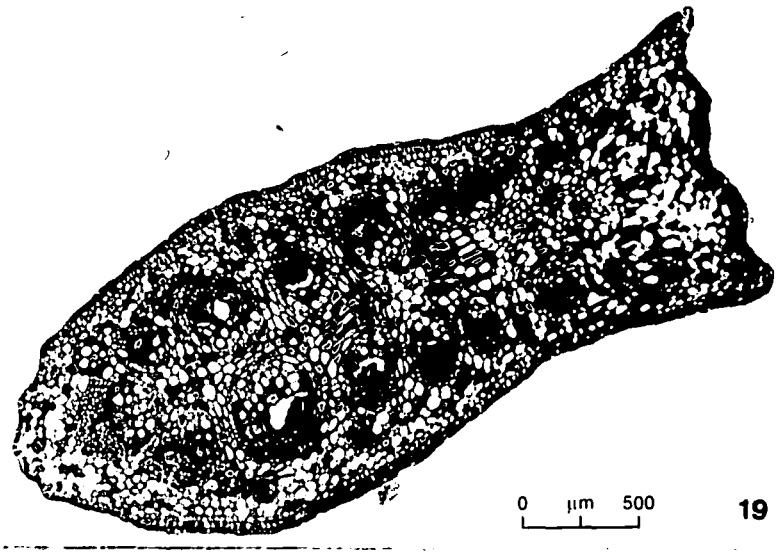
20

Loc. Gibb River - Kalumburu Mission road, 42 km S of Carson River crossing.

Lat. **Long.**

Coll. A.C. Beauglehole 52131 4 June 19 76

Figs. 19 and 21-25. - 19, *G. mimosoides* (CSIRO 4843). Leaf base, transverse section. - 21, *G. nematophylla* (ADN 26518). Leaf base, transverse section. - 22, *G. pyramidalis* (McGillivray 3769). Leaf base, transverse section. - 23, *G. saccata* (McGillivray 3277). Stoma, transverse section. - 24-25, *G. pteridifolia* (Hoogland 8487). - 24, Midrib, transverse section. - 25, Leaf margin, transverse section.



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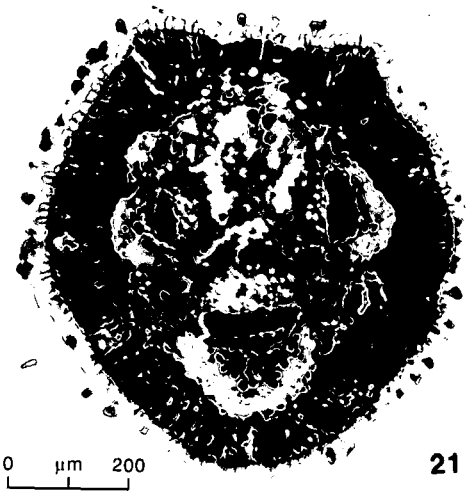

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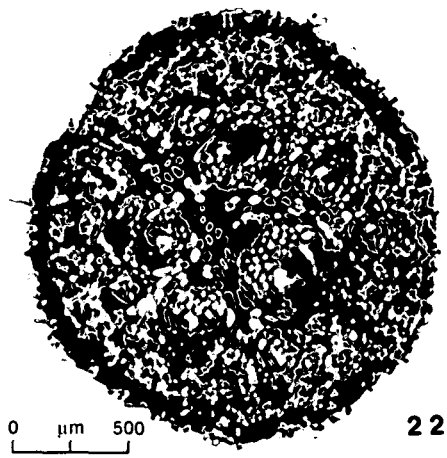

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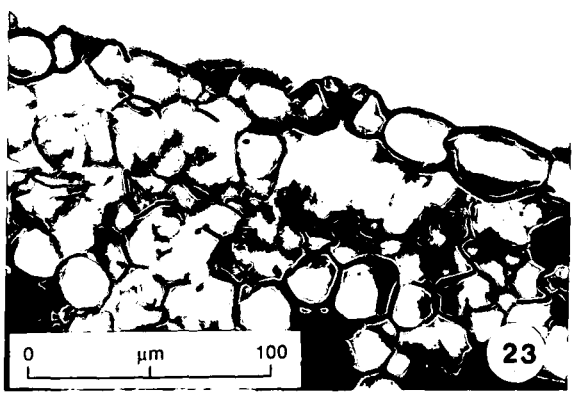

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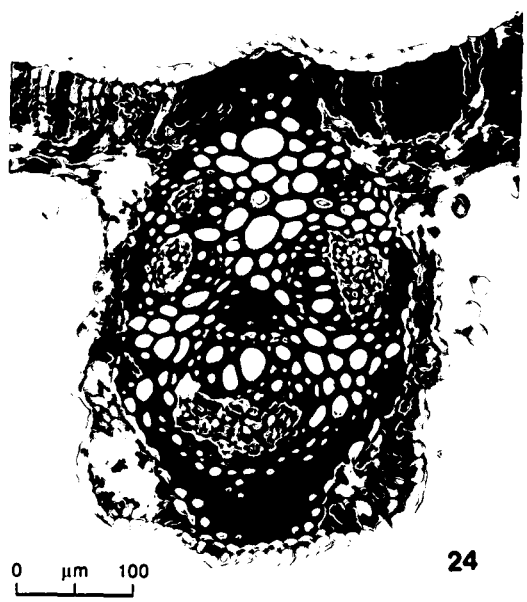

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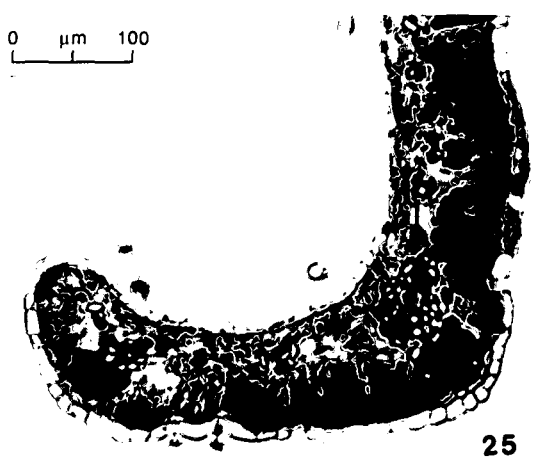
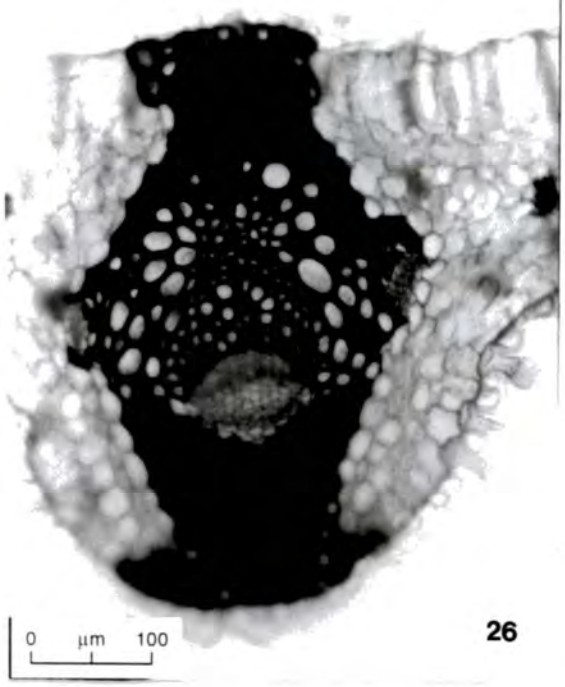


25

Figs. 26-31. - 26, *G. speciosa* ssp. *oleoides* (Sikes 101). Midrib, transverse section. - 27, *G. australis* var. *montana* (T.E. Burns 5302/9013). Midrib, transverse section. - 28, *G. australis* (Strid 22016). Midrib, transverse section. - 29, *G. acuaria* (Melville 71.442). Midrib, transverse section. - 30, *G. victoriae* (Darbyshire 70). Leaf margin, transverse section. - 31, *G. victoriae* (C.J. Everist). Leaf margin, transverse section.



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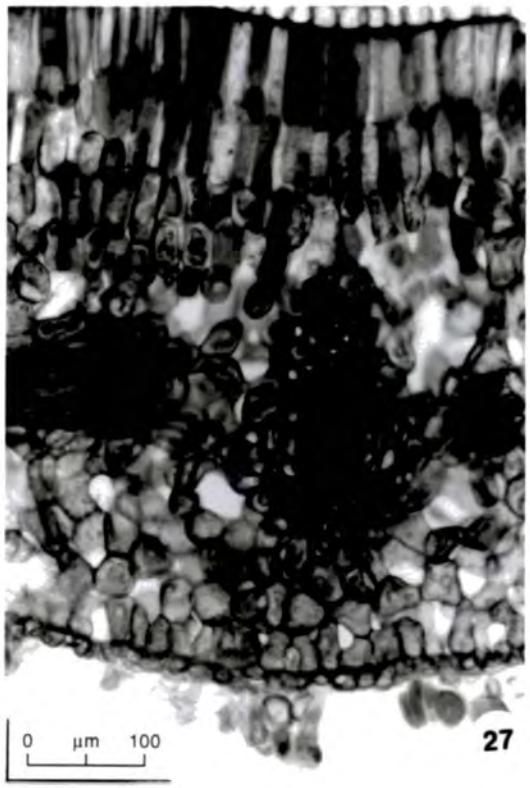

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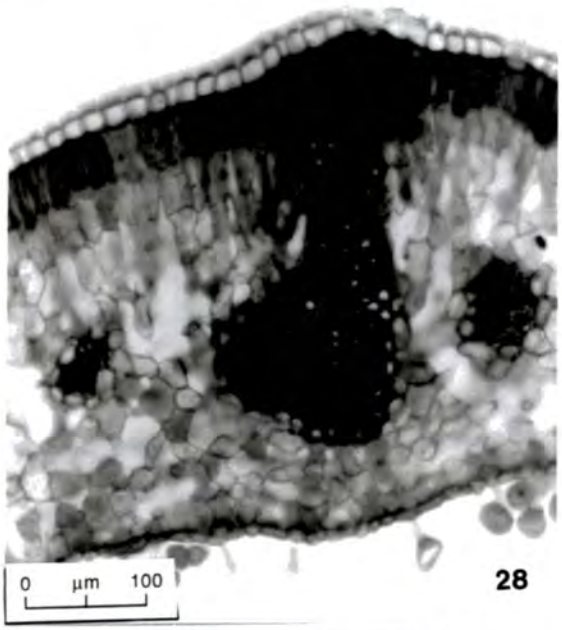

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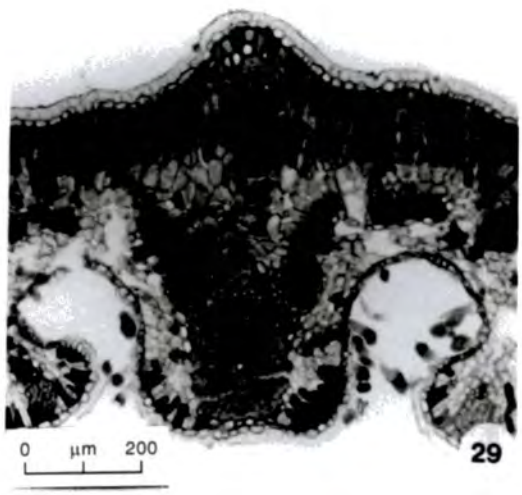

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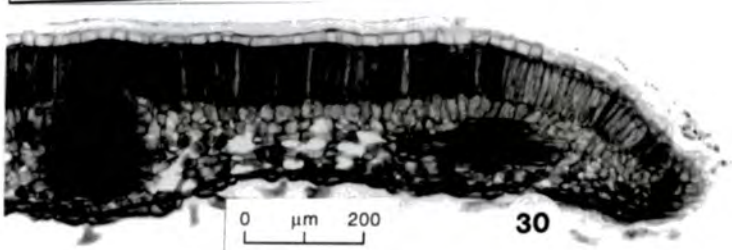

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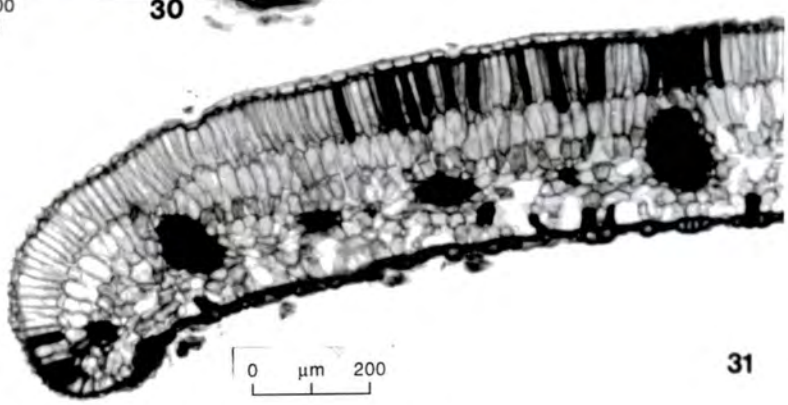
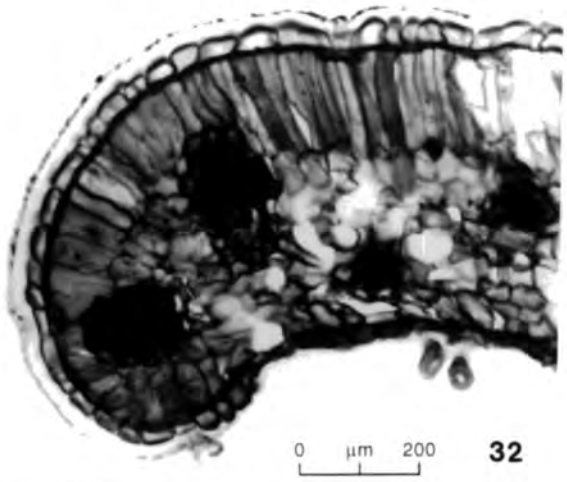


31

Figs. 32-37. - 32, *G. victoriae* (Herb. Chas. Walker). Leaf margin, transverse section. - 33, *G. australis* (Strid 22016). Leaf margin, transverse section. - 34, *G. sparsiflora* (Johnson 2151). Leaf, transverse section. - 35, *G. acuaria* (Tindale 3756). Leaf, transverse section. - 36, *G. acuaria* (DFB W75/45). Leaf margin, transverse section. - 37, *G. pauciflora* (George 13107). Leaf margin, transverse section.



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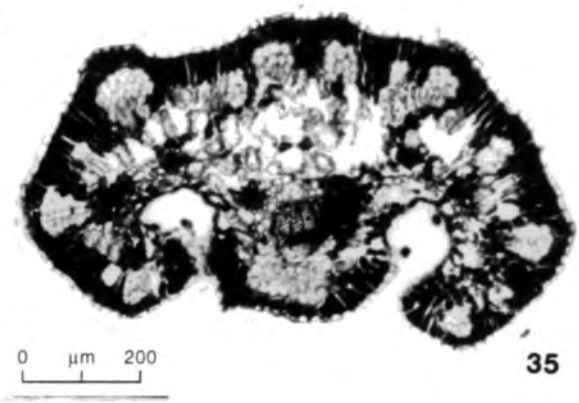

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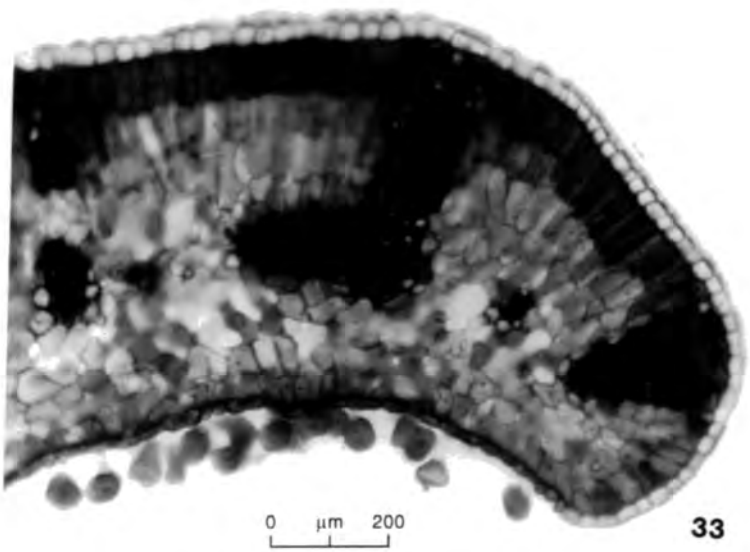

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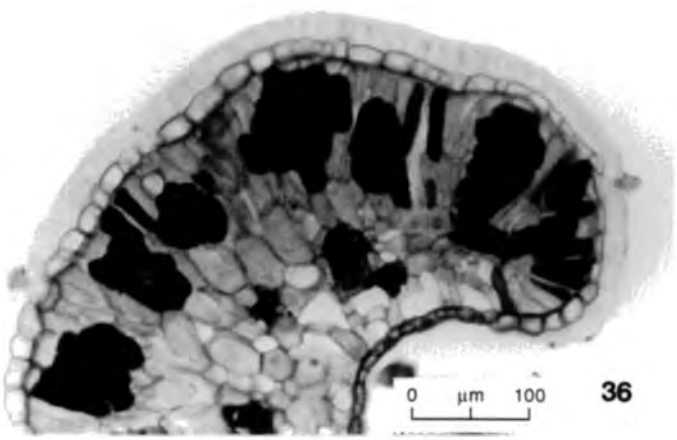

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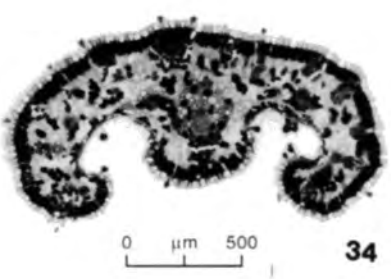

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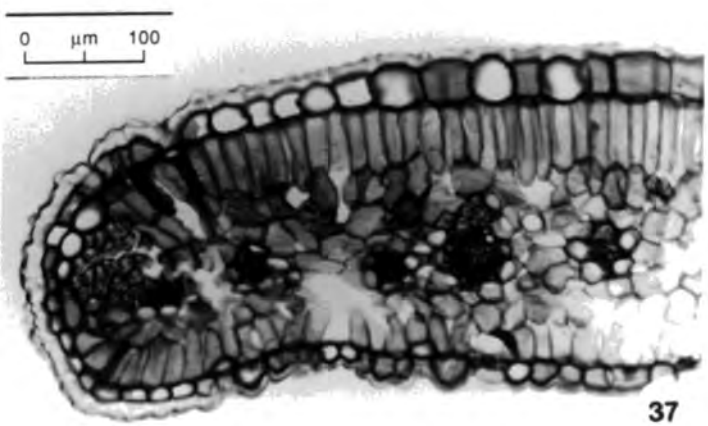
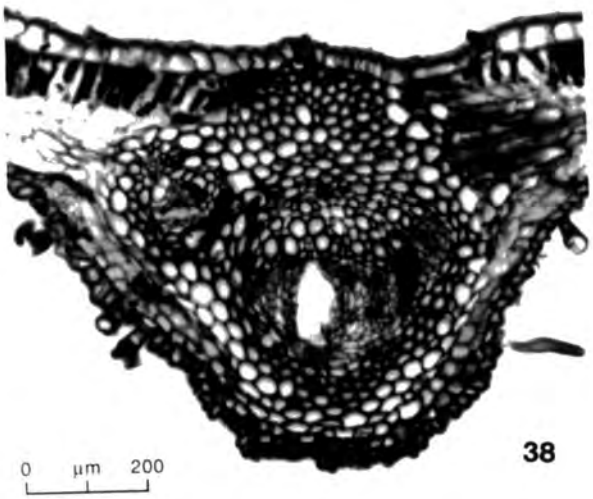


37

Figs. 38-43. - 38, *G. robust* (Hubbard 5416). Midrib, transverse section. - 39-40, *G. robusta* (Hubbard 5416). Lignified sheath cells. - 41, *G. meisneri* (Vieillard 3092). Midrib, transverse section. - 42, *G. papuana* (NGF 38967). Midrib, transverse section. - 43, *G. papuana* (NGF 38967). Leaf margin, transverse section.



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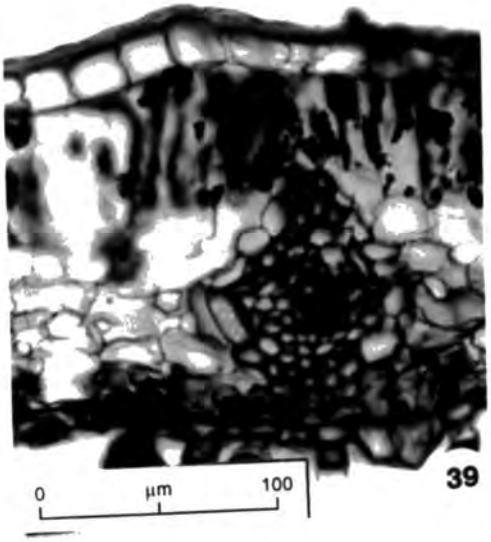

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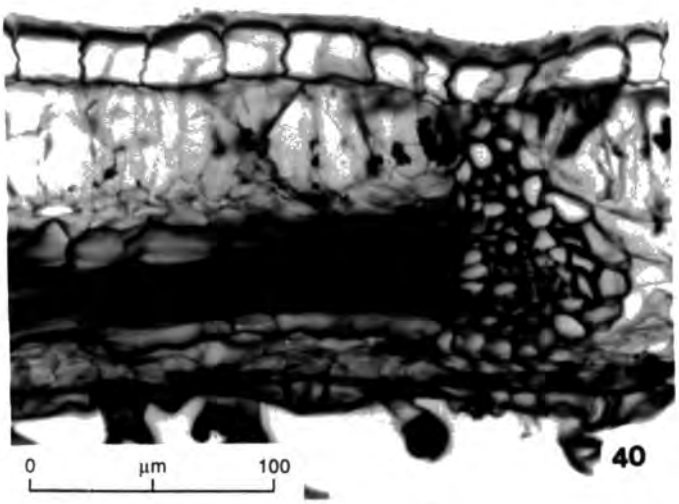

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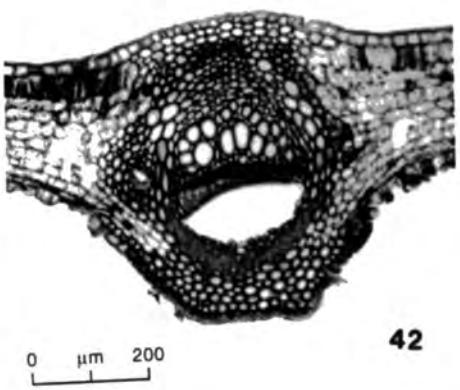

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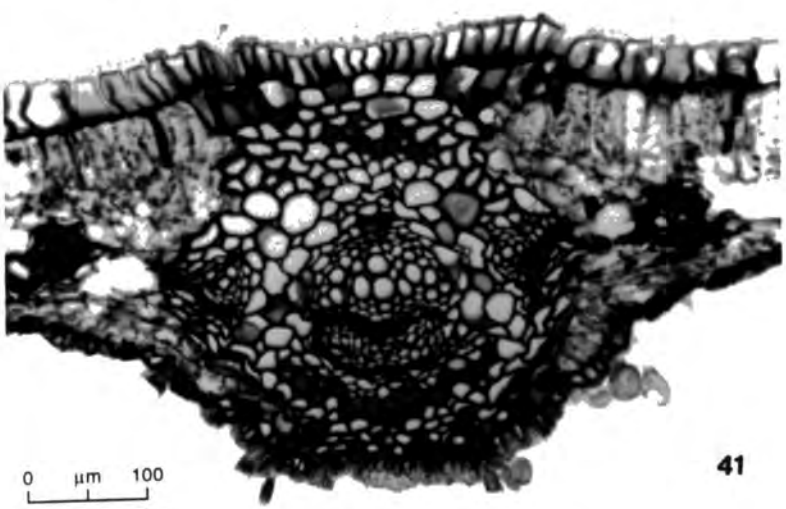

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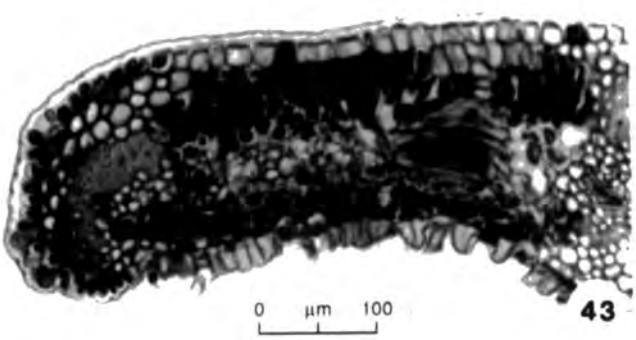
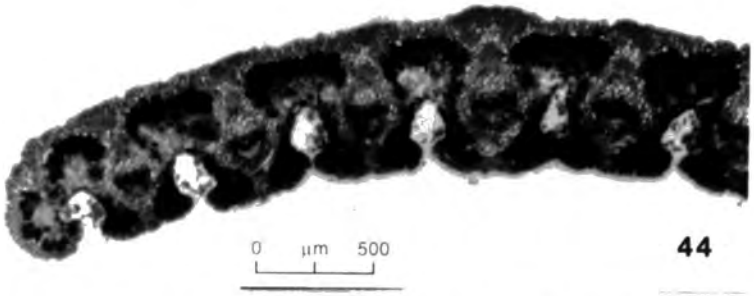


43

Figs. 44-49. - 44, *G. striata* (Flora Australiensis). Leaf, transverse section. - 45, *G. polybotrya* (Kew no. H973/80 243). Leaf margin, transverse section. - 46, *G. polybotrya* (Kew no. H973/80 243). Midrib, transverse section. - 47, *G. integrifolia* (Tindale 207 & Maslin). Midrib, transverse section. - 48-49, *G. pyramidalis* (McGillivray 3277). Leaf, transverse section.



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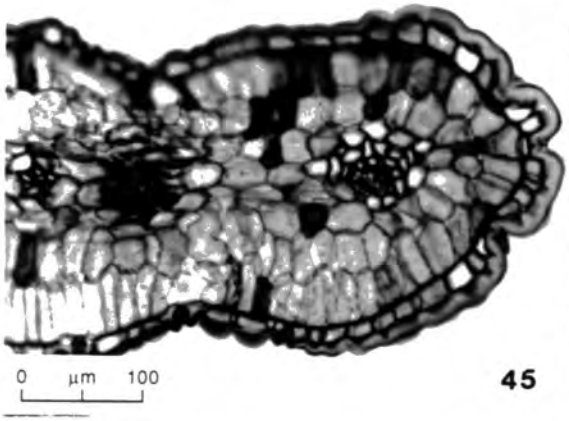

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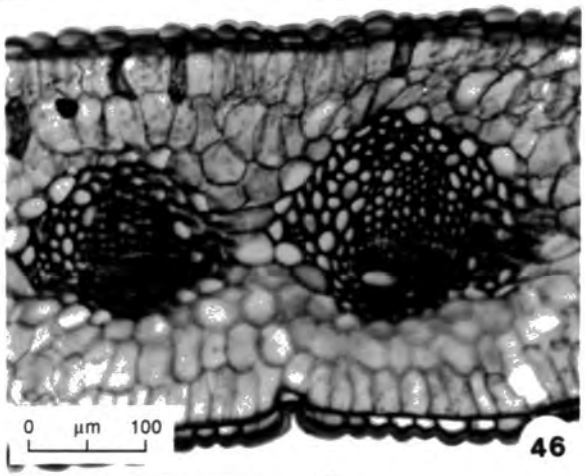

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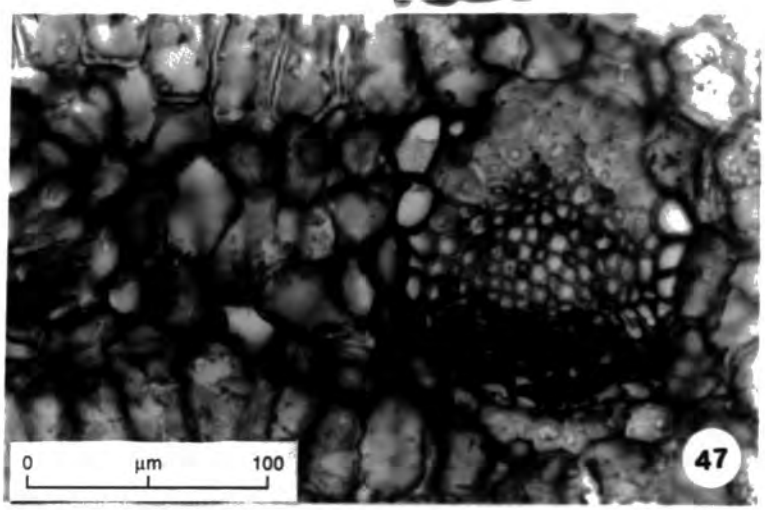

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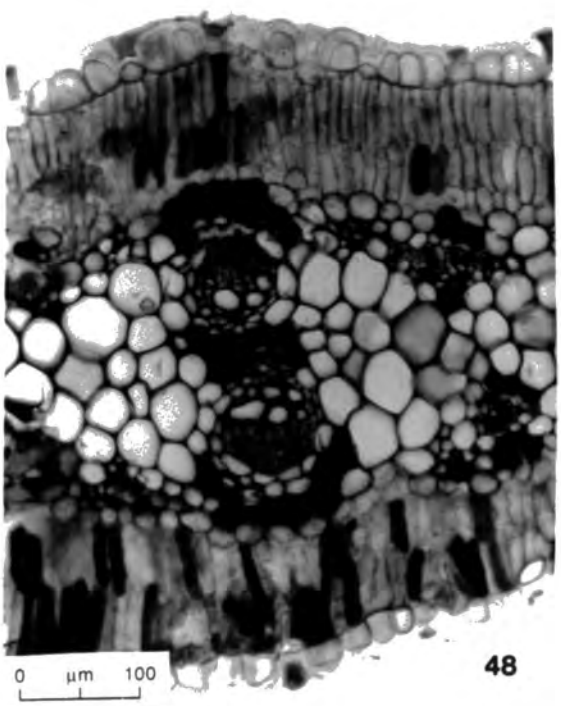

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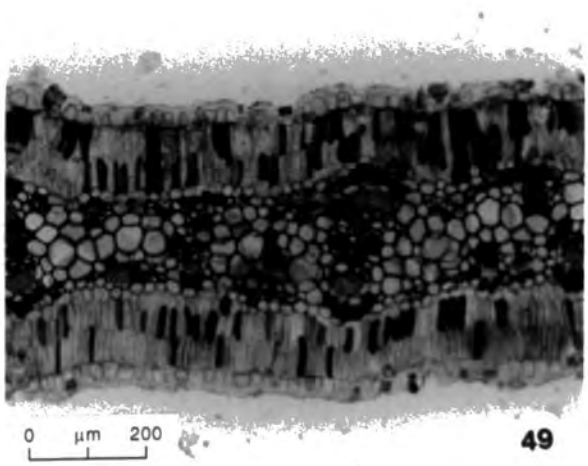

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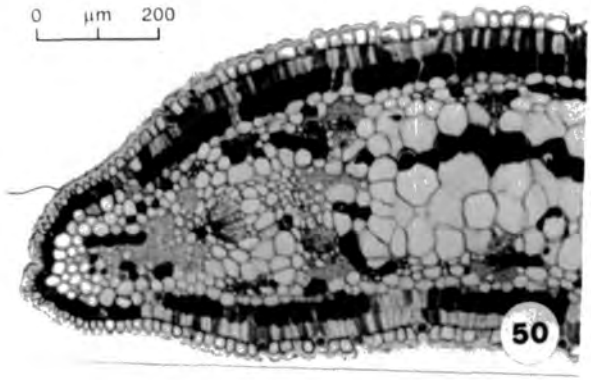
Figs. 50-55. - 50-52, *G. mimosoides* (CSIRO 4843). Leaf, transverse section. - 53-55, *G. dimidiata* (Kew no. H11/177 154). Leaf, transverse section.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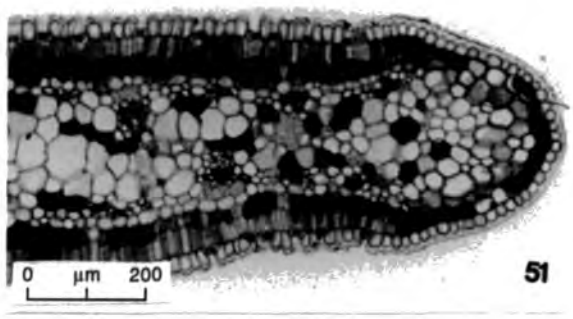
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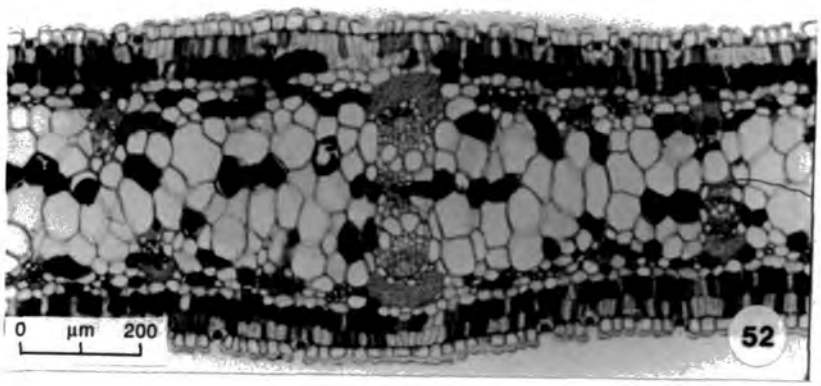
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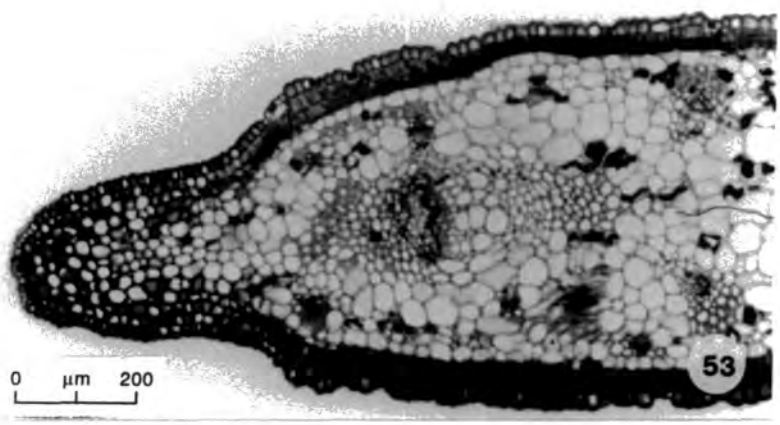
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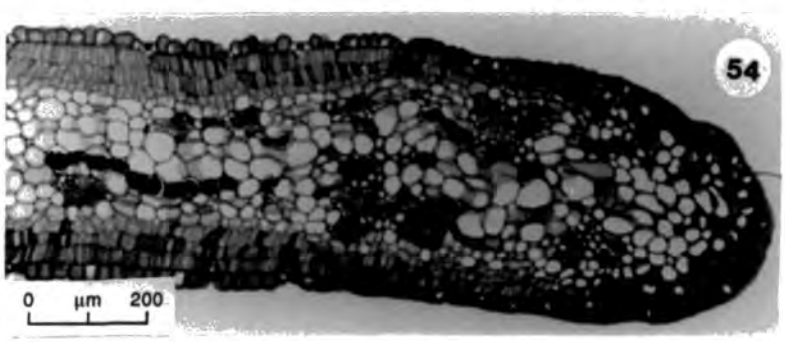
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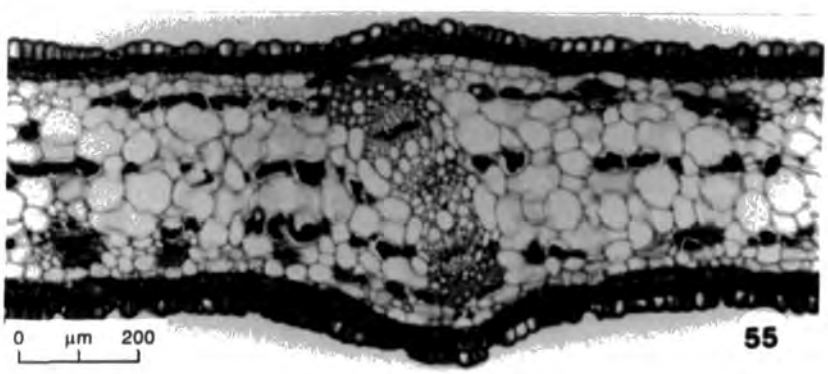
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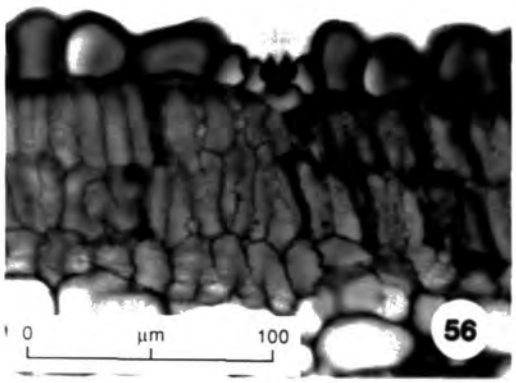
Figs. 56-61. - 56, *G. dimidiata* (Kew no. H11/177 154). Stoma, transverse section. - 57-58, *G. dimidiata* (Kew no. H11/177 154). Stomata, epidermal preparation. - 59, *G. wickhamii* (Letz 7163). Midrib, transverse section. - 60-61, *G. wickhamii* (Carolin 6200). Leaf, transverse section.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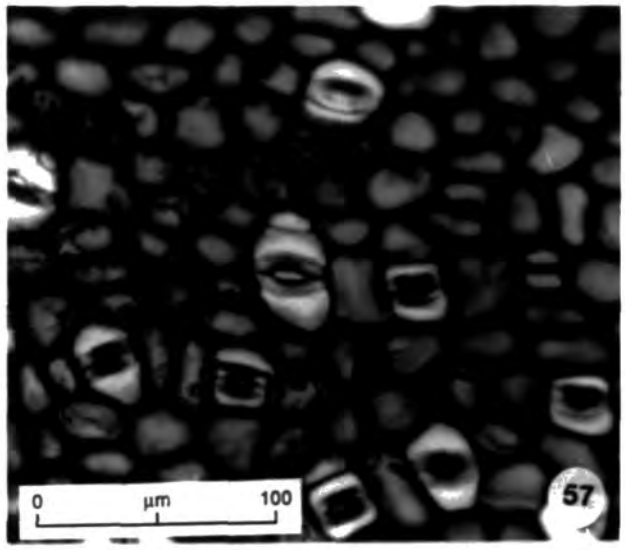
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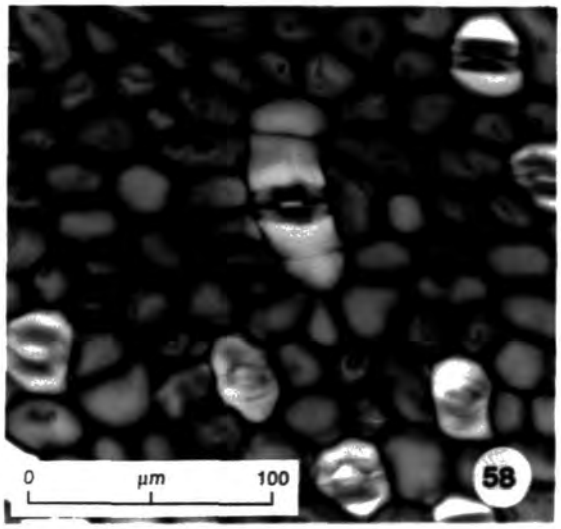
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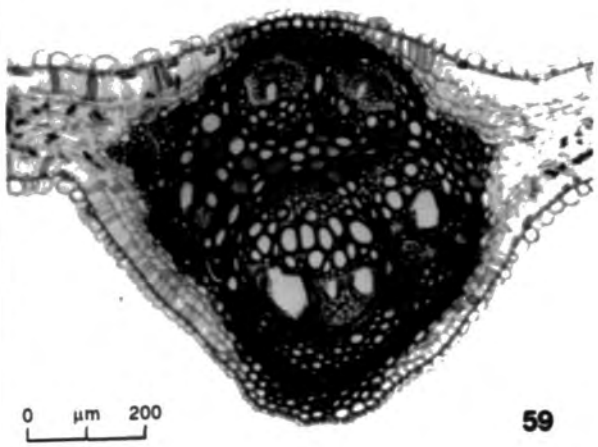
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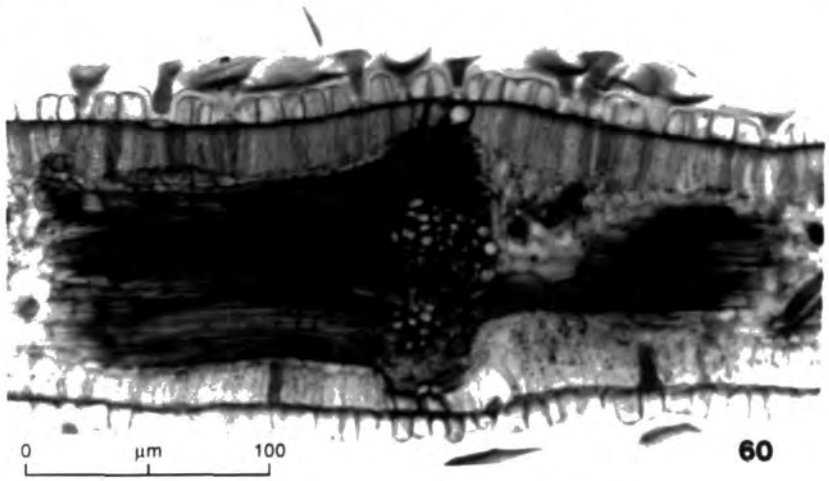
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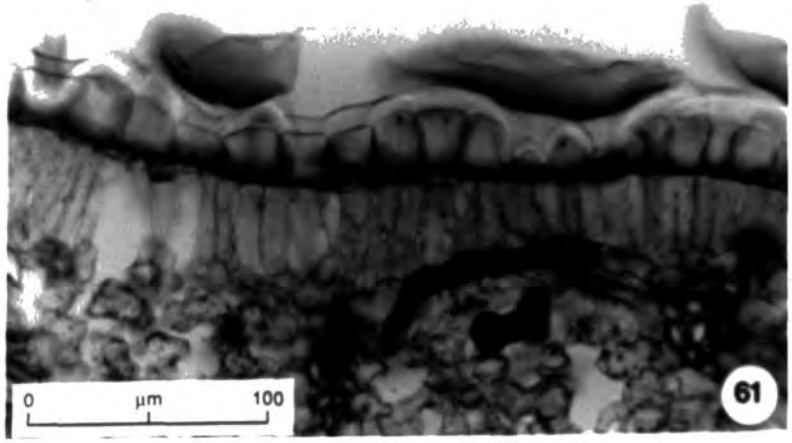
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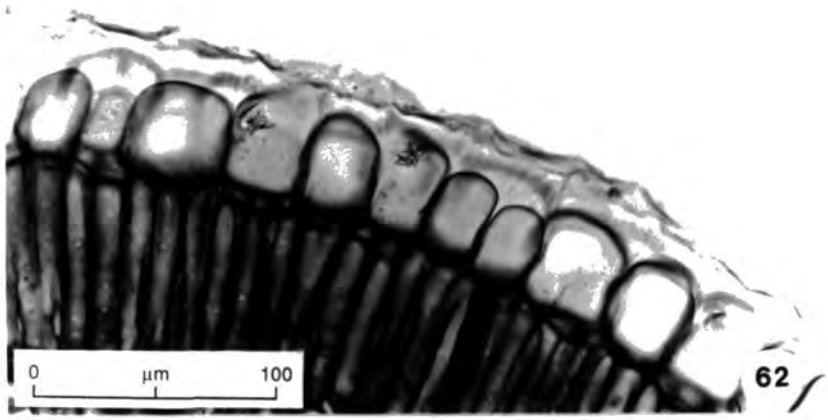
Figs. 62-66. - 62, *G. patentiloba* (Melville & George 71.273). Leaf, transverse section. - 63, *G. patentiloba* (Melville & George 71.273). Leaf margin, transverse section. - 64, *G. hakeoides* (Kew no. H973/80 187). Leaf, transverse section. - 65, *G. commutata* (McGillivray 3329 & George). Midrib, transverse section. - 66, *G. commutata* (McGillivray 3229 & George). Leaf margin, transverse section.



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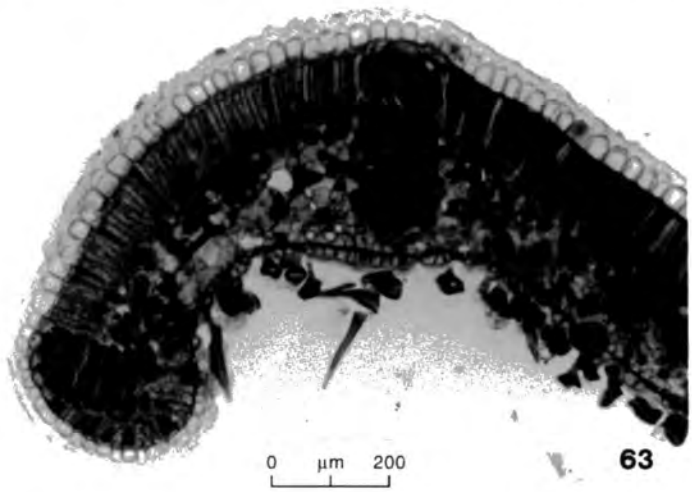

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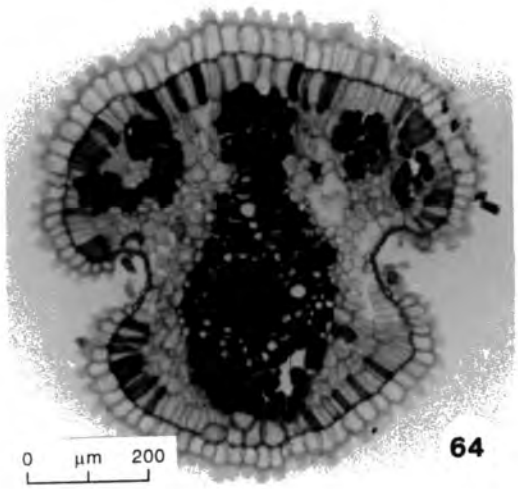

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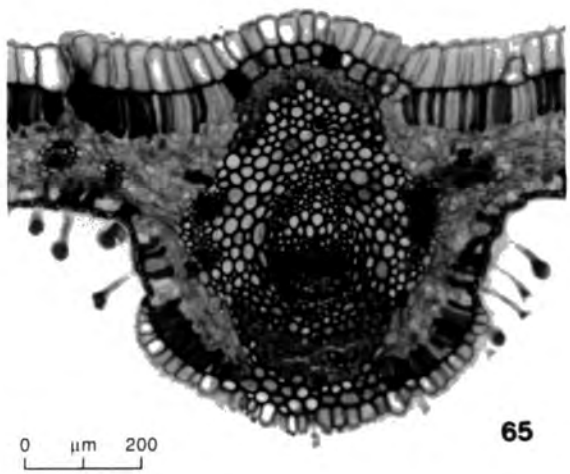

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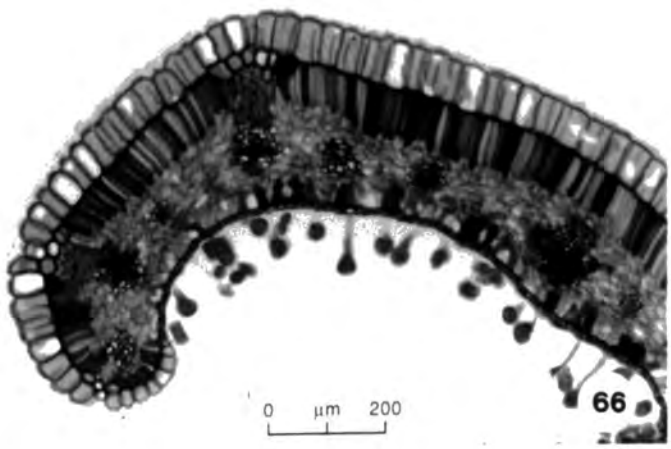
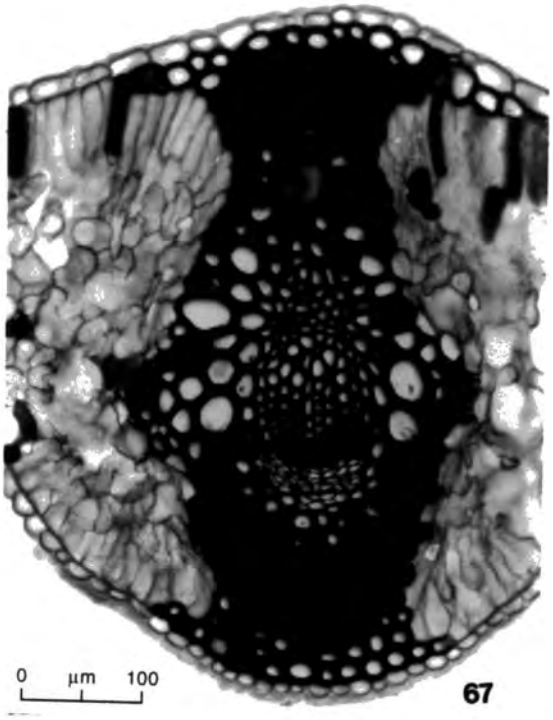


66

Figs. 67-72. - 67-69, *G. diversifolia* (H973/80 175). - 67, Midrib, transverse section. - 68, Leaf margin, transverse section. - 69, Leaf, transverse section. - 70-71, *G. heliosperma* (McGillivray 3914). - 70, Midrib, transverse section. - 71, Leaf margin, transverse section. - 72, Vascular bundle, transverse section.



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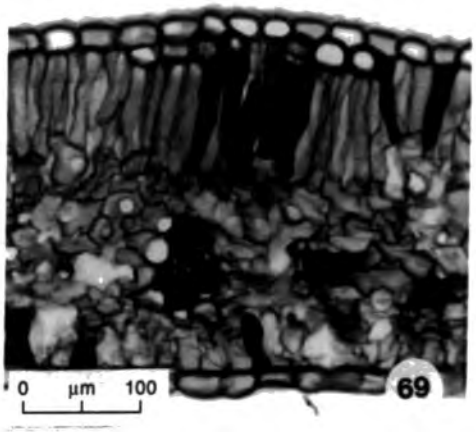

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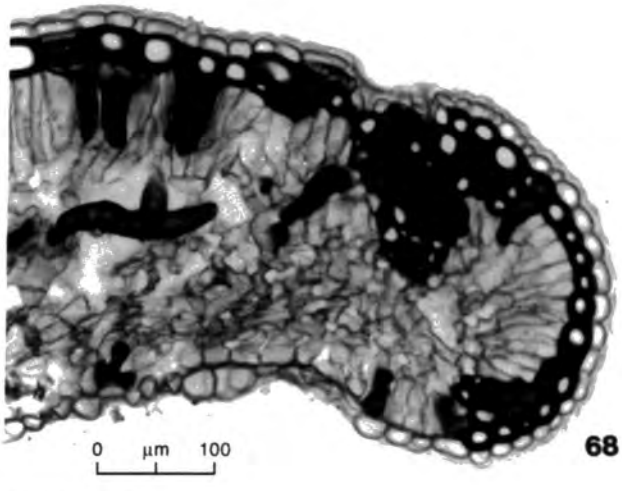

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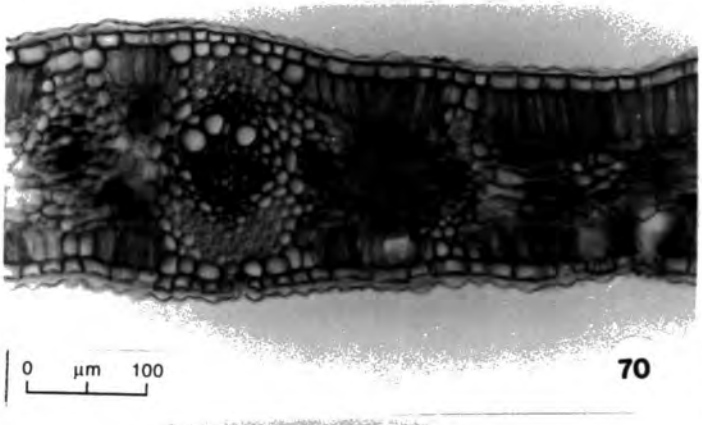

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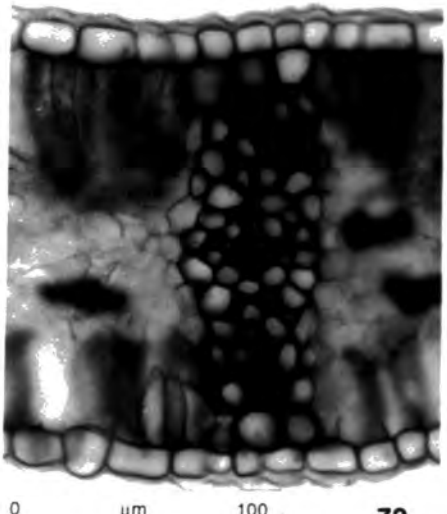

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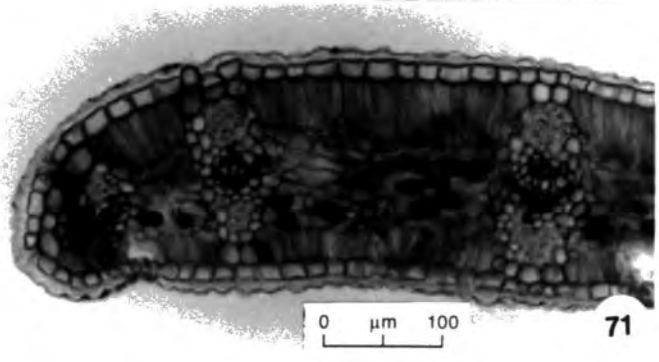

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OBSERVATIONS

Each specimen was described in detail. Descriptions have been retained in Durham.

Grevilleeae

Grevillea

Stem (Fig. 1)

Stems included in the stem-node-leaf continuum were between 1 and 2.5 mm in diameter. There were numerous hairs within the epidermis. Where cork had formed, it was superficial. The cortex, composed of unlignified parenchyma, was between 2 and 7 cells wide. In 2 specimens of *G. acuaria* (Melville and George 71.442 and Blaxell DFB/W75/45), there were 6 or 7 rows of regular, square cork cells and, below these, some 4 rows of unlignified cortical parenchyma (Fig. 2). In the third specimen (Tindale 3756), two regions of cork were separated by 2-3 rows of cortical parenchyma. In *G. sparsiflora*, there were 4 rows of cork and 1-3 rows of cortical parenchyma. In most specimens, there were no sclereids in the cortex. In *G. glauca* and in one specimen of *G. mimosoides* (CSIRO 4843), there were occasional sclereids among cortical parenchyma. In *G. meisneri*, *G. striata* and *G. nematophylla*, sclereids were well developed. Many cortical cells contained tannin. Pericyclic fibres, loosely associated with vascular bundles, formed a more or less continuous ring. In some specimens, among the pericyclic sclerenchyma, often opposite rays, there were sclereids (Fig. 3); in others, there was lignified parenchyma (Fig. 4). Vascular tissues were eustelic to siphonostelic. A continuous cambial zone was recognisable. There were interxylary fibres in all the specimens examined. Pith was lignified. In *G. glauca*, *G. meisneri*, *G. didymobotrya*, *G. striata* and *G. insignis*, there were large, well developed sclereids within the pith. There were sclereids in *G. speciosa*. In one specimen of *G. sericea*

(NSW 17828), there were no sclereids (Fig. 5), in another (NSW 8504), sclereids were weakly developed and, in the third (NSW 18628), there were occasional groups of large sclereids (Fig. 6).

Nodal anatomy

Leaf traces did not extend into adjacent nodes but spanned only a short distance between the stele and the leaf base. Below the node, near leaf traces, there was some dividing and merging of stelar bundles. This feature was marked in all the specimens from Group 8, in *G. buxifolia*, *G. sparsiflora*, *G. acuaria*, *G. pauciflora*, *G. brachystachya*, *G. glauca*, *G. striata* and *G. insignis*.

In some specimens, leaf traces coincided with pronounced ridges in the stem; this feature varied within species.

At low levels, leaf traces were recognised by wider rays bordering them and by modified xylem which consisted of simple vascular elements and weakly lignified parenchyma (Fig. 7). Fibre caps were enlarged and, in lateral leaf traces, orientated towards the leaf base.

In *G. sparsiflora*, *G. pauciflora* and *G. acuaria*, at the lowest levels, there was modified xylem in one region of the stele. There was dividing and merging of stelar tissues below the node. At higher levels, within a single leaf gap, 2 small bundles, associated with the vascular supply to the axillary bud, alternated with 3 leaf traces (Fig. 8). In each specimen, several nodes were similar. The single specimen of *G. insignis* had 4 lacunae and 4 traces; there was an extra lateral trace on one side. In *G. glauca*, in the position of each lateral leaf trace, xylem was modified in 2 stelar bundles which combined to form one trace before leaving the stele. In a second node, there were 2 bundles in each lateral position. On one side, tissues combined outside the stele, within the cortex. On the other, the bundles were separate

to the leaf base. With, these exceptions, all the nodes examined had 3 lacunae and 3 leaf traces.

In one specimen of *G. integrifolia* (H973/80 288), there was a small strand of stelar tissue to one side of a lateral trace; within the cortex, it was separate but merged with the lateral trace within the leaf base. A similar strand was associated with the median leaf trace and merged with it within the cortex. There were no vascular strands in the supradjacent node of this specimen or in the second specimen (Tindale 207). In *G. trifida*, a vascular strand separated from the median leaf trace in the cortex and remained separate until it formed a small bundle, next to the central bundle, in the leaf base. No similar strands were seen in 2 adjacent nodes in this specimen. In *G. polybotrya*, there was an ephemeral vascular strand associated with a lateral leaf trace in one of 3 nodes studied.

At progressively higher levels, increased amounts of unlignified parenchyma occurred among fibres and caps associated with leaf traces were dispersed. No fibres crossed the abscission layer.

Leaf base

At the lowest levels, the leaf base was first recognised by an absence of cork and, often, an increased occurrence of hairs. Below the epidermis, within the outline of the stem or in a projection on the side of the stem, there was a group of lignified parenchyma cells surrounded by unlignified parenchyma (Fig. 9). At higher levels, discreet bundles of fibres, separated by lignified parenchyma, were radially aligned with leaf traces. The unlignified parenchyma of the abaxial cortex was continuous with the abscission layer. There were sclereids in nodal regions in many specimens; their abundance varied within species. Only in *G. australis* and *G. polybotrya* were no sclereids seen. In *G. meisneri*, *G. brachystachya*, *G.*

glauca, *G. striata*, *G. pyramidalis*, *G. mimosoides* and *G. dimidiata*, there were large sclereids in leaf bases.

In *G. sparsiflora*, *G. acuaria*, *G. pauciflora* and *G. insignis* and in specimens from Groups 7 and 8 in which a complete node was examined, there was a band of lignified parenchyma and/or sclereids, sometimes mixed with fibres, on the adaxial side of the abscission layer, below the level of separation of the leaf base (Fig. 10).

In *G. ramosissima* and *G. insignis*, the abscission layer was not seen at low levels. In *G. ramosissima*, thick walled fibres were surrounded by unlignified parenchyma between the phloem and fibre cap of the median leaf trace. At higher levels, the abscission layer was on the adaxial side of this region. In *G. insignis*, opposite the median leaf trace, the outer region of the stem was composed of lignified parenchyma, sclereids and fibres. At higher levels, on the adaxial side of these tissues, the abscission layer was seen as an irregular band of unlignified cells among leaf traces. Higher still, in both species, the structure of the leaf base was similar to that in other specimens.

Leaf traces crossed the abscission layer. Often, they branched within the stem. At higher levels, there were divisions and mergers of vascular tissues within the leaf base.

Inversely orientated bundles

Inversely orientated vascular bundles occurred in the leaf bases of *G. pyramidalis*, *G. dimidiata*, *G. mimosoides* and *G. wickhamii*. In *G. laurifolia* and *G. insignis*, there was an adaxial bundle at ninety degrees to the main arc. In *G. meisneri*, towards the adaxial side of the leaf base, there was a double bundle with shared xylem and 2 phloem caps.

Table 5.

Petiolate, Compound and Lobed Leaves in *Grevillea*

Petiolate	Compound	Lobed
G. laurifolia	*G. pteridifolia*	*G. ilicifolia*
G. repens	*G. banksii*	*G. ramosissima*
G. victoriae	*G. pulchella*	*G. trifida*
G. speciosa		
ssp. *dimorpha*	*G. pyramidalis*	*G. vestita*
ssp. *oleoides*	*G. paniculata*	*G. patentiloba*
G. wickhamii	*G. heliosperma*	
G. insignis	*G. robusta*	
G. glauca		
G. papuana		
G. meisneri		

The distal end of the leaf base

Within the leaf base, divisions and mergers of vascular tissues were more or less complicated and differed among species, within species and within specimens. Leaf bases were not always symmetrical. Of the species examined, 9 were petiolate (Table 5). In species with short leaf bases, the arrangement of vascular bundles was stable for only a short distance before expansion into the leaf.

In 48 of the specimens examined, there were 3 main bundles, sometimes with an additional small bundle between the central bundle and the lateral bundle and/or a small bundle outside the lateral bundle towards the margin. Main bundles had well developed abaxial fibre caps. Adaxial fibres were less well developed and, sometimes, combined in an adaxial band.

In some species, all the bundles within the leaf base were large and of more or less equal size (Fig. 11). In *G. laurifolia*, *G. insignis*, *G. victoriae*, *G. glauca*, *G. papuana* and *G. striata* each had between 7 and 10 large bundles in the distal end of the leaf base. In one specimen of *G. mimosoides* (Evans 3356), there was an arc of 9 vascular bundles. Outside the main arc, on the adaxial side, there were occasional small bundles. In the second specimen (CSIRO 4843), the network of bundles was more complex and there were some sixteen bundles within the arc; vascular bundles associated with the median leaf trace were in a group slightly separated from those associated with lateral traces. In one specimen of *G. dimidiata* (Perry 2073), there was an arc of more than twenty vascular bundles in which 3 complexes were recognisable. In the second specimen (H1193/77154), there were 8 bundles; complexes associated with individual leaf traces were less well defined. In *G. pyramidalis*, leaves were compound. Changes were associated with the dividing petiole. At a high levels, there was an arc of some 9 vascular

bundles. Outside the main arc, there were numerous small bundles in the abaxial cortex.

The transition from leaf base to leaf

Because there were mergers and divisions among vascular tissues in leaf bases, bundles were seldom unchanged leaf traces. Except in *G. nematophylla*, *G. pyramidalis*, *G. mimosoides* and *G. dimidiata*, leaf bases were tangentially extended (Figs. 12, 13). In some species, there was a pronounced expansion of parenchyma between central and lateral bundles. The central bundle followed a direct course between leaf base and leaf tip. A lateral bundle followed each margin and joined the midrib at the tip. In some species, expansions were more even throughout the leaf. Vascular tissues which were components of central or lateral bundles in the leaf base were separate, lower order veins at higher levels. Veins towards the margins of the leaf base did not retain their identities at higher levels.

In *G. meisneri*, as well as tangential extension of the leaf base, there were changes in the arrangement of central bundles. On the abaxial side, there was an arc of 3-5 bundles. Towards the adaxial side, there was a complex of 5 variously orientated bundles and, among them, there was some merging of tissues (Fig. 14).

In one specimen of *G. integrifolia* (H973/80 288) and in *G. biformis* leaves were narrow and linear and in *G. didymobotrya* they were linear-terete. There was limited expansion of the leaf base and an increase in the number of vascular bundles which were arranged in a circle towards the outside of the central parenchyma (Figs. 15-18).

In *G. mimosoides* and *G. dimidiata*, the extension of leaf base was in the radial plane and the leaf blade was laterally flattened. In a double row of vascular bundles, the median leaf trace was at one margin and, at the other, there were smaller bundles (Fig. 19). Especially towards the abaxial end,

there were smaller bundles outside the main group. At a low level, main bundles divided into a series of veins which followed a more or less parallel course to meet at the leaf tip (Fig. 20, 20A).

The leaves of *G. nematophylla* were linear-terete. There were only small changes in dimensions between the leaf base and the leaf. In both specimens, there was radial elongation of the leaf base. Palisade which surrounded the leaf base was interrupted by a small region of more isodiametric parenchyma cells associated with the reduced adaxial surface (Fig. 21).

Compound leaves

Of 10 species which had compound leaves (Table 5), 9 had tangentially extended leaflets. At lower levels, main vascular bundles in the leaflets were seen as components of the central bundle in the rachis. Where leaves were lobed, main vascular bundles in the lobes were seen as components of the midrib.

In *G. pyramidalis*, the leaf base was radially extended. Changes in the petiole were associated with the separation of the vascular supply to leaflets. Weakly developed, subepidermal palisade cells surrounded the leaf base, interrupted only by a small group of more nearly isodiametric cells associated with the reduced adaxial surface (Fig. 22). Outside the central, double row of main vascular bundles, there were smaller bundles and, outside these, around the periphery of the central parenchyma, there were many small bundles and vascular strands. Phloem was towards the epidermis. At higher levels, in the region outside the main bundles, some smaller bundles were orientated with their phloem towards the centre of the petiole. Higher still, there was parenchyma between the main bundles and these reorientated bundles and, above this, the rachis and rachilla were separate. Similar changes were associated with higher lobes. At all levels,

the rachis and rachillae were radially elongated and leaf lobes were laterally flattened.

Leaf anatomy

Group 1

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were weakly recurved. Slight adaxial ridges were associated with main veins. A pronounced abaxial ridge was associated with the midrib.

In *G. repens*, margins were hardly recurved and there were abaxial ridges over main veins.

Anatomy: general description

Leaves were dorsiventral (sensu Metcalfe and Chalk, 1950; Esau, 1965). Hairs occurred on both surfaces but were more numerous on the abaxial surface. The epidermis consisted of a single row of cells. Outer walls were cutinised on the adaxial surface, around margins and on the abaxial side of the midrib. Stomata which were restricted to the abaxial surface, and especially to abaxial grooves, were paracytic and had a single subsidiary cell on either side of the guard cells (Fig. 23). Below the adaxial epidermis, there was a single row of tall, narrow palisade cells with pits in projections in anticlinal walls. Below the abaxial epidermis there were 4-7 rows of spongy mesophyll cells. In palisade and mesophyll cells, some walls were weakly lignified and some contents gave positive reactions for tannin. Vascular bundles were collateral. Phloem was abaxial. At the midrib, there was an arc of 3-5 vascular bundles. Lignified parenchyma occurred among the bundles and, in some specimens, there were peripheral bundles (Fig. 24). Large abaxial and adaxial caps of thick walled fibres associated with the complex were separated from the epidermises by 1-3 rows of parenchyma (Fig. 24). At the margins, there was palisade and mesophyll (Fig. 25).

Towards each margin, there were 2 bundles with well developed adaxial fibre caps, separated from the epidermis by a single row of parenchyma cells (Fig. 25). Abaxial fibres were within the mesophyll. Lower order veins of various sizes had abaxial and adaxial fibres, adaxial fibres or were without fibres. Minor bundles were within the mesophyll. Some small bundles contained only large, simple tracheary elements. Similar cells were on the periphery of larger bundles. Occasional, short, irregular, thick walled fibres or sclereids were associated with vascular bundles. Bundle sheaths were weakly developed.

In some specimens, characteristics were different:-

Epidermis: Cuticle was hardly developed on the abaxial surface of *G. repens*.

Palisade: In *G. laurifolia* and *G. ilicifolia*, there was a second and weakly developed third row of adaxial palisade. Pits in projections in anticlinal walls were not an obvious feature in *G. laurifolia, G. ilicifolia* and *G. repens*. In *G. repens*, occasional palisade cells had uneven ends and there was some intrusion among mesophyll and epidermal cells. In 2 specimens of *G. pteridifolia* (McKee 9237 and Hoogland 8487) and in *G. ilicifolia*, there was weakly developed palisade below the abaxial epidermis.

Leaf margins: In 1 specimen of *G. pteridifolia* (Thorne & Jones 21170) there was a third bundle with a well developed adaxial fibre cap towards each margin. In another specimen, (Hoogland 8487), there were 2 on one side and 3 on the other. Three similar bundles occurred towards each margin in *G. ilicifolia*. In *G. laurifolia, G. repens* and *G. ramosissima*, there were no palisade and mesophyll tissues at the margins. Thick walled fibres associated with a small vascular bundle were separated from the epidermis by a single row of parenchyma. In *G. ramosissima*, near to the margin, there was a

bundle with an adaxial fibre cap separated from the epidermis by a single row of parenchyma; abaxial fibres were within the mesophyll.

Vascular bundles: In *G. repens*, there was one bundle of similar extent to the midrib between the centre of the leaf and the bundle at the margin and, in *G. laurifolia*, there were 2. All lower order veins were within the mesophyll.

Tracheary elements: In *G. ilicifolia*, *G. repens* and *G. ramosissima*, large tracheary elements on the edges of vascular bundles rarely occurred.

Group 2.

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were weakly recurved but rounded in *G. pauciflora*. Except in *G. pauciflora* and *G. australis*, there was an abaxial ridge associated with the midrib; in *G. australis* var. *montana*, it was slight. On both surfaces, the prominence of veins was different among specimens and species.

Anatomy: general description

Leaves were dorsiventral. Hairs occurred on both surfaces but were more numerous on the abaxial surface. The epidermis consisted of a single row of cells. Outer walls were cutinised on the adaxial surface, around margins and on the abaxial side of the midrib. Stomata which were restricted to the abaxial surface were paracytic and had a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a single row of tall, palisade cells. Below the abaxial epidermis, there were 4-7 rows of spongy mesophyll cells. Some palisade and mesophyll cells had weakly lignified walls; some contained tannin. Vascular bundles were collateral. Phloem was abaxial. At the midrib, there was a single vascular bundle with well developed abaxial and adaxial caps of thick walled fibres separated from the epidermises by 1-4 rows of parenchyma (Fig. 26). In

some specimens, there was a small vascular bundle on either side of the midrib. Palisade was continuous around margins. Towards each margin, there were 2 bundles with well developed adaxial fibre caps separated from the epidermis by a single row of parenchyma cells. Abaxial fibres were within the mesophyll. Lower order veins of various sizes had abaxial and adaxial fibres, adaxial fibres or were without fibres. Minor bundles were within the mesophyll. Occasionally, small bundles contained only large, simple tracheary elements. Similar cells were on the periphery of some larger bundles. Occasional, short, irregular, thick walled fibres or sclereids were associated with vascular bundles. Bundle sheaths were weakly developed.

In some specimens, characteristics were different:-

Hairs: In *G. mucronulata* and *G. saccata* hairs were infrequent on both surfaces.

Epidermis: In *G. pauciflora* outer walls of epidermal cells were weakly cutinised on both surfaces of the leaf. In *G. saccata*, the abaxial side of the midrib was not well cutinised. In 6 specimens of *G. speciosa*, epidermal cell walls were heavily cutinised on the adaxial surface, around margins and on the abaxial surface of the midrib and more weakly cutinised on the rest of the abaxial surface. In *G. australis*, outer walls were cutinised on the adaxial surface and around margins only.

Palisade: In *G. australis* var. *montana* there were 2 rows of palisade and weakly developed third and fourth rows. In *G. australis* and 2 specimens of *G. victoriae* (Darbyshire 70 and C.J. Everist) there were 2 rows and a weakly developed third. In the third specimen of *G. victoriae* (Herb. Chas. Walker) and in *G. sparsiflora* there was a weakly developed second row.

Table 6.

Group 2. Tissue patterns at the margins of leaves

Species/Specimen	
G. mucronulata	There were no vascular bundles with adaxial fibres separated from the epidermis by a single row of parenchyma or modified palisade. Across the leaf, there were many bundles with well developed adaxial fibre caps which extended into the modified palisade.
G. occidentalis	There were no vascular bundles with adaxial fibres separated from the epidermis by a single row of parenchyma or modified palisade. Lower order veins hardly extended into the palisade, most were within the mesophyll.
G. victoriae Darbyshire 70	There were 2 secondary veins of similar extent to the midrib on each side of the leaf but no bundles with well developed adaxial fibres near the margins (Fig. 30).
S.J. Everist	There were no bundles with well developed adaxial fibres near the margins. Adaxial fibres associated with other vascular bundles did not extend into the outer palisade (Fig. 31).
Herb. Chas. Walker	There was a secondary bundle of similar extent to the midrib on either side of the leaf. Near each margin, there were 2 small bundles with adaxial fibre caps separated from the epidermis by one row of modified palisade cells (Fig. 32).
G. australis	As well as 2 bundles towards each margin, between the margin and the midrib, but not associated with a vascular bundle, there was a group of fibres separated from the abaxial epidermis by one row of parenchyma (Fig. 33).
G. australis var. *montana*	There were no vascular bundles with adaxial fibres separated from the epidermis by a single row of parenchyma or modified palisade. All the bundles were within the central mesophyll. Near the inner boundary of the palisade, there were small fibre groups.
G. sparsiflora	In the 2 bundles towards the margin, adaxial fibre caps were small. The cap associated with the inner bundle was within the modified palisade. Groups of fibres not associated with vascular bundles were within the modified palisade (Fig. 34)

G. acuaria	This specimen conformed to the general description (Fig. 35).	Numerous adaxial groups of fibres which were not associated with vascular bundles were separated from the epidermis by a single row of parenchyma or modified palisade (Fig. 36).
Tindale 3756		
Melville & George 71.442	Towards each margin, there were 3 bundles with well developed adaxial fibre caps.	
DFB/W75/45	2 bundles towards each margin were small and fibre caps were only loosely associated with them (Fig. 36).	

G. pauciflora — There were no vascular bundles with adaxial fibres separated from the epidermis by a single row of parenchyma or modified palisade. All lower order veins were within the mesophyll. There were many small groups of fibres, particularly on the inner edge of the palisade. At each margin, but not associated with a vascular bundle, there was a group of fibres separated from the epidermis by one row of parenchyma (Fig. 37).

G. speciosa Ashby B.	There were 2 bundles with well developed adaxial fibre caps at the margin. Between the margin and the midrib, there were 3 large, similar bundles on one side of the leaf and 4 on the other.
Ashby A.	There were 3 bundles with well developed adaxial fibre caps towards each margin.
Sikes 101.	There were 2 bundles with well developed adaxial fibre caps towards each margin and a third between the margin and the midrib.
V 468. H 973/80460. NSW 19368.	These specimens conformed to the general description.

G. saccata, *G. buxifolia*, *G. sericea* and *G. linearifolia* conformed to the general description.

In *G. speciosa*, except in specimen NSW 19368 and *G. speciosa* ssp. *dimorpha* (Kew no. H973/80 460), in all 3 specimens of *G. sericea*, in *G. pauciflora* and one specimen of *G. linearifolia* (NSW 18004), there was some abaxial palisade. In *G. sparsiflora* and *G. acuaria*, there was some palisade on the abaxial side of the midrib.

There were pits in projections in anticlinal walls in *G. occidentalis*, *G. buxifolia*, *G. speciosa* and *G. pauciflora*.

Mesophyll: In *G. australis* there were 9 rows of mesophyll.

In *G. linearifolia*, there were occasional, extremely small druses in some mesophyll cells.

Midrib: In *G. australis* var. *montana*, abaxial and adaxial fibres were within the mesophyll (Fig. 27). In *G. australia*, abaxial fibres were within the mesophyll and adaxial fibres were separated from the epidermis by 1-2 rows of parenchyma (Fig. 28). In *G. acuaria* and *G. sparsiflora*, adaxial fibres were within the mesophyll. In one specimen of *G. acuaria* (Melville and George 71.442) a large group of fibres separated from the adaxial epidermis by a row of parenchyma cells was aligned with the midrib but not continuous with it (Fig. 29).

Margins: In *G. occidentalis*, *G. buxifolia*, *G. victoriae* and *G. sparsiflora* there was palisade and mesophyll at the margins.

Variations in tissue patterns at the margins of leaves are shown in Table 6.

Group 5.

G. pulchella

Leaves were compound. Leaflets were described.

Outline in transverse section

Leaflets had parallel abaxial and adaxial surfaces. Margins were weakly recurved. Leaflets were slightly thicker over main veins.

Anatomy

Leaflets were dorsiventral. There were few hairs on either surface. The epidermis consisted of a single row of cells. Outer walls were cutinised especially on the adaxial surface and around margins. Stomata which were restricted to the abaxial surface were paracytic and had a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a row of palisade cells with pits in projections in anticlinal walls and a second, more weakly developed row of shorter cells. Some palisade cells contained tannin. Below the abaxial epidermis, a single row of mesophyll cells contained tannin. In the middle of the leaf, there were some 4-5 rows of mesophyll cells many of which were orientated with their long axes parallel to the leaf surface. Vascular bundles were collateral. Phloem was abaxial. At the midrib, there was a vascular bundle with an abaxial cap of thick walled fibres separated from the epidermis by 1-3 rows of parenchyma. The adaxial side of the bundle was enclosed in thin walled fibres and lignified parenchyma which were within the outer palisade. On the edges of the midrib, there were small bundles and vascular strands. At the margins, there was palisade and mesophyll; cells contained tannin. On each side of the leaflet, a single lower order vein had well developed abaxial and adaxial fibres. Minor bundles were within the mesophyll. Occasional bundles contained only large, tracheary elements. Similar cells sometimes occurred on the edges of larger bundles. Bundle sheaths were weakly developed.

Group 7.

G. robusta. Leaves were compound; leaflets were described.

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were weakly recurved. Abaxial ridges were associated with main veins.

Anatomy

Leaves were dorsiventral. Hairs were abundant on the abaxial surface and rare on the adaxial. The epidermis consisted of a single row of cells; outer walls were cutinised on the adaxial surface and around margins and weakly cutinised on the abaxial side of major veins. Stomata which were restricted to the abaxial surface were paracytic and had a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, was a single row of high, narrow palisade cells. Below the palisade, there were some 5-7 rows of mesophyll. Occasional palisade and mesophyll cells had weakly lignified walls; a few contained tannin. Vascular bundles were collateral. Phloem was abaxial. At the midrib, there was a smaller bundle on either side of a large central bundle. Vascular bundles were separated by lignified parenchyma. Fibre caps were weakly defined. Towards the adaxial side, there was a group of fibres separated from the epidermis by parenchyma. On the abaxial side, a more or less continuous zone of fibres was separated from the epidermis by some 4 rows of parenchyma (Fig. 38). At the margins, there was palisade and mesophyll. On one side of the leaflet, there were 2 bundles with well developed abaxial and adaxial fibre caps which extended nearly to the epidermis and, on the other side, there were 3. Lower order veins were of various sizes; some had adaxial fibre caps which extended into the palisade. Minor veins were within the mesophyll. Some small bundles contained only large tracheary elements. There were similar cells on the periphery of some bundles. Around some bundles, sheath like cells were lignified and heavily pitted (Figs. 39, 40).

Occasional short, irregular thick walled fibres were associated with vascular bundles.

G meisneri

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were hardly recurved. Abaxial ridges were associated with main veins.

Anatomy

Leaves were dorsiventral to weakly isolateral. Hairs occurred on the abaxial surface and were rare on the adaxial. The epidermis consisted of a single row of cells; outer walls were heavily cutinised on the adaxial surface, around margins and on the abaxial side of main veins. Stomata which were restricted to the abaxial surface were paracytic and had a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis was a single row of tall narrow palisade cells with pits in projections in anticlinal walls. Abaxial palisade was weakly developed and interrupted; cells were shorter and wider. Between the palisade, there was some 5-7 rows of spongy mesophyll. Occasional palisade and mesophyll cells had weakly lignified walls; some contained tannin. Vascular bundles were collateral. Phloem was abaxial. At the midrib, there was a smaller bundle on either side of a large central bundle. Vascular bundles were separated by lignified parenchyma; occasional large sclereids occurred among the parenchyma. On the adaxial side, within the lignified parenchyma, there was a small group of fibres. On the abaxial side, there was a band of fibres separated from the epidermis by some 4 rows of lignified parenchyma (Fig. 41). At the margins, the fibre cap associated with a small bundle was separated from the epidermis by 2-3 rows of large, lignified parenchyma cells. On either side of the leaf, there were 2 or 3 bundles with well developed fibre caps separated from the adaxial epidermis by a single row of large, upright parenchyma cells

and from the abaxial by 2-3 rows of lignified parenchyma. Lower order veins were of various sizes; some had adaxial fibre caps which extended into the palisade. Minor veins were within the mesophyll. Some bundles contained only large tracheary elements. There were similar cells on the periphery of some bundles. Occasional, short, irregular, thick walled fibres were associated with vascular bundles. Bundle sheaths were hardly developed.

G. brachystachya

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were recurved and there was a pronounced abaxial ridge associated with the midrib so that the abaxial surface was deeply grooved.

Anatomy

Leaves were dorsiventral to weakly isolateral. Hairs were abundant in abaxial grooves and rare on the adaxial surface. The epidermis consisted of a single row of cells with heavily cutinised outer walls on the adaxial surface, around margins and on the abaxial surface of the midrib. Stomata which were restricted to the abaxial grooves were paracytic and had a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there were 1-4 rows of lignified parenchyma and, below these, 2-3 rows of palisade. On the abaxial ridge, there was lignified parenchyma below the epidermis. On the edges of the ridge, there were palisade cells below the parenchyma. Opposite abaxial grooves, there were some 7-9 rows of mesophyll. Many palisade and mesophyll cells had lignified walls and contained tannin. Vascular bundles were collateral. Phloem was abaxial. Abaxial and adaxial caps of thick walled fibres associated with the midrib extended to the sub epidermal parenchyma. A single row of lignified parenchyma which extended around each margin separated the epidermis

from thick walled fibres associated with a vascular bundle. On each side of the leaf, between the midrib and the margin, there were 4 vascular bundles with well developed adaxial caps of thick walled fibres which extended to the parenchyma. Minor bundles which were without fibres were within the mesophyll. Bundle sheaths were not an obvious feature.

G. papuana

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were hardly recurved. Ridges over main veins were well developed on the abaxial surface and less pronounced on the adaxial.

Anatomy

Leaves were dorsiventral. Hairs were abundant on the abaxial surface and rare on the adaxial. The epidermis consisted of a single row of cells; outer walls were cutinised on the adaxial surface, around margins and on the abaxial side of main veins. Especially where sub epidermal cells were lignified, occasional epidermal cells had lignified walls. Stomata which were restricted to the abaxial surface, were paracytic and had a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a row of tall, narrow palisade cells; some had irregular ends which intruded among other cells. Many palisade cells were weakly lignified; some were heavily lignified and resembled columnar sclereids. Irregular, lignified cells occurred among the 5-7 rows of more or less rectangular mesophyll cells. Many palisade and mesophyll cells contained tannin. Vascular bundles were collateral. Phloem was abaxial. At the midrib, there was a single large bundle. A tangentially extended abaxial fibre cap was separated from the epidermis by some 5 rows of lignified parenchyma. Adaxial fibres were mixed with lignified parenchyma; there were 2-3 rows of lignified parenchyma below the epidermis (Fig. 42). On each side of the complex,

there was a small vascular bundle. At each margin, a tangentially extended band of fibres associated with a small vascular bundle was separated from the epidermis by 3 rows of small parenchyma cells which had lignified walls and contained tannin (Fig. 43). On each side of the leaf, there were several (>10) bundles which, with their associated tissues, spanned the thickness of the leaf and were separated from the epidermises by lignified parenchyma. Often, this parenchyma was extended tangentially and, particularly on the edges of groups, was large and well pitted. Occasional groups of lignified parenchyma cells which were not obviously associated with vascular bundles, interrupted the palisade. Minor bundles were within the mesophyll. Some bundles contained only large tracheary elements. There were similar cells on the periphery of some bundles. Bundle sheaths were weakly developed.

G. glauca

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were rounded. There was a slight widening of the leaf near the midrib and main veins.

Anatomy

Leaves were isolateral. Hairs were abundant on both surfaces. The epidermis consisted of a single row of cells; outer walls were weakly cutinised. Stomata which occurred on both surfaces were paracytic with a single subsidiary cell on either side of the guard cells. There was a single row of palisade cells below each surface. Some cells had irregular ends which intruded among other cells, many had weakly lignified cell walls and some contained tannin. Between the palisade, there were some 4 rows of rectangular, thin walled mesophyll cells orientated with their long axes parallel to the leaf surface. Occasional palisade and mesophyll cells

contained silica. At the midrib, there was a tangentially spread complex which included 3 bundles. Between the bundles, there was lignified parenchyma. Each bundle had a well developed abaxial and adaxial cap of fibres. Around the complex, there was a single row of sheath like cells which contained silica bodies. A row of unlignified parenchyma or, in places, modified palisade cells separated these tissues from the epidermises. At each margin, there was a weakly developed vascular bundle separated from the epidermis by some 2 rows of unlignified parenchyma. On either side of the leaf, there were 6 to 9 bundles with well developed abaxial and adaxial fibre caps most of which were separated from the epidermises by heavily modified palisade and surrounding sheath like cells which often contained silica. Minor bundles were within the palisade, many contained only large simple tracheary elements. There were similar cells on the periphery of some bundles. Sheath cells sometimes contained silica bodies.

G. striata

Outline in transverse section

The adaxial surface was weakly convex. Margins were rounded. On the abaxial surface ridges and deep grooves alternated.

Anatomy (Fig. 44)

Leaves were dorsiventral to weakly isolateral. There were occasional hairs on the adaxial surface and on abaxial ridges. In abaxial grooves, hairs were abundant. The epidermis consisted of a single row of cells with heavily cutinised outer walls on the adaxial surface, around margins and on abaxial ridges. Stomata which were restricted to abaxial grooves were paracytic with a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there were some 4 rows of lignified parenchyma; around margins and on abaxial ridges, there were 1-3 rows. Especially on the adaxial side of

the leaf and around margins and, less frequently, on abaxial ridges, there were groups of fibres among the parenchyma.

Below the adaxial parenchyma, there were 2 rows of palisade and a weakly developed third row. There were also palisade cells towards the margins of abaxial ridges. Spongy mesophyll coincided with abaxial grooves. The walls of some palisade and mesophyll cells were weakly lignified; some cells contained tannin. Vascular bundles were collateral. Phloem was abaxial. Associated with each ridge, there was a large vascular bundle with well developed abaxial and adaxial caps of thick walled fibres separated from the epidermises by 1-3 rows of lignified parenchyma. Lignified parenchyma surrounded the vascular tissues and, on the edge of it, there were numerous small vascular strands. Towards each margin, there were 2 smaller vascular bundles with well developed adaxial girders of thick walled fibres separated from the epidermis by 2-3 rows of lignified parenchyma; abaxial fibres were weakly developed. Minor bundles, some of which had fibres associated with them, were within the mesophyll. In some minor bundles, vascular tissues were not precisely delimited and orientated. Some small groups contained only large, simple, tracheary elements. Similar cells occurred on the edges of larger vascular bundles or as isolated cells among leaf tissues. Occasional, irregular, thick walled fibres or sclereids were associated with vascular bundles. Bundle sheaths were not an obvious feature.

Group 8.

G. nematophylla

Outline in transverse section

Leaves were linear terete and, in transverse section, almost circular. A flattened region corresponded to the reduced adaxial surface of the leaf base and, on either side of it, there was a small, shallow groove.

Anatomy (Fig. 21)

Leaves were more or less terete. Hairs were numerous over the whole surface. The epidermis consisted of a single row of cells with cutinised outer walls. There were small druses, acicular and rhombic crystals in epidermal cells. Stomata occurred over the entire surface, except in the flattened adaxial region, and were numerous in adaxial grooves. They were paracytic with a single subsidiary cell on either side of the guard cells and, except in grooves, were sunken. Below the epidermis, there was a row of tall narrow palisade cells, a more weakly developed second and, in places, a third row. Cells had numerous pits in projections in anticlinal walls. Some palisade cells had lignified walls. Near stomata and in adaxial grooves, palisade cells were irregular and had thin walls. At the centre of the adaxial region, palisade was interrupted by a group of large lignified parenchyma cells which contained tannin. Parenchyma, sometimes containing tannin, filled the centre of the leaf; vascular bundles and their fibres were within this region. The midrib was towards the abaxial side of the leaf and, on either side of it, were 3 main bundles in a radial file. Fibre caps associated with the phloem were well developed, fibres associated with xylem were few. Around the periphery of the central region, parenchyma was unlignified and there were numerous small bundles and vascular strands. In some, tissues were not precisely delimited and orientated. Large, simple tracheary elements occurred on the edges of vascular groups or as isolated cells.

G. polybotrya

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were rounded.

Anatomy

Leaves were isolateral. Occasional hairs occurred on both surfaces. The epidermis consisted of a single row of cells. Outer walls were cutinised, especially at margins. Stomata which occurred on both surfaces were paracytic with a single subsidiary cell on either side of the guard cells. Below the epidermis, there was a row of palisade cells and a weakly developed second row. Between the palisade were some 4 rows of more or less rectangular mesophyll cells. Around margins, the outer palisade was continuous (Fig. 45). Vascular bundles were within the mesophyll. Bundles were collateral. Phloem was abaxial. The midrib, and 4 bundles of similar extent, were surrounded by abaxial and adaxial fibres and lignified parenchyma (Fig. 46). Some lower order veins were similar in form but smaller, many were without fibres. Some small bundles contained only large, simple tracheary elements. Similar cells occurred on the edges of larger bundles. Bundle sheaths occurred especially around small bundles.

G. integrifolia (Tindale 207 & Maslin)

Outline in transverse section

Abaxial and adaxial surfaces were more or less parallel. Margins were rounded.

Anatomy

Leaves were isolateral. Hairs occurred on both surfaces. The epidermis consisted of a single row of cells. Except at margins, outer walls were hardly cutinised. Stomata, which occurred on both surfaces, were paracytic and had a single subsidiary cell on either side of the guard cells. Below each epidermis, there were 2 rows of palisade cells with pits in projections in anticlinal walls; especially in the outer rows, cells contained tannin. In the centre of the leaf, there were 3-4 rows of mesophyll cells similar in shape and orientation to palisade cells (Fig. 47). Bundles were

collateral. Phloem was abaxial. The midrib which had abaxial and adaxial fibre caps was within the outer palisade. It was distinguished only by its position; many other bundles were of similar size and structure. At the margins, there was mesophyll. Many other bundles were well developed and had abaxial and adaxial fibres or adaxial fibres only. Occasional small bundles contained only large tracheary elements. Similar cells occurred around the edges of larger bundles. Bundle sheaths were well developed.

G. integrifolia ssp. biformis

Outline in transverse section

Leaves were linear terete and, in transverse sections, were oval, laterally extended and ridged.

Anatomy (Fig. 18)

Leaves were linear terete. Hairs occurred over the whole surface but were more frequent in grooves. The epidermis consisted of a single row of cells. Cutinised outer walls were thicker over ridges and only weakly developed in grooves. Stomata which occurred in grooves were paracytic with a single subsidiary cell on either side of the guard cells. Below the epidermis, there was a single row of tall narrow palisade cells with abundant pits in projections in anticlinal walls. Rounded parenchyma cells filled the centre of the leaf. The walls of many palisade cells and occasional mesophyll cells were lignified. Palisade cells contained tannin. Mesophyll cells, especially sheath like cells associated with vascular bundles contained large silica bodies. Vascular bundles which often coincided with ridges were in a ring towards the outside of the central mesophyll. At the centre of the abaxial side of the leaf, there was a large bundle which was continuous with the median leaf trace. Phloem was towards the palisade except in 2 small bundles at the centre of the adaxial side which were turned through ninety

degrees (Fig. 18). With the exception of these bundles which had fibres associated with the xylem only, all the bundles had fibres associated with phloem and xylem. Large, simple tracheary elements occurred on the edges of vascular bundles. Bundle sheaths were hardly developed.

A second specimen (Strid 20757) was similar to H973/80 288, except that the anticlinal walls of the palisade were less well pitted, palisade and mesophyll cells were not lignified and palisade cells did not contain tannin. There were bundle sheaths.

G. didymobotrya

Descriptions of *G. integrifolia* ssp. *biformis* described this species but mesophyll cells, as well as palisade cells, contained tannin. Bundle sheaths were not an obvious feature and no silica bodies were seen. With the exception of the two adaxial bundles, all the bundles had well developed caps of thick walled fibres associated with phloem and xylem. Those associated with the phloem interrupted the palisade and were separated from the epidermis by a single row of parenchyma. There were small peripheral bundles associated with some main bundles. Minor bundles occasionally occurred within the mesophyll. Large, simple tracheary elements were numerous, especially outside the fibre caps associated with the xylem.

G. pyramidalis

Leaves were once or twice pinnate. Leaflets were sectioned.

Outline in transverse section

The abaxial and adaxial surfaces were more or less parallel and slightly undulating over large vascular bundles. Margins were rounded, square or extended and pointed.

Anatomy (Figs. 48, 49)

Leaflets were isolateral. On both surfaces, the epidermis consisted of a single layer of cells with cutinised outer walls. Hairs and stomata occurred on both surfaces. Stomata were sunken and paracytic with a single subsidiary cell on either side of the guard cells. In epidermal cells, there were druses and acicular crystals; prismatic and rhombic crystals occurred and, sometimes, they were twinned. Below the epidermis, there were 2 rows of palisade cells. Many cells had lignified walls; many contained tannin. At the margins, palisade was interrupted by rounded parenchyma cells. Within the leaflets, parenchyma formed the ground tissue. Cells were large, angular and weakly lignified in the centre and smaller, more rounded and unlignified near the palisade. Within the central parenchyma, vascular bundles were in a double row. Phloem was towards the palisade. In the 2 rows, major bundles coincided. There were fibre caps associated with the phloem. Sometimes, fibres associated with the xylem merged (Fig. 48). At the 2 margins, the arrangement of vascular bundles was different. At one, there was a single large bundle which was continuous with the median leaf trace and, at the other, small bundles. Around the periphery of the central parenchyma, there were small bundles and vascular strands (Fig. 49). In many, phloem was towards the palisade but, in some, vascular tissues were not precisely delimited and orientated. Occasionally, a small fibre cap was associated with the phloem or, less often, with the xylem. Scattered fibres were loosely associated with the bundles or occurred in groups or as isolated cells near the periphery of the central region. There were well developed fibres among the parenchyma at the margins. Large, simple, vascular elements occurred on the edges of vascular bundles or in groups or as isolated cells, near the periphery of the central mesophyll.

G. mimosoides

Outline in transverse section

The outline in transverse section was similar to *G. pyramidalis*.

Anatomy (Figs. 50-52)

Generally, the description of *G. pyramidalis* described this species. Some characteristics were different:-

Stomata: Occasional stomata had 2 parallel subsidiary cells on one or, less often, on both sides of the guard cells.

Palisade: Outer palisade cells had abundant pits in projections in anticlinal walls. The inner row was weakly developed and cells were shorter and wider. In the outer row, some darkly stained cells were narrower than others and had a tendency to branch and intrude into the second layer.

Central mesophyll: Cells were lignified and some contained tannin. Sclereids occurred frequently.

Margins: Fibres were associated with vascular bundles only.

A second specimen (Evan 3356) was similar to CSIRO 4843 but the inner row of palisade cells was more strongly developed. In both rows, cells had lignified walls and contained tannin. There were no sclereids in the central mesophyll.

G. dimidiata

Outline in transverse section

The outline in transverse section was similar to *G. pyramidalis*.

Anatomy (Figs. 53-55)

Generally, the description of *G. pyramidalis* described this species. Some characteristics were different:-

Hairs: No hairs were seen.

Stomata: On both surfaces, some stomata with 2 subsidiary cells on one or both sides of the guard cells regularly occurred (Fig. 56). In epidermal preparations, there were some stomata with large subsidiary cells which showed indications of dividing into 2 (Fig. 57). Other stomata had 2 subsidiary cells on one or both sides of the guard cells (Fig. 58).

Palisade: A third row of palisade was weakly developed in some parts of the leaf. Cells had numerous pits in projections in anticlinal walls, did not have lignified walls and did not contain tannin. End walls were slightly irregular but there was no evidence of intrusive growth.

Central mesophyll: Cells were irregular and had thin walls. Some contained tannin.

Margins: Fibres were associated with vascular bundles only. Some parenchyma cells were lignified.

Vascular bundles: At the periphery of the central mesophyll, bundles had fibre caps associated with the phloem and, sometimes, fibres associated with the xylem. Others were without fibres. There were few isolated groups of fibres or single fibres.

A second specimen (Evans 2073) was similar to H173/77 154 but crystals in epidermal cells occurred rarely and were weakly developed. There were

only 2 rows of palisade cells. Especially in the inner row, cell walls were lignified and cells contained tannin.

Group 9.

G. trifida. Leaves were 3 lobed and each lobe was 3 toothed.

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were weakly recurved. A pronounced abaxial ridge was associated with the midrib.

Anatomy

Section from the middle of a lobe - Leaves were dorsiventral. The epidermis consisted of a single row of cells with weakly cutinised outer walls on the adaxial surface, round margins and on the abaxial surface of the midrib. Stomata which were restricted to the shallow abaxial grooves were paracytic with a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis was a single row of tall narrow palisade cells. There were occasional arm palisade cells. There were some 5 rows of mesophyll cells. Particularly near vascular bundles, occasional mesophyll cells were weakly lignified. Vascular bundles were collateral. Phloem was abaxial. At the midrib, fibres associated with the single large vascular bundle were separated from the adaxial epidermis by modified palisade and from the abaxial by 1-2 rows of modified mesophyll cells. At the margins, palisade was continuous. Lower order bundles which were within the mesophyll had small adaxial fibre caps or were without fibres. Large, simple, tracheary elements occurred on the edges of some bundles.

Section at the junction of 3 lobes - At the midrib, there was a broad arc of 5 vascular bundles each with an abaxial fibre cap separated from the epidermis by 2 rows of parenchyma. Adaxial fibres were united in a more or

less continuous band separated from the epidermis by a single row of parenchyma. Other features were similar to those in the middle of the lobe.

Section from the middle of a tooth - At the midrib, there was a single vascular bundle. Large amounts of lignified parenchyma were associated with the bundle. An abaxial fibre cap and an arc of fibres which enclosed the adaxial side of the complex were separated from the epidermises by 1 row of parenchyma. There was a small vascular bundle on each edge of the complex. Other features were similar to those in the middle of the lobe.

G. paniculata. Leaves were once or twice divided into 3 segments.

Outline in transverse section

Abaxial and adaxial surfaces were parallel. Margins were strongly recurved. The midrib was radially extended into a pronounced abaxial ridge; there was a slight adaxial ridge. Towards the margins, there were adaxial ridges over main veins.

Anatomy

Leaves were dorsiventral. Hairs occurred on both surfaces. The epidermis consisted of a single row of cells with cutinised outer walls on the adaxial surface, around margins and on the abaxial surface of the midrib. Stomata which were restricted to the abaxial grooves were paracytic with a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a single row of tall narrow palisade cells. There were some 4-5 rows of mesophyll. Near the midrib, there was some development of abaxial palisade and, below it, there were 2-4 rows of mesophyll cells. Occasional druses and acicular crystals occurred in epidermal and mesophyll cells. Many palisade and mesophyll cells had weakly lignified walls; some contained tannin. Vascular bundles were collateral. Phloem was abaxial. Within the radially elongated midrib, there was a large bundle towards the abaxial side and, adaxial to it, were two radial files of small bundles and

vascular strands. Palisade and mesophyll extended around the sides of the midrib. Within the complex, there was lignified parenchyma. Fibres which were not closely associated with vascular tissues were separated from the abaxial and adaxial epidermises by a single row of parenchyma. Towards each margin there were 3 bundles with well developed caps of adaxial fibres, separated from the epidermis by a single row of parenchyma. Between the midrib and the margin, there was a slightly smaller bundle with fibres separated from the adaxial epidermis by modified palisade cells. Lower order bundles were within the mesophyll. On the edges of some bundles large simple tracheary elements occurred and there were occasional irregular thick walled fibres.

The structure was similar at all levels within the leaf except that, nearer the tip, there were only 3 more or less evenly spaced veins with well developed adaxial fibre caps.

G. vestita

Outline in transverse section

Abaxial and adaxial surfaces were parallel. Margins were weakly recurved. Abaxial ridges were pronounced over main veins. There was an adaxial groove over the midrib and slight undulations over other major bundles.

Anatomy

Leaves were weakly isolateral. Hairs occurred on both surfaces. On the abaxial and adaxial surfaces, the epidermis consisted of a single row of cells with cutinised outer walls. Stomata which were restricted to the abaxial surface were paracytic with a single subsidiary cell on either side of the guard cells. There was a single row of adaxial palisade cells and an interrupted row of shorter, wider abaxial palisade. Between the palisade, there were some 5 rows of mesophyll. Palisade and mesophyll cells had

weakly lignified walls; some contained tannin. In some vascular bundles, vascular tissues were not precisely orientated or delimited; often there were vessels on the abaxial side of the phloem in addition to the larger xylem group on the adaxial side. Fibres associated with the midrib were separated from the epidermises by 1-3 rows of parenchyma. At the margins, there was palisade and mesophyll. On each side of the leaf, there was a vein which was of almost similar extent to the midrib; adaxial fibres were separated from the epidermis by modified palisade cells. Lower order veins had abaxial and adaxial caps of thick walled fibres; occasionally, fibres extended into the palisade. Minor veins which were within the mesophyll had adaxial fibres or were without fibres. Some small bundles contained only large, simple tracheary elements. Short, irregular thick walled fibres or sclereids were on the periphery of some bundles. Bundle sheaths were hardly developed.

Group 11.

G. wickhamii

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were rounded. There were abaxial and adaxial ridges over main veins and abaxial ridges over lesser veins.

Anatomy

Leaves were isolateral. Hairs were few. The epidermis consisted of a single row of cells. Outer walls were weakly cutinised, particularly on the abaxial surface. Small crystals, particularly druses, occurred in epidermal cells. Stomata which were frequent on both surfaces were sunken and paracytic with a single subsidiary cell on either side of the guard cells. On each side of the leaf, there was a single row of palisade cells with pits in projections in anticlinal walls. Between the palisade, there were 5-8 rows of

mesophyll cells. Some palisade and mesophyll cells contained tannin, the walls of some were weakly lignified. At the midrib, there was a complex which contained an arc of 3 bundles with abaxial phloem and, towards the adaxial side, 2 inverted bundles (Fig. 59). There was lignified parenchyma within the complex and, on each edge, there was a small vascular bundle. Fibres associated with the midrib were separated from the epidermises by 1-3 rows of parenchyma (Fig. 59). There were 2 bundles of similar extent to the midrib on either side of the leaf. At each margin, thick walled fibres associated with a vascular bundle were separated from the epidermis by 1-2 rows of parenchyma. In many bundles, there was xylem on both sides of the phloem (Fig. 60). Especially in smaller bundles, vascular tissues were not precisely delimited and orientated. Some contained only large, simple, tracheary elements. Similar cells occurred on the edges of larger bundles. Many lower order veins had well developed abaxial and adaxial caps of thick walled fibres which extended into the palisade or were within the mesophyll. Minor bundles which were within the mesophyll had abaxial and adaxial fibres, adaxial fibres or were without fibres. Sheath cells were associated with vascular bundles but did not always surround them. Short, irregular thick walled fibres were associated with some bundles.

In a second specimen (Carolin 6200) some characteristics were different:

Epidermis: Cell walls were heavily cutinised and there were abundant hairs on both surfaces.

Midrib: There was an arc of 5 bundles with phloem towards the abaxial side. Towards the adaxial side, there was one inverted bundle and one double bundle with phloem on each side of the xylem. Around the periphery of the complex, there were small vascular bundles and vascular strands.

Margins: There was modified palisade tissue between the fibres and the epidermis.

Vascular bundles: There were 6 bundles of similar extent to the midrib on either side of the leaf.

Short, irregular thick walled fibres or sclereids occurred associated with vascular bundles or as idioblasts, particularly at the boundary between palisade and mesophyll (Fig. 61).

Group 12.

G. insignis

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were rounded. There were abaxial and adaxial ridges over major veins and abaxial ridges over lesser veins.

Anatomy

The leaf was isolateral. Hairs were few. On both surfaces, the epidermis consisted of a single row of cells with cutinised outer walls. Stomata which were on the abaxial surface were paracytic with a single subsidiary cell on either side of the guard cells. On each side of the leaf, there was a single row of palisade cells with pits in projections in anticlinal walls; abaxial cells were shorter and wider than adaxial cells. Between the palisade, there were some 4-5 rows of mesophyll cells. There were occasional small crystals in epidermal or mesophyll cells. Some palisade and mesophyll cells contained tannin; some had lignified walls. Vascular bundles were collateral. Phloem was abaxial. Within the midrib, there were 4 vascular bundles. Between the bundles there was lignified parenchyma. On the periphery of the complex there were small vascular bundles and, in some sections, there were 2 amphivasal bundles towards the adaxial side. Large abaxial and adaxial caps of thick walled fibres were separated from the epidermises by 1-3 rows of parenchyma. On either side of the leaf, there were 2 or 3 bundles of similar abaxial-adaxial extent to the midrib. Wings of

parenchyma were associated with major bundles and there were small bundles at the periphery. At each margin, thick walled fibres associated with a vascular bundle were separated from the epidermis by a single row of parenchyma. Lower order bundles of various sizes which extended into the palisade or were within the mesophyll, had abaxial and adaxial fibres, adaxial fibres or were without fibres. In some smaller bundles, xylem and phloem were not always precisely orientated and delimited. Some contained only large simple tracheary elements. Similar cells occurred on the edges of larger bundles. Short, irregular, thick walled fibres or sclereids were associated with many bundles or, occasionally, occurred as idioblasts. Bundle sheaths were hardly developed.

Group 13.

G. patentiloba

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were recurved. Over main veins, there were large abaxial ridges.

Anatomy

Leaves were dorsiventral. Hairs occurred occasionally on the adaxial surface, around margins and on the abaxial side of major veins and were numerous on other parts of the abaxial surface. The epidermis consisted of a single row of cells. On the adaxial surface, around margins and on the abaxial side of major veins, outer walls were cutinised. Epidermal cells contained large numbers of cluster crystals and acicular crystals (Fig. 62), rhombic crystals also occurred and, sometimes, they were twinned. Stomata which occurred on the abaxial surface were paracytic with a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a single row of tall, narrow palisade cells with pits in projections on anticlinal walls and a second row of more nearly isodiametric cells. On the

abaxial side, there were some 9 rows of spongy mesophyll. The walls of many palisade and mesophyll cells were lignified; many cells contained tannin. Occasional crystals occurred in mesophyll cells. Bundles were collateral. Phloem was abaxial. Within the midrib and a second, similar major vein, there were 3 vascular bundles. Between the bundles, there was lignified parenchyma and fibres. Associated with each complex, there were large abaxial and adaxial fibre caps separated from the epidermises by 1 to 2 rows of parenchyma. Around margins, there was palisade. Near to each margin, there were 2 vascular bundles with well developed adaxial caps of thick walled fibres separated from the epidermis by a single row of parenchyma (Fig. 63). Abaxial fibres were within the mesophyll. Lower order veins which were within the mesophyll had abaxial and adaxial fibres, adaxial fibres or were without fibres. Bundle sheaths were hardly developed. Occasional large, simple tracheary elements were associated with vascular bundles. Short, irregular thick walled fibres or sclereids were associated with many bundles; some occurred as idioblasts.

Group 19.

G. hakeoides

Outline in transverse section

Leaves were linear terete. There was a deep lateral groove on either side of the leaf.

Anatomy (Fig. 64)

Leaves were nearly terete. Hairs were in lateral grooves. The epidermis consisted of a single row of cells. Except in lateral grooves, outer walls were heavily cutinised. Stomata were in lateral grooves, were paracytic and had a single subsidiary cell on either side of the guard cells. Except in grooves where there was spongy mesophyll, there was a single row of palisade cells below the epidermis. Spongy mesophyll filled the centre of

the leaf. The walls of occasional palisade and mesophyll cells were lignified. Associated with the midrib, there was lignified parenchyma and abaxial and adaxial fibres which were separated from the epidermises by a row of heavily modified palisade cells. Around the periphery of the complex, there were several small vascular groups on which tissues were not precisely delimited and orientated. Simple tracheary elements and sclereids occurred in this region. On either side of the midrib, there were 2 bundles with well developed adaxial fibre caps. Abaxial fibres were absent or very weakly developed.

G. hakeoides subsp. *commutata*

Outline in transverse section

Abaxial and adaxial surfaces were parallel. Margins were recurved. There were adaxial ridges over main veins and a pronounced abaxial ridge over the midrib.

Anatomy

Specimens were compared to *G. hakeoides*. Where there was no comment, characters were similar.

Leaves were weakly isolateral. Hairs occurred on the adaxial surface and were more frequent on the abaxial. Epidermal cells had cutinised outer walls on the adaxial surface, around margins and on the abaxial surface of the midrib. Stomata occurred on the abaxial surface only. Below the adaxial epidermis there was a single row of tall narrow palisade cells. On the abaxial side, palisade was more weakly developed. Many palisade cell walls were weakly lignified. Between the palisade, there were some 8 rows of spongy mesophyll. Abaxial and adaxial fibres associated with the midrib were separated from the epidermis by 1-3 rows of parenchyma (Fig. 65). Vascular tissues in bundles on the periphery of the midrib were more precisely orientated and delimited than in *G. hakeoides*. Towards each

margin, there were 3 bundles with well developed adaxial fibre cups separated from the epidermis by a single row of parenchyma (Fig. 66). Lower order veins which were within the mesophyll had abaxial and adaxial fibres, adaxial fibres or were without fibres. Large, simple tracheary elements occurred on the edges of some bundles and some small bundles were composed entirely of these cells.

G. diversifolia

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were incurved. There were abaxial and adaxial ridges associated with major veins.

Anatomy

Leaves were weakly isolateral. On both surfaces, hairs were few. The epidermis consisted of a single row of cells with cutinised outer walls on the adaxial surface, around margins and on the abaxial surface of the midrib. Some epidermal cells contained small acicular crystals. Stomata which were restricted to the abaxial surface were paracytic with a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a single row of tall narrow palisade cells. Abaxial palisade was weakly developed. There were some 7-8 rows of mesophyll. The walls of some palisade and mesophyll cells were weakly lignified. Vascular bundles were collateral. Phloem was abaxial. Fibres associated with the midrib were separated from the abaxial and adaxial epidermises by 1-2 rows of lignified parenchyma which extended laterally beyond the bundle (Fig. 67). On each side, at the periphery of the midrib and its associated tissues, there was a small vascular bundle. Palisade extended around the margins. At each margin, there was a group of fibres and, near to it, 2 bundles with well developed caps of adaxial fibres. Fibres were separated from the epidermis by a single row of lignified parenchyma cells which was extended laterally

and sometimes merged to form a sub epidermal row (Fig. 68). Some groups of similar parenchyma occurred where there were no vascular bundles (Fig. 69). Lower order veins which were within the mesophyll had abaxial and adaxial fibres, adaxial fibres or were without fibres. Some small bundles contained only large, simple tracheary elements. Similar cells were found on the edges of larger bundles. Bundle sheaths were weakly developed. Short irregular thick walled fibres or sclereids were associated with some bundles.

Group 21.

G. heliosperma

Leaves were compound, leaflets were described.

Outline in transverse section

Leaflets had parallel abaxial and adaxial surfaces. Margins were rounded, hardly recurved. Abaxial and adaxial ridges were associated with major bundles.

Ridges were not an obvious feature in 2 specimens (McGillivray and Dunlop 3914; Blake 16979).

Anatomy

Leaflets were isolateral. Hairs which occurred on both surfaces were more numerous in abaxial intercostal regions. The epidermis consisted of a single row of cells with cutinised outer walls which were thinner in abaxial intercostal regions. Stomata which were sunken and abundant in abaxial intercostal regions, were paracytic with a single subsidiary cell on either side of the guard cells. Small crystals, especially druses, occurred in epidermal cells. Below the epidermis, there was a single row of palisade cells. On the abaxial side, these were shorter and wider. Between the palisade, there were some 7 rows of more or less rectangular mesophyll cells; the innermost cells were orientated with their long axes parallel to the surface of the leaflet (Fig.

70). Xylem was predominantly adaxial to the phloem but, in many bundles, vessels were well developed on the abaxial side also (Fig. 72). At the midrib well developed abaxial and adaxial fibre caps were separated from the epidermis by 1-2 rows of lignified parenchyma (Fig. 70). On the abaxial side, fibres were thick walled but, on the adaxial, they were less well developed and associated with large amounts of lignified parenchyma. On the periphery of the complex, there were small vascular groups. On either side of the leaflet, there were 7 or 8 bundles of similar structure and extent to the midrib. At the margins, there were modified palisade cells and, inside these, a small vascular bundle (Fig. 71). Many lower order bundles had well developed abaxial and adaxial caps of thick walled fibres which extended into the palisade or were within the mesophyll. Minor bundles which were within the mesophyll had abaxial and adaxial fibres, adaxial fibres or were without fibres. Large, simple tracheary elements frequently occurred on the periphery of bundles. Sheath cells were associated with vascular bundles but did not always surround them. Short, irregular thick walled fibres or sclereids were associated with some bundles. Occasional, isolated, heavily lignified cells occurred among the mesophyll.

In a second, smaller leaflet from the same specimen (McGillivray 3891) there were 2 bundles of similar extent to the midrib on either side.

In 2 specimens (McGillivray and Dunlop 3914; Blake 16979) intercostal grooves were not a feature of the abaxial epidermis and hairs were less numerous. Outer epidermal walls were cutinised over the whole surface of the leaflet. Stomata were not sunken and none was seen on the adaxial surface. Palisade and mesophyll cells contained tannin. Many bundles were of similar extent to the midrib. At the margins, palisade cells were highly modified and a single row of parenchyma cells separated the bundle from the epidermis.

G. bracteosa

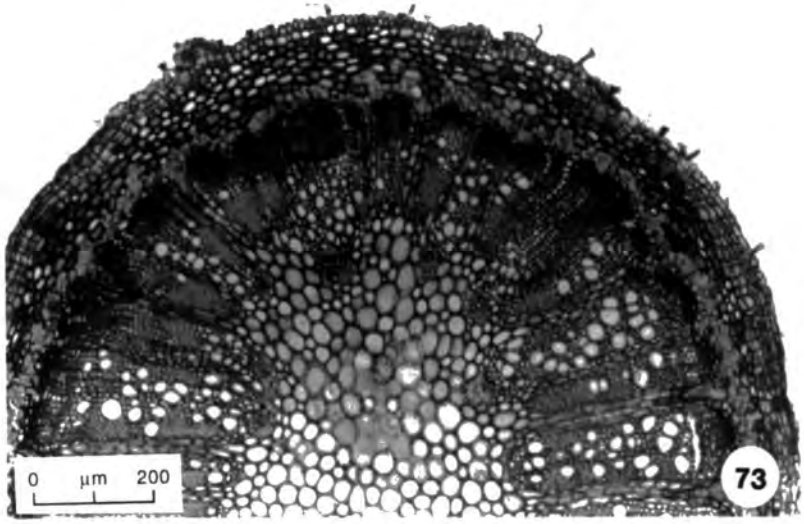
Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were incurved. There was a pronounced abaxial ridge on either side of the midrib.

Anatomy

Leaves were weakly isolateral. Hairs were few. The epidermis consisted of a single row of cells with cutinised outer walls on the adaxial surface, around margins and on the abaxial side of the midrib. There were occasional acicular crystals and druses in epidermal cells. Stomata which were restricted to the abaxial surface were paracytic with a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a single row of tall, narrow palisade cells. Abaxial palisade was more weakly developed. Between the palisade, there were some 6-7 rows of mesophyll cells. Some palisade cells had weakly lignified walls; some contained tannin. Vascular bundles were collateral. Phloem was abaxial. Abaxial and adaxial fibres associated with the midrib were separated from the epidermis by a single row of parenchyma cells. There was lignified parenchyma associated with the midrib. At the periphery of the complex there were several small vascular groups. At each margin, there was a vascular bundle with a well developed fibre cap separated from the epidermis by a single row of parenchyma cells and, near the margin, there were 2 bundles with well developed adaxial caps of thick walled fibres separated from the epidermis by a single row of parenchyma. Abaxial fibres were within the mesophyll. Lower order veins which were within the mesophyll had adaxial and abaxial fibres, adaxial fibres or were without fibres. Bundle sheaths were not developed. Short, irregular, thick walled fibres or weakly developed sclereids were associated with some bundles.

Figs. 73-77. - 73, *H. arborescens* (WRB 5543). Stem, near node, transverse section. - 74, *H. orthorrhyncha* (WRB 5451). Median leaf trace, transverse section. - 75, *H. rostrata* (WRB 5488). Node, transverse section. - 76, *H. platysperma* (Melville 148). Node, transverse section. - 77, *H. trineura* (WRB 5653). Lateral leaf trace, transverse section.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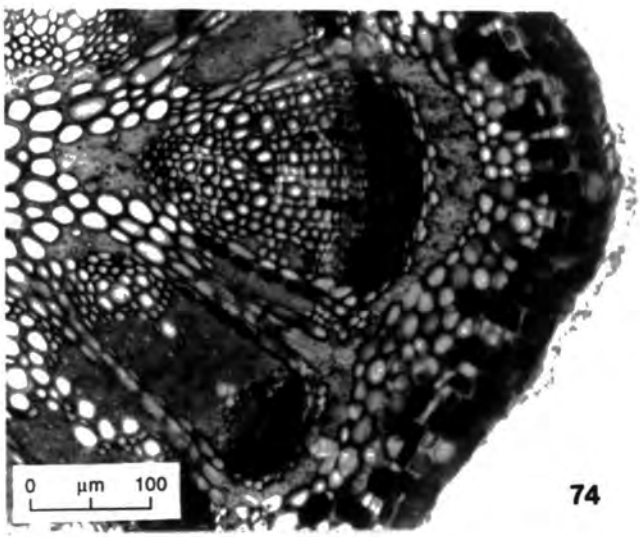
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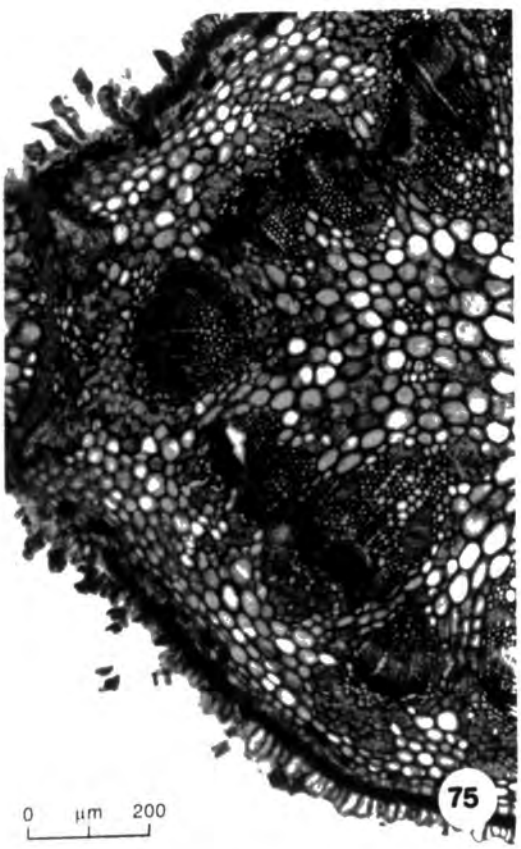
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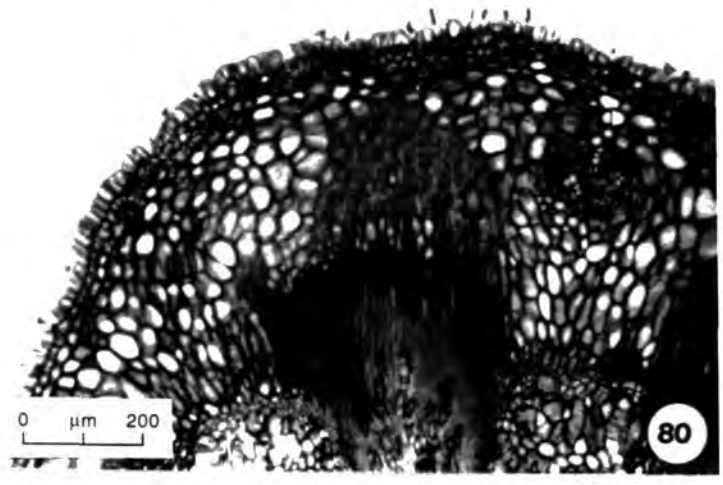

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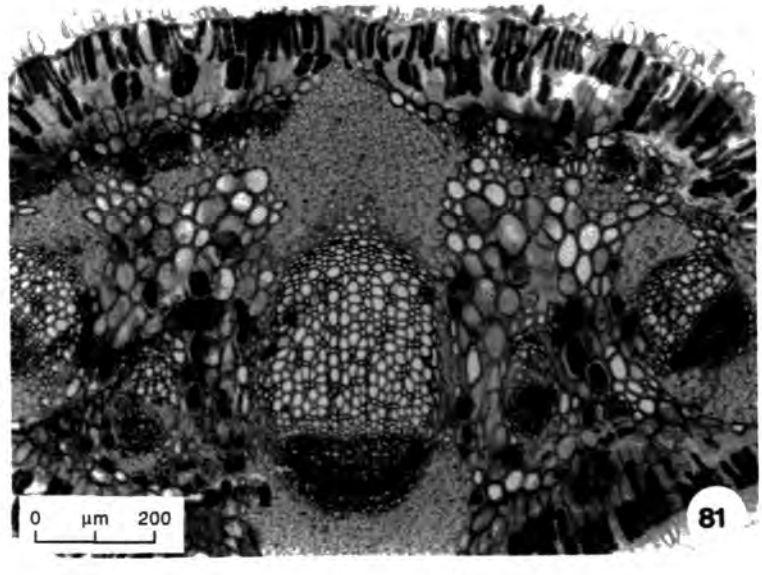

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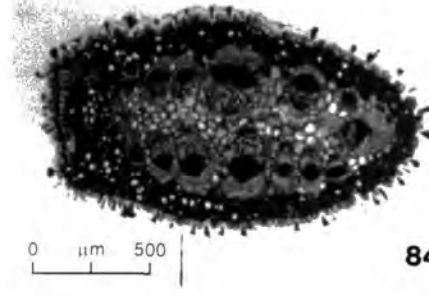

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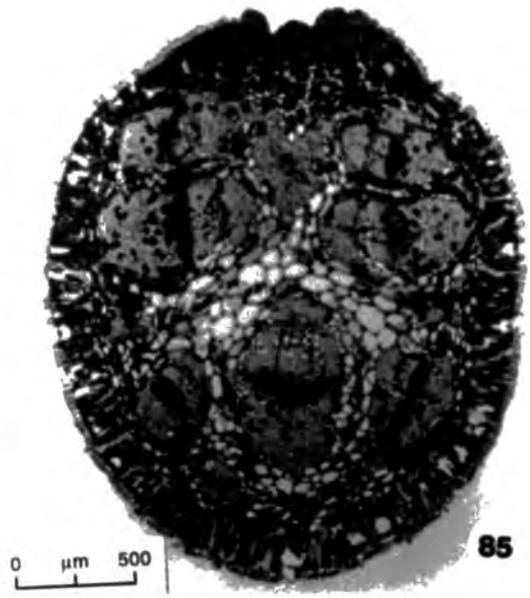
Figs. 78-84. - 78, *H. trineura* (WRB 5654). Node, transverse section. - 79, *H. salicifolia* var. *salicifolia* (WRB 5638). Node, transverse section. - 80, *H. arborescens* (WRB 5343). Leaf base, transverse section. - 81, *H. laurina* (WRB 5082). Leaf base, transverse section. - 82, *H. elliptica* (H 1128/86 422). Leaf base, transverse section. - 83, *H. ambigua* (H 1128/86 500). Leaf base, transverse section. - 84, *H. pandanicarpa* (Orchard 1536). Leaf base, transverse section.

Figs. 85-89. - 85, *H. clavata* (Strid 22500). Leaf base, transverse section. - 86, *H. brownii* (H 1128/86 59). Leaf base, transverse section. - 87, *H. baxteri* (Melville & George 71.114). Leaf base, transverse section. - 88, *H. eriantha*, (P.R. H. St. John). Leaf, X-radiograph. - 89, *H. dactyloides* (WRB 5614). Leaf, X-radiograph. 16 & 17 x 3.



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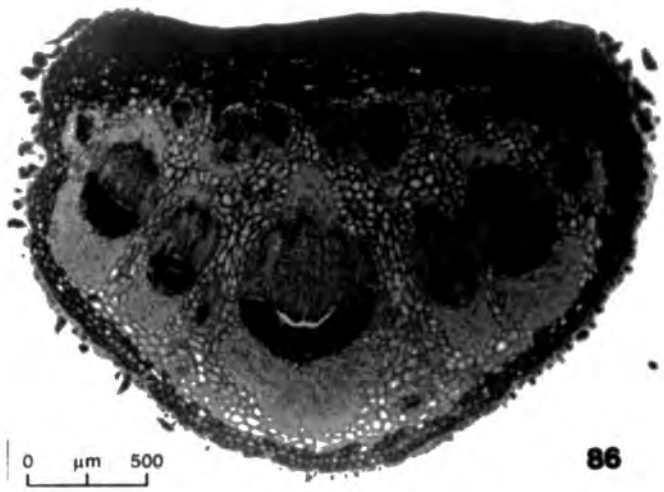

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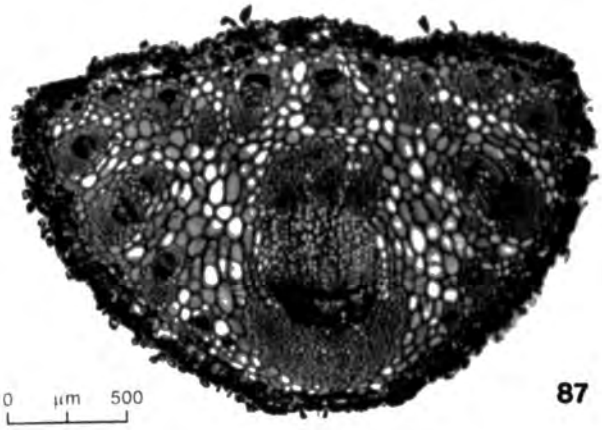

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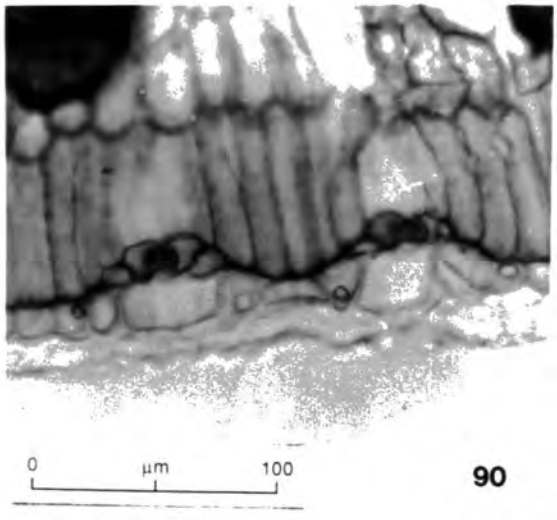
Figs. 90-95. - 90, *H. neurophylla* (Cranbourne). Leaf, transverse section. - 91, *H.* "Dorrigo" (WRB 5634). Leaf, transverse section. - 92, *H. suberea* (Nelson 1507). Leaf, transverse section. - 93-95, *H. trineura* (WRB 5654). Leaf, transverse section.



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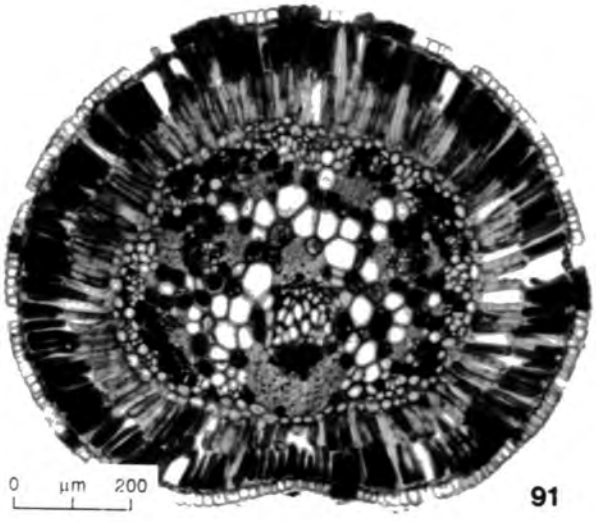

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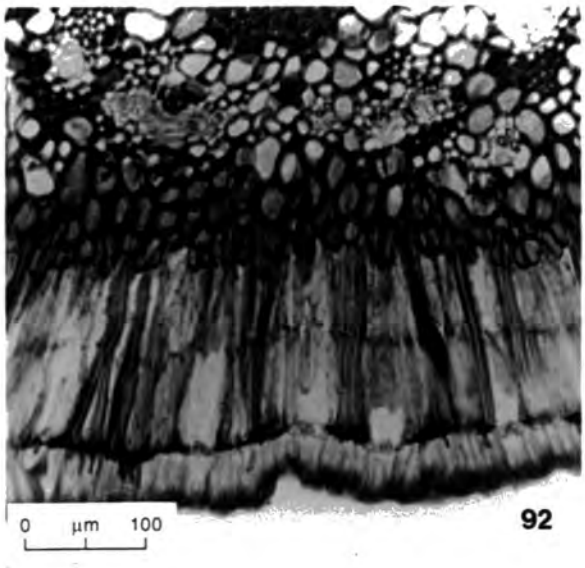

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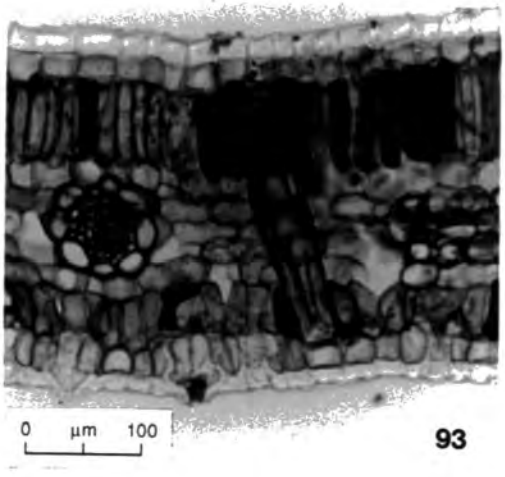

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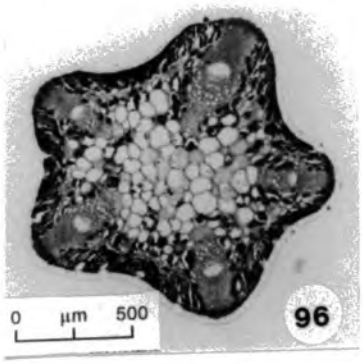
Figs. 96-101. - 96, *H. sulcata* (Coveny 8106). Leaf, transverse section. - 97, *H. plurinervia* (R. W. Johnson 825). Leaf, transverse section. - 98-99, *H. dactyloides* (WRB 5617). Leaf, transverse section. - 100, *H. falcata* (Kew H1128/86 462). Leaf, transverse section. - 101, *H. lasiantha* (Melville 4443). Leaf, longitudinal section.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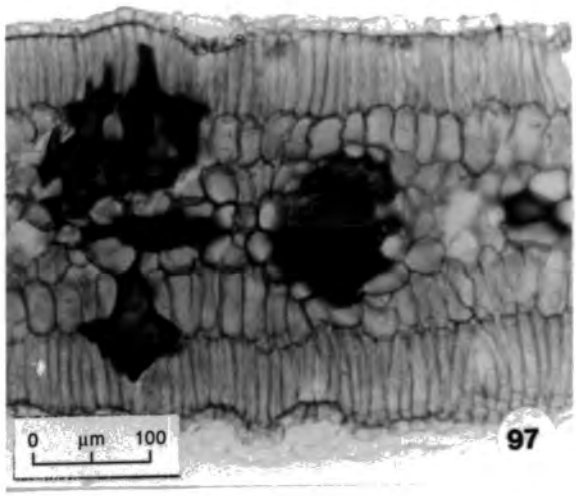
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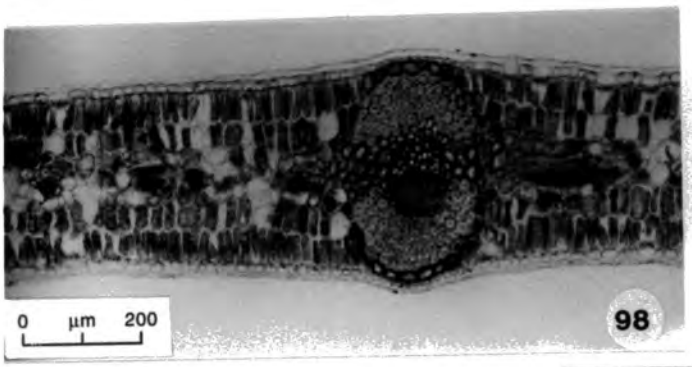
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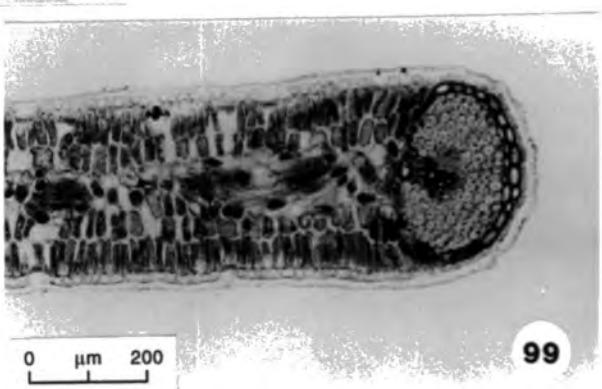
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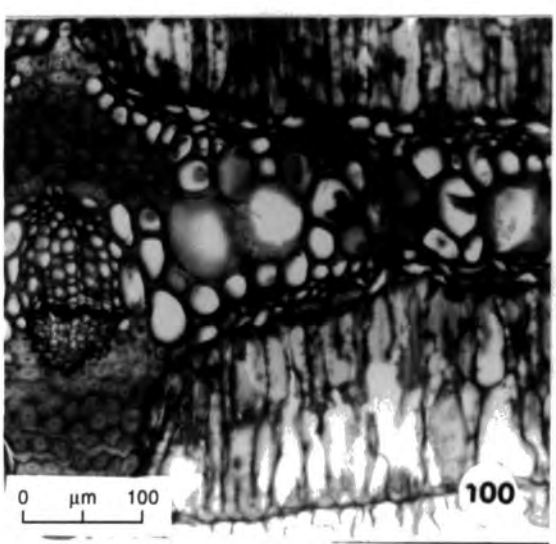
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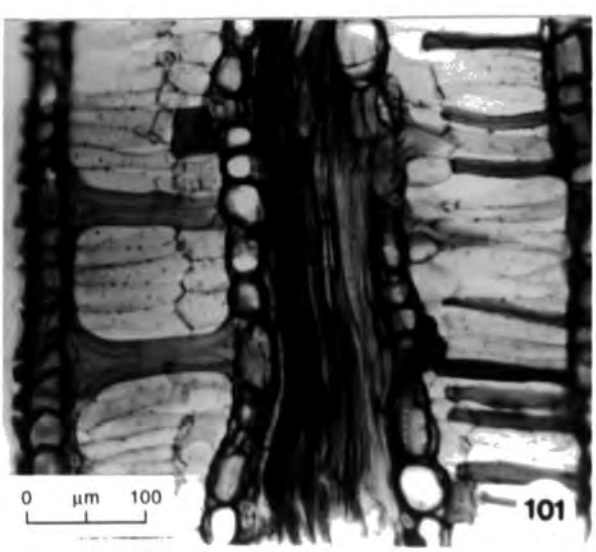
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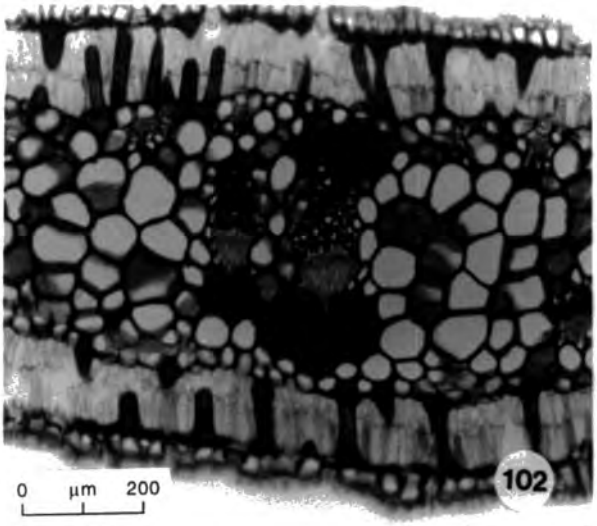
Figs. 102-107. - 102, *H. ceratophylla* (Cunningham 19073). Leaf, transverse section. - 103-104, *H. pandanicarpa* (Orchard 1536). Leaf, transverse section. - 105, *H. lasiantha* (Melville 4443). Leaf, transverse section. - 106, *H. eriantha* (WRB 5623). Leaf, transverse section. - 107, *H. baxteri* (Melville & George 71.114). Midrib, transverse section.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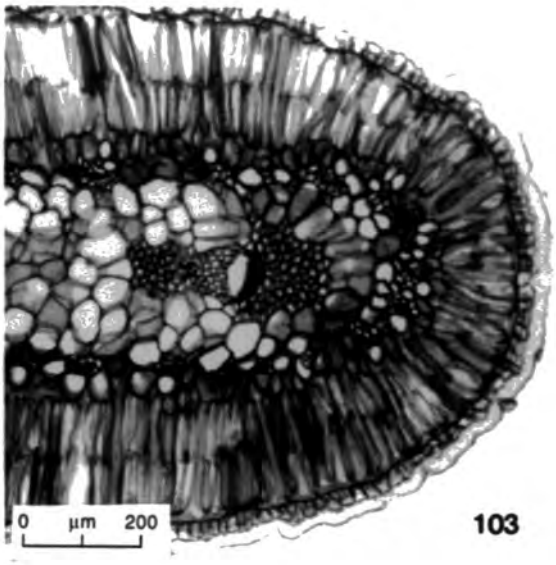
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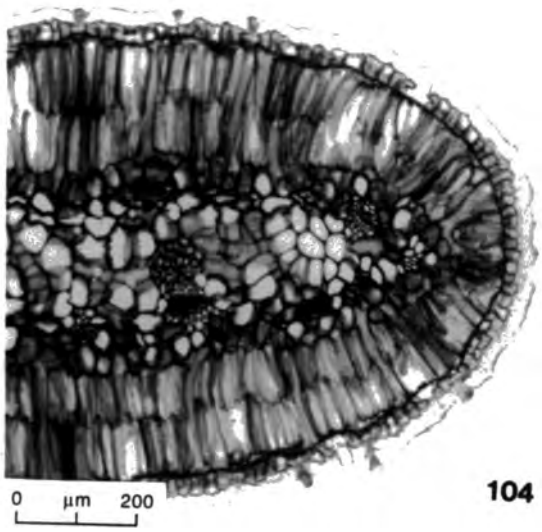
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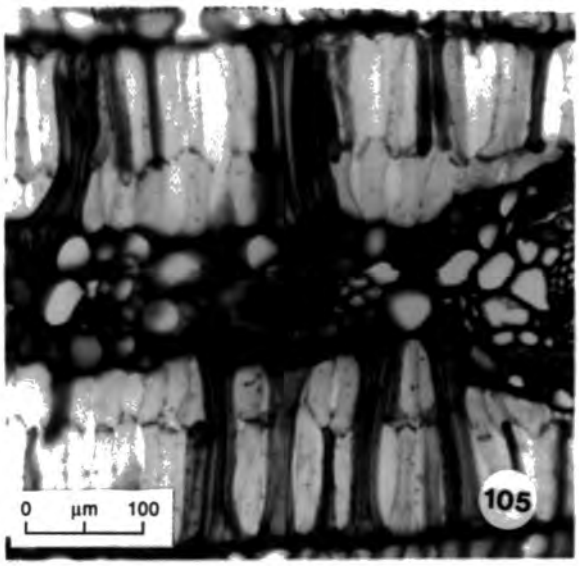
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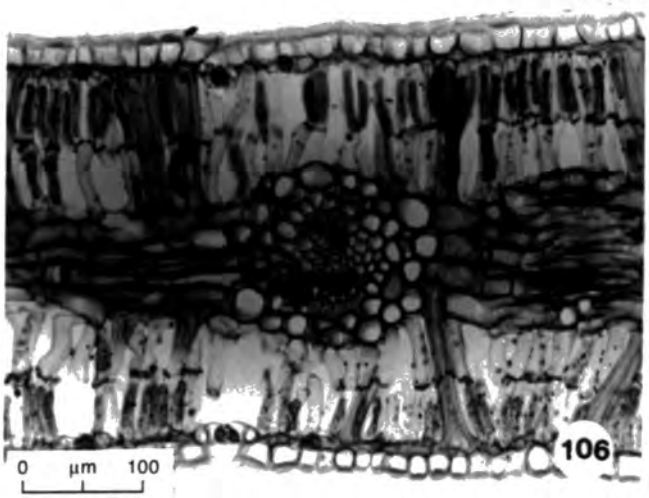
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Table 7.

***Hakea*. Nodes with more than 3 traces and/or inverted bundles in the ~~idrib~~ leaf base**

Specimen	Nodes with more than 3 traces. Median position	Lateral 1	Lateral 2	Inverted bundles in the leaf-base
Sub-division 1				
H. ivoryi WRB 5590.				3
H. trineura WRB 5653.	5	2	1	
Sub-division 2				
H. laurina WRB 5082.				Numerous throughout petiole.
H. loranthifolia Patrick 120.				2
H. elliptica Kew H1128/86 422.	2	2	2	
H. falcata Drummond Kew H1128/86 462.				2 at lower levels. At higher levels small bundles and vascular strands surrounded the central region.
Sub-divison 3				
H. linearis Drummond 335.				
Node.				2
Separate leaf-base.				2
H. eriantha WRB 5623.				2 vascular strands in which tissues were not precisely delimited and orientated.
RBG Sydney 13385.				2
Loa Monga.				1 vascular strand in which tissues were not precisely delimited and orientated.

H. obliqua WRB 5430 Node 2.	2	1	1	
H. baxteri Kew 1128/86 696.	5	1	1	2, 4 or 6 at different levels.
Melville & George 71.114.	5	1	1	2, 4 or 6 at different levels.
H. brownii Kew H1128/86 30.	4	2	1	Numerous adaxial bundles.
Kew H1128/86 59.	5 + 3 small strands at higher level.	1	1	Numerous adaxial bundles.
H. ceratophylla Strid 21634.				
Node.				Vascular strands at 90° to the central bundle.
Separate leaf-base.				Vascular strand at 90° to the central bundle and 1 inverted bundle.
Kew H1128/86 120. Leaf-base.				2 large and many small bundles towards the adaxial side.
H. flabellifolia Kew H128/86 695.	3	1	1	
H. hookeriana Kew H1128/86 699.				2 adaxial bundles at low levels. Many adaxial bundles at higher levels.
H. pandanicarpa and *H. pandanicarpa* ssp. *crassifolia* - all specimens.				In the upper leaf base, a double row of primary bundles in which phloem is towards the palisade. Minor bundles peripheral to central region.
H. platysperma Melville 148.	2	1	1	
Kew H1128/86 70.	3	1	1	

Hakea

Stem (Fig. 73)

Stems included in the stem-node-leaf continuum were between 1 mm and 3.5 mm in diameter.

Where cork had formed it was superficial. The unlignified cortex varied from 2 to 8 cells in width, complementing the size of caps of thick walled fibres associated with vascular bundles. There was a more or less continuous ring of pericyclic sclerenchyma. As well as fibres, this included sclereids which often, though not necessarily, coincided with medullary rays. Vascular tissues were eustelic to siphonostelic. A continuous cambial zone was recognisable. In most specimens there were interxylary fibres. Pith was lignified and, in some species, there were sclereids.

Nodal anatomy

Vascular bundles spanned only a short distance between the stele and leaf base. They did not extend into adjacent nodes.

Below the node, near leaf traces, stelar bundles divided or merged and there were small bundles (Fig. 73). Leaf traces were recognised by wider rays bordering them and by their modified xylem which consisted of simple vascular elements and unlignified parenchyma (Fig. 74). Fibre caps were enlarged and, in lateral leaf traces, orientated towards the leaf base. Near leaf traces, the cortex was expanded and there were numerous sclereids. In 37 of the specimens examined, nodes had 3 traces (Fig. 75), in 10 there were more (Fig. 76). 'Extra' bundles were in median or lateral positions (Table 7).

In seventeen specimens, there were small vascular strands close to leaf traces where they were within or just outside the stele (Fig. 77). Ten were associated with median leaf traces and twenty two with lateral traces. At higher levels, twelve of these vascular strands were close to the leaf traces, but separate from them, throughout the cortex and abscission layer. Twenty

were not seen as individual strands but were components of the leaf trace or of neighbouring stelar bundles. Other vascular strands were first associated with traces where they were outside the stele, within the cortex. At lower levels, they were seen as components of the leaf trace or as isolated groups of weakly differentiated cells. All were close to lateral traces. Four were continuous to the leaf base, 3 were ephemeral.

The occurrence of small vascular strands associated with leaf traces varied among species, within species and within specimens. Nodes were seldom symmetrical.

Abscission layer

In some specimens there were weakly differentiated vascular tissues within the abscission layer. Sometimes they occurred close to leaf traces, sometimes they were separated from them by lignified cells (Fig. 78). At higher levels, bundles were fully differentiated and contributed to the vascularisation of the leaf base, often merging with leaf traces.

Leaf base

At the lowest levels, the leaf base was first recognised by the absence of cork and by a sub-epidermal proliferation of small, closely packed, deeply stained, unlignified parenchyma cells, sometimes within the outline of the stem or, sometimes, within a projection on the side of the stem. At higher levels, a group of lignified parenchyma and, sometimes, sclereids occurred within the unlignified cells (Fig. 79). At lower levels these were in a central group but, above this, they were in discrete bundles radially aligned with leaf traces and separated by lignified parenchyma (Fig. 80). The unlignified parenchyma of the abaxial cortex was continuous with the abscission layer.

No sclerenchyma crossed the abscission layer. Within the stem, at progressively higher levels, increased amounts of unlignified parenchyma

occurred among fibres. Caps associated with leaf traces were dispersed. Generally, there were numerous sclereids in the cortex.

In a few specimens, the abscission layer was not continuous at lower levels. There was an arc of unlignified parenchyma associated with each trace. At higher levels they joined. In a small number of specimens, the abscission layer was not seen at low levels. There was unlignified parenchyma between the phloem and fibre cap of the median leaf trace bundle. At higher levels, there was a group of thick walled fibres within this parenchyma. Unlignified parenchyma bordered a central wedge of lignified tissues. Above this, the leaf base was tangentially extended and the structure was similar to that in other specimens. Such variations occurred within species and were of no taxonomic significance. In some leaf bases, among lignified tissues, there were groups of unlignified, weakly differentiated cells which were at the lower limits of small vascular bundles (Fig. 80). Similar tissues also occurred at higher levels where leaf traces were within the leaf base. Such vascular strands were not consistent within specimens or species.

Leaf traces crossed the cortex. Often, they branched at the boundary between stem and leaf base. At higher levels, there were divisions and mergers of vascular tissues within the leaf base. Separate abaxial fibre caps were associated with main vascular bundles.

The arrangement of vascular tissues was different among species, within species and within specimens.

Inversely orientated bundles

Inversely orientated vascular bundles were seen in the leaf bases of some specimens (Table 7; Figs. 81, 86 and 87).

The distal end of the leaf base

In the most simple arrangement there were 3 main vascular bundles. In some specimens there was a small bundle between the lateral bundle and the central bundle and/or a small bundle outside the lateral bundle, towards the margin. Leaf bases were not always symmetrical. In other specimens, the leaf base contained an arc of 5, 7 or 9 large vascular bundles of more or less equal size (Fig. 82). There was a well developed abaxial and adaxial fibre cap associated with each main bundle. In some specimens, adaxial fibre caps merged in a continuous band. Main bundles were separated by lignified parenchyma. The leaf base was surrounded by several rows of unlignified parenchyma.

At upper levels there were palisade cells in the cortex and sclereids occurred.

The transition from leaf base to leaf

In most broad leaved species, leaf bases were tangentially extended into a dorsiventrally flattened blade. In some species, there was a pronounced expansion of the parenchyma between the central and marginal regions (Fig. 83). The central main bundle followed an uninterrupted course between the leaf base and leaf tip. A lateral bundle followed each margin and joined the midrib at the tip so that the venation was acrodromous (Fig. 88). In many specimens, the vein at the margin contained 2 vascular bundles of which the outer was smaller. Other main bundles in the leaf base, or branches of primary veins, sometimes followed a direct course to the leaf tip so that venation was parallelodromous (Fig. 89).

In *H. pandanicarpa* and *H. pandanicarpa* ssp. *crassifolia* the extension of the leaf base was in the radial plane and the leaf blade was laterally flattened (Fig. 84). The median leaf trace was at one margin and, at the other, there were smaller bundles. At a low level, there was a main branch

Table 8.

Hakea. Terete leaves. Outline in tranverse sections

Species		
sub-division 1		
Needlewoods		
Group A.	*H. lissosperma*	abaxial surface flattened
	H. 'Wallum'	adaxial surface flattened
Group B.	*H. leucoptera*	circular
	H. tephrosperma	circular
Group E.	*H. macraena*	abaxial surface flattened
	H. 'Dorrigo'	abaxial surface grooved
Group G.	*H. bakeriana*	abaxial surface grooved
Corkwoods		
	H. ivoryi	oval
	H. suberea	abaxial surface grooved
	H. fraseri	circular
sub-division 3		
Microcarpa group	*H. microcarpa*	circular, slightly irregular
	H. clavata	oval
Rostrata group	*H. rostrata*	circular
Verrucosa group	*H. verrucosa*	circular
Obliqua group	*H. obliqua*	abaxial surface flattened
	H. platysperma	circular
	H. adnata	circular
	H. orthorrhyncha	adaxial surface flattened, abaxial surface grooved

of the median leaf trace which followed a direct course to the leaf tip, more or less in the position of a midrib. *H. clavata* had oval terete leaves and, in this species also, the leaf base was radially extended (Fig. 13). In most species with terete leaves there was little expansion of the leaf base or increase in the number of main veins.

In species with terete leaves, in the Obliqua group of sub division 3, in *H. persiehana* and *H. arborescens* of sub division 1 and in *H. falcata*, there were small bundles and vascular strands around the central mesophyll at higher levels in the leaf base.

Leaf anatomy

All the specimens examined had either terete or isolateral leaves. The epidermis consisted of a single row of cells with cutinised outer walls. Stomata which were sunken and occurred on both surfaces were paracytic and had 2 subsidiary cells on either side of the guard cells (Fig. 90). Mesophyll cells, especially in the outer palisade, contained tannin.

Terete leaves

Outline in transverse sections

There were terete leaves in sub divisions 1 and 3. Leaf shapes are described in Table 8.

Anatomy: general description (Fig. 91).

Two rows of subepidermal palisade cells had numerous pits in projections in anticlinal walls. Columnar sclereids which branched and spread at their limits crossed the palisade. Within the leaf, parenchyma formed the ground tissue. Cells were large, lignified and angular in the centre and smaller, less lignified and round nearer the palisade. Within the central parenchyma there were 3, 5 or 7 main bundles in a circle or arc. Large bundles had caps of

thick walled fibres associated with xylem and phloem. Other bundles had fibres associated with xylem only or were without fibres. Small groups of fibres or individual cells occasionally occurred among the ground tissue or near its outer edge. Around the periphery of the central parenchyma there were numerous small bundles and vascular strands. In many, phloem was towards the palisade but, in some, vascular tissues were not precisely delimited and orientated. Large, isolated vascular elements occurred in this region.

In some species, characteristics were different:-

Palisade: In *H.* 'Dorrigo' and *H. bakeriana*, palisade was interrupted by a small group of round parenchyma cells at the abaxial groove. There were 3 rows of palisade cells in *H. microcarpa*. Pits in anticlinal walls were not an obvious feature in *H. lissosperma*, *H. leucoptera*, *H. tephrosperma* and *H. suberea*.

Central parenchyma: In *H. ivoryi*, *H. suberea* and *H. fraseri* 2-3 rows of lignified parenchyma with thickened, heavily pitted walls formed an uninterrupted band on the periphery of the central parenchyma (Fig. 92).

Vascular bundles: In *H. orthorrhyncha* there were 8 main bundles and in *H. leucoptera* 9. Both specimens of *H. platysperma* had eleven and *H. suberea* fifteen.

Broad leaves

Sub division 1

Outline in transverse section

Mature leaves of *H. arborescens* had flat adaxial and weakly convex abaxial surfaces. Two leaves from specimen WRB 5543 had slight abaxial grooves. In immature leaves both surfaces were weakly convex. In *H.*

persiehana adaxial surfaces were concave and abaxial convex. In immature leaves surfaces were more strongly curved.

H. florulenta had a weakly convex adaxial and a weakly concave abaxial surface.

In 3 specimens of *H. salicifolia* var. *salicifolia* both surfaces were flat. *H. trineura* was ridged over main veins on both surfaces.

In all the species, margins were rounded. They were also bulbous in *H. trineura* and in some specimens of *H. salicifolia* var. *salicifolia*.

Anatomy: general description

H. trineura

On each side of the leaf there was a single row of palisade cells. Abaxial palisade cells were shorter and wider than the adaxial. Pits in anticlinal walls were present but few. Between the palisade there were 5 to 7 rows of unlignified parenchyma. Large columnar sclereids crossed the whole leaf (Fig. 93). Vascular bundles were collateral. Phloem was abaxial. Large abaxial and adaxial caps of thick walled fibres associated with the midrib were separated from the epidermis by 1-3 rows of lignified parenchyma (Fig. 94). There were 1 or 2 bundles of similar extent to the midrib on either side of the leaf. At each margin palisade was continuous (Fig. 95). Close to the margin there was a bundle whose abaxial fibre cap was separated from the epidermis by a row of lignified parenchyma. In some specimens there was a row of lignified parenchyma below the adaxial epidermis and, in others, there was slightly modified palisade. Lower order veins which were of various sizes had abaxial and adaxial fibres, adaxial fibres or were without fibres. Minor veins were within the central mesophyll. In the smallest vascular groups xylem and phloem were not always precisely delimited and orientated. Some contained only large, simple tracheary elements. Wings of lignified parenchyma were associated with large

vascular bundles and, on the edges of these, there were small bundles or vascular strands. Bundle sheaths were well developed. Prismatic, rhombic and cluster crystals occurred in epidermal cells.

H. arborescens and *H. persiehana*

Generally, the description of terete leaves described these species. Some characters were different:-

Palisade: There was one row of palisade cells and, occasionally, a suggestion of a second row. In some specimens, palisade tissues were interrupted at the margins by a group of small round unlignified cells.

Vascular bundles: 5 or 7 main vascular bundles were regularly spaced across the width of the leaf. Phloem was abaxial.

Fibres: Fibre caps associated with vascular bundles were more weakly developed and there were few individual fibre cells.

H. salicifolia var. *salicifolia* and *H. florulenta*

Generally, the description of the trifurcata group of sub division 3 described these species. Some characters were different.

Palisade: There was one row of palisade cells.

Central parenchyma: There were 5-6 rows of mesophyll between the palisade. The innermost cells were rectangular, irregular and orientated with their long axes parallel to the leaf surface.

Vascular bundles: At the midrib abaxial fibres were separated from the epidermis by 1-2 rows of weakly lignified parenchyma in *H. florulenta* and in 2 leaves of 1 specimen of *H. salicifolia* var. *salicifolia* (WRB 5687).

Sub division 2

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces and were of constant thickness except where ridges were associated with main vascular bundles. Generally, ridges occurred on both surfaces. *H. neurophylla* and *H. falcata* had ridges on the abaxial surface only. Margins were rounded and, in *H. undulata* and *H. elliptica*, bulbous. *H. loranthifolia* and *H. plurinervia* were hardly ridged and margins were sloping. Superficially, *H. sulcata* leaves were terete. Five ridges coincided with fibre caps associated with major vascular bundles (Fig. 96).

Anatomy: general description

On each side of the leaf there were two rows of palisade cells with numerous pits in projections in anticlinal walls. Between the palisade, there were 2-4 rows of unlignified mesophyll cells. Large irregular sclereids in the central mesophyll often spread into the palisade (Fig. 97). Vascular bundles were collateral. Phloem was abaxial. Large abaxial and adaxial caps of thick walled fibres associated with the midrib were separated from the epidermis by 1-3 rows of lignified parenchyma (Fig. 98). 2, 4, 6 or, occasionally, more major bundles were of similar extent to the midrib. Wings of lignified parenchyma were associated with major bundles. At each margin thick walled fibres associated with a vascular bundle were separated from the epidermis by 1-3 rows of lignified parenchyma (Fig. 99). Lower order veins had abaxial and adaxial fibres, adaxial fibres or were without fibres. Minor veins were within the central mesophyll. In the smallest vascular groups xylem and phloem were not always precisely orientated and delimited. Some contained only large, simple tracheary elements. Similar cells occurred on the edges of large bundles. Bundle sheaths were present

although sometimes weakly developed. In epidermal cells, acicular, prismatic and rhombic crystals were sometimes twinned (Fig. 90).

In some species characteristics were different:-

Palisade: In *H. ambigua, H. undulata* and both specimens of *H. elliptica* there was 1 row of palisade on each side of the leaf. In both specimens of *H. loranthifolia* the second layer was hardly developed. Pits were not an obvious feature in the palisade of *H. laurina, H. neurophylla* and *H. sulcata*.

Central parenchyma: Cells were rectangular and orientated with their long axes parallel to the leaf surface in both specimens of *H. elliptica*. In *H. falcata* and *H. sulcata* cells were lignified. In *H. undulata* there were some weakly lignified cells.

Sclereids: In *H. falcata* columnar sclereids were associated with the palisade (Fig. 101). In *H. undulata, H. elliptica* and *H. sulcata* no sclereids were seen.

Main vascular bundles: In *H. plurinervia* there were 7 main bundles, in *H. undulata* and *H. ambigua* there were 8. In both specimens of *H. elliptica* there were eleven. Ten leaves of *H. dactyloides* from 7 specimens were of different sizes. Most contained 5 main bundles but 2 contained 3, 2 had seven and another 10.

Fibre caps: In the more or less terete leaves of *H. sulcata* fibres associated with the phloem were separated from the epidermis by a single row of parenchyma. Fibres associated with the xylem were within the leaf (Fig. 96).

Minor bundles: In *H. falcata* minor bundles were peripheral to the central mesophyll and phloem was towards the palisade (Fig. 100).

Bundle sheaths: In *H. sulcata* bundle sheaths were not an obvious feature. In *H. falcata* individual bundle sheaths were absent. A continuous row of morphologically distinct cells surrounded the central mesophyll (Fig. 100).

Sub division 3

Outline in tranverse section

Most leaves had unridged, more or less parallel surfaces. *H. baxteri* was weakly ridged over main veins on the adaxial surface. *H. brownii* and *H. linearis* were weakly ridged on both surfaces. 3 out of 4 specimens of *H. eriantha* were abaxially ridged at the midrib. Margins were rounded.

Anatomy: general description

It was convenient to consider species in the Obliqua group separately from those in other groups in this sub division.

Obliqua group

The general description of terete leaves described these species. In some specimens, the inner palisade cells were shorter and wider than the outer. Sometimes palisade tissues were interrupted at the margin by a group of small, round, unlignified parenchyma cells. Primary veins were more numerous and regularly spaced across the width of the leaf. Phloem was towards the abaxial surface (Fig. 102). There were lower order veins of different sizes within the central parenchyma. On the outer edges of larger bundles there were large simple tracheary elements.

In some species characteristics were different:

Vascular bundles: In *H. brownii* and *H. baxteri* inverted bundles of intermediate size occurred towards the adaxial surface.

In *H. pandanicarpa* and *H. pandanicarpa* ssp. *crassifolia* primary vascular bundles were oriented with phloem towards the abaxial or adaxial

surface. Margins of leaves were different. At one there was a single large vascular bundle and, at the other, small bundles (Figs. 103 and 104).

Trifurcata group and species of uncertain affinity

Two rows of subepidermal palisade cells had numerous pits in projections in anticlinal walls. Columnar sclereids which branched and spread at their limits crossed the palisade and penetrated into the inner mesophyll where they were closely associated with vascular bundles (Figs. 101 and 105). Between the palisade there were 2-4 rows of irregular, rectangular, unlignified parenchyma cells orientated with their long axes parallel to the leaf surface (Fig. 106). Vascular bundles were collateral. Phloem was abaxial. Abaxial and adaxial caps of thick walled fibres associated with the midrib were within the heavily modified palisade. At the margins palisade was continuous. Lower order veins which were within the central mesophyll had abaxial and adaxial fibre caps, adaxial fibres or were without fibres. In small bundles tissues were not always precisely orientated and delimited. Some contained only large simple tracheary elements. Wings of lignified parenchyma were associated with larger vascular bundles and, on the edges, there were small bundles or vascular strands. Bundle sheaths were well developed and sometimes merged to form a continuous row of cells around several bundles.

In some species characteristics were different:-

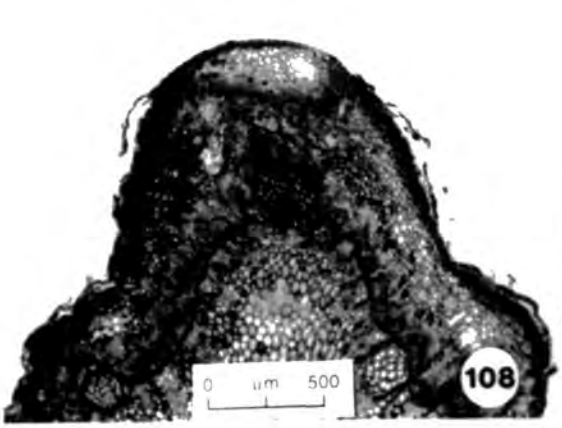
Palisade: In *H. lasiantha*, the inner layer of palisade was more weakly developed (Figs. 101 and 105).

Vascular bundles: In 4 specimens of *H. eriantha* the midrib had abaxial and adaxial fibre caps separated from the epidermis by 1 or 2 rows of parenchyma. In the 5th specimen, RBG Sydney 13385, there was modified outer palisade on the adaxial side. 4 or 6 bundles of similar extent to the

midrib occurred in *H. lasiantha*. There were no bundles of similar extent to the midrib in *H. eriantha* but several lower order veins of various sizes extended into the modified palisade.

Bundle sheaths: In *H. eriantha* bundle sheaths were well developed but rarely merged to enclose more than one bundle.

Figs. 108-114. - 108-113, *Finschia chloroxantha* (NGF 9123). - 108, Node, transverse section. - 109, Leaf base, transverse section. - 110, Vascular bundles in nodal region and leaf base, transverse section. - 111, Leaf base, transverse section. - 112, Leaf base, transverse section. - 113, Leaf base, transverse section. - 114, *F. chloroxantha* (NGF 10358). Leaf base, transverse section.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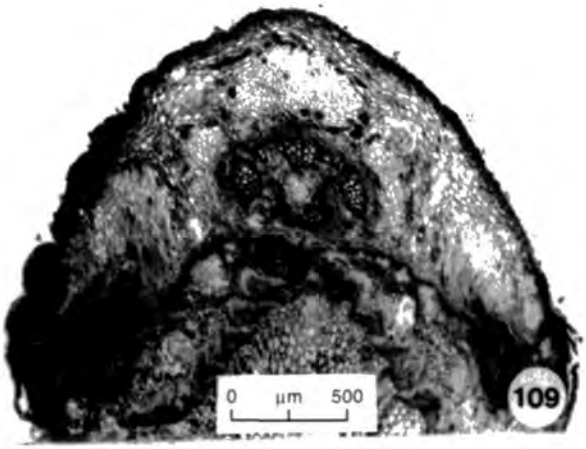
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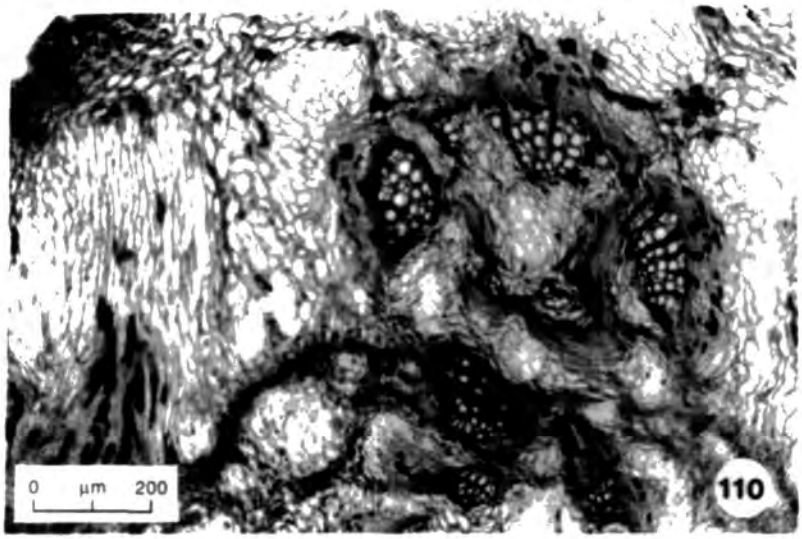
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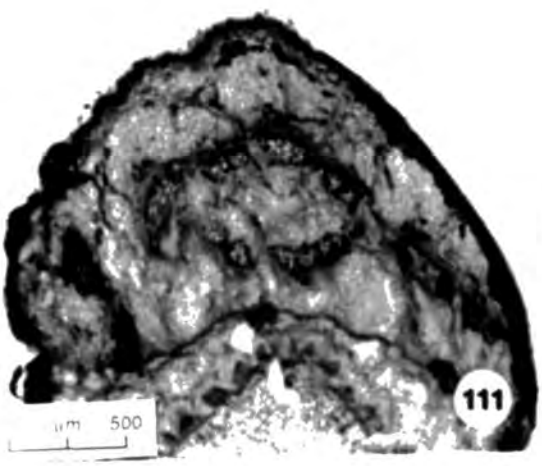
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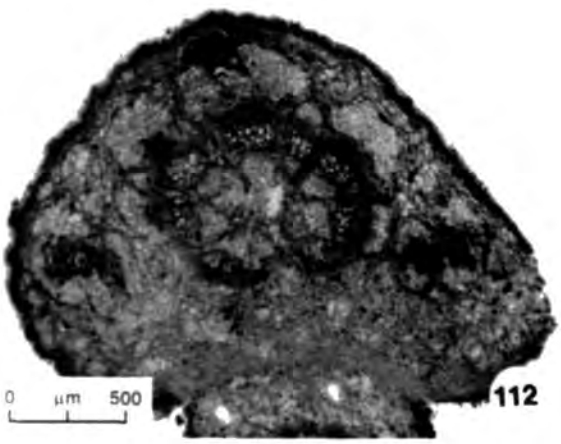
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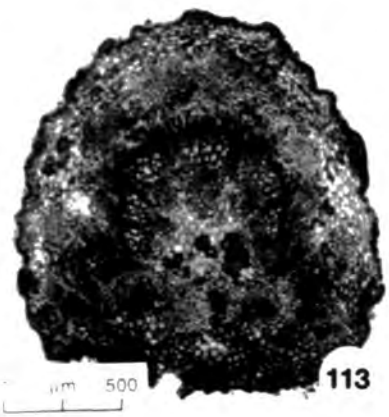
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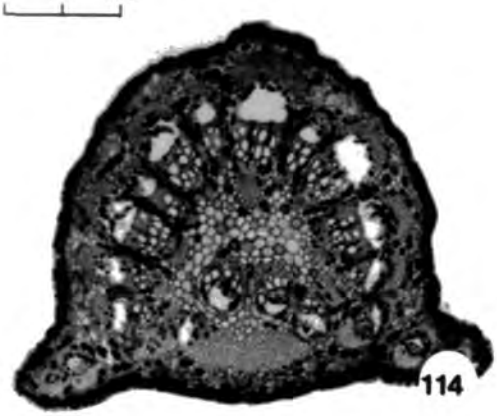
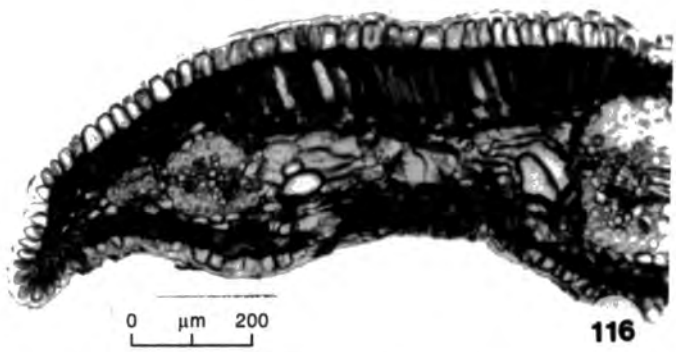

114

Figs. 115-119. - 115-117, *Finschia chloroxantha* (NGF 9123). - 115, Midrib, transverse section. - 116, Leaf margin, transverse section. - 117, Leaf, transverse section. - 118, *F. chloroxantha* (NGF 10358). Midrib, transverse section. - 119, *F. rufa* (Department of Forests, Lae 59040). Main vein, transverse section.

115



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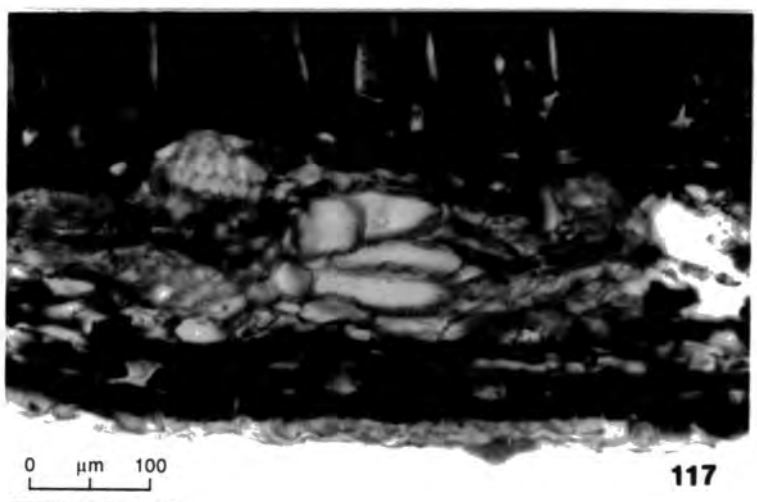

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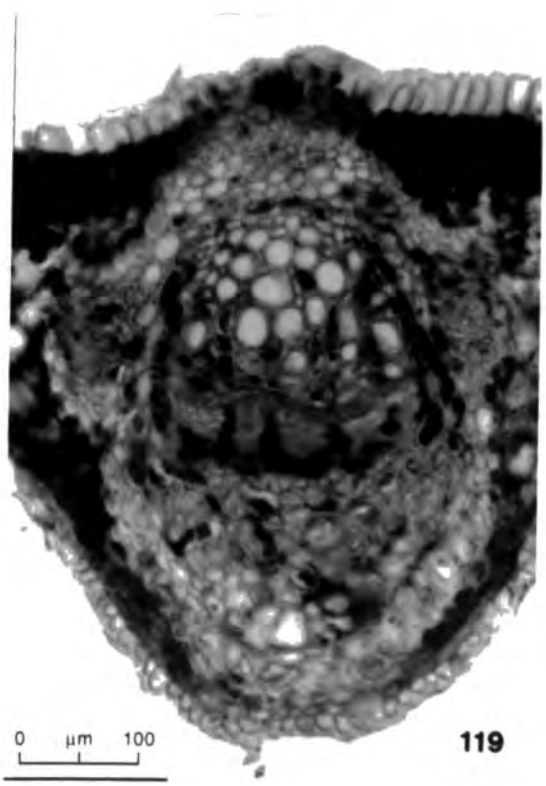


119

Finschia

F. chloroxantha

Stem

The stem included in the stem-node-leaf continuum was 3 mm in diameter. Cork was superficial. The cortex which, in places, was weakly lignified, was 3-10 cells wide, complementing the size of fibre caps associated with vascular bundles. Within the cortex, groups of sclereids were strongly developed. There was a more or less continuous ring of pericyclic sclerenchyma. As well as fibres, this included large sclereids which often, though not necessarily, coincided with medullary rays. Vascular tissues were weakly eustelic. A continuous cambial zone was recognisable. Interxylary fibres were well developed. Within the pith, some cells were lignified and there were groups of sclereids.

Nodal anatomy

Below the node, near leaf traces, stelar bundles divided and merged. At low levels, leaf traces were recognised by modified xylem which consisted of simple vascular elements and unlignified parenchyma. There was some lignified and unlignified parenchyma among pericyclic fibres and caps were somewhat dispersed. In the median position, changes were seen in 3 adjacent bundles and in part of a fourth. In each lateral position, one bundle had modified xylem. At higher levels, the 3 bundles in the median position were combined. On either side of the complex, there were changes in 2 small stelar bundles (Fig. 108). Outside the leaf traces, cork was continuous, the cortex was wide and, within it, there were numerous sclereids.

At the supradjacent node, changes were generally similar. At the lowest levels, xylem was modified in 6 adjacent bundles in the median position, 4 in one lateral position and 3 in the other. There was a constant

combining and separating of vascular tissues. At the level where it left the stele, the median leaf trace had 3 components and, at a higher level, 2 bundles on either side of the complex had modified xylem. In each lateral trace, modified xylem tissues were combined in one bundle.

Leaf base

Leaves were petiolate.

The base of the petiole was first recognised by the absence of cork. At the same level, the abscission layer was within the stem (Fig. 108). No sclerenchyma crossed the abscission layer. Within the stem, at progressively higher levels, fibre caps associated with leaf traces were dispersed. Within the petiole, there was lignified parenchyma and fibres (Fig. 108) and, at the level where the median leaf trace crossed the abscission layer, there was a weakly developed fibre cap ahead of it. Lateral leaf traces were within the cortex. Near the adaxial edge of the petiole, the median trace divided into 3 and, associated with each bundle, there was a weakly developed fibre cap. At higher levels, small groups of vascular tissues which had separated from the 3 main bundles alternated with them (Fig. 109). The 4 stelar bundles which, at lower levels, had shown changes in the xylem, passed to the petiole (Fig. 110). Within the petiole, they were inversely orientated and completed a ring of vascular bundles. Lateral leaf traces passed to the petiole; near the abscission layer, they bifurcated. At higher levels there were more, smaller separate bundles within the circle (Fig. 111). There were numerous groups of sclereids in the petiole and in the cortex of the stem; some were close to the adaxial side of the abscission layer (Fig. 112). At the level where the petiole was separate from the stem, it contained a ring of small bundles and, towards each margin, 2-3 closely associated lateral bundles.

At higher levels, lateral bundles and bundles towards the abaxial side of the leaf were in a broad arc. Abaxial fibre caps were almost completely merged; adaxial fibres were in discreet groups. Towards the adaxial side of the petiole, there was a line of small bundles in which vascular tissues were not well orientated or delimited. On both sides, there were fibres which were loosely associated with these bundles. Some 9 rows of cortical parenchyma surrounded the petiole. Within the cortical and central parenchyma there were groups of large sclereids (Fig. 113). At still higher levels, there were fewer bundles in the adaxial line and in the arc where bands of parenchyma separated a large central bundle.

In a second specimen (NGF 10358) the petiole was in a better condition and was used to study the anatomy, particularly at the distal end. The petiole was similar to that examined in NGF 9123 but bundles were larger and adaxial bundles were few and precisely inversely orientated (Fig. 114).

The transition from leaf base to leaf

Towards the distal end of the petiole, there were 2 adaxial marginal extensions. Two lateral bundles were separated from the main arc by unlignified parenchyma (Fig. 114).

Leaf Anatomy

Outline in transverse section

Leaves had parallel abaxial and adaxial surfaces. Margins were hardly recurved. The leaf was thicker over main veins. At the midrib, the abaxial side of the leaf was convex and there was a pointed adaxial ridge.

Anatomy

Leaves were dorsiventral. Hairs occurred occasionally on both surfaces. The epidermis consisted of a single row of cells. Outer walls were cutinised on the adaxial surface and at margins and more weakly cutinised

on the abaxial surface. Stomata which were restricted to the abaxial surface were paracytic and had a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a row of tall, narrow palisade cells and a weakly developed second row of shorter, wider cells. Below the abaxial epidermis there was a row of square cells. In the centre of the leaf there was spongy mesophyll. Palisade cells had lignified walls and contained tannin. Some mesophyll cells had weakly lignified walls; some contained tannin. Main bundles were predominantly collateral with abaxial phloem. At the midrib, towards the abaxial side, there was an arc of 7 or 8 vascular bundles; there was some merging of tissues. Weakly defined abaxial caps of thin walled fibres were associated with bundles. Among vascular tissues and fibres, there were weakly lignified parenchyma cells, some of which contained tannin, and large, simple tracheary elements which occurred singly or in groups. There were adaxial fibres associated with each bundle. Some 7 rows of cortical parenchyma surrounded the abaxial side of the midrib. On the adaxial side of the midrib, there was weakly lignified parenchyma and thin walled fibres. Large simple tracheary elements occurred singly or in groups. Large unlignified or weakly lignified parenchyma cells filled the centre of the midrib. In this region, there were groups of large sclereids (Fig. 115). Towards the margin, palisade was reduced and, close to the tip, there were small rounded parenchyma cells; many contained tannin. A short distance from the tip, within the mesophyll, there was a group of fibres and, close to it, a vascular bundle with well developed abaxial and adaxial fibre caps (Fig. 116). Other vascular bundles which were of various sizes had well developed abaxial and adaxial fibre caps. In the largest, fibres were separated from epidermises by 3 or 4 rows of parenchyma, others were within the mesophyll and palisade was more or less modified. Large simple tracheary elements occurred among vascular tissues and on the periphery of bundles. Much of the centre of the leaf was

filled by very large simple tracheary elements (Fig. 117). Bundle sheaths were fairly well developed.

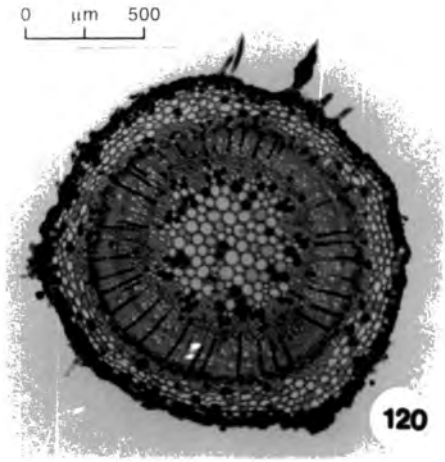
Generally, the second specimen (NGF 10358) was similar to NGF 9123. The second row of adaxial palisade was hardly developed. Throughout the leaf, there were occasional large sclereids. At the midrib, vascular bundles were larger and discreet. Abaxial and adaxial fibre caps were associated with individual bundles. Towards the adaxial side of the midrib, there was a tangentially spread, inversely orientated bundle and, adaxial to it, were 2 closely associated bundles with abaxial phloem and a single, tangentially spread, adaxial fibre cap (Fig. 118). There were fewer large tracheary elements within the midrib. At margins, bundles were further from the tip and fibres were less well developed; there was a group of large, lignified, thick walled parenchyma cells among rounded parenchyma cells. In the centre of the leaf, tracheary elements occupied less space.

F. rufa

It was possible to obtain only a small piece from the margin of one leaf. The sample did not include the midrib.

Generally, characters which were available for examination were similar to *F. chloroxantha*. Inner rows of palisade were hardly developed below the adaxial epidermis. On the abaxial side, there were some 9 rows of spongy mesophyll. In a large vein, vascular tissues were not precisely orientated and delimited and large, simple tracheary elements occurred among them (Fig. 119). Near the margin, there were small rounded parenchyma cells and, within them, there was a group of tracheary elements.

Figs. 120-125. - 120, *Persoonia mollis* (Weston 1267). Stem, transverse section. - 121, *P. hirsuta* (N.S.W. 20893). Node, transverse section. - 122-123, *P. gunnii* (Lord Talbot de Malahide). - 122, Node, transverse section. - 123, Leaf base, transverse section. - 124, *P. laurina* (Weston, Blue Mountains). Leaf base, transverse section. - 125, *P. rufiflora* (CSIRO). Leaf base, transverse section.



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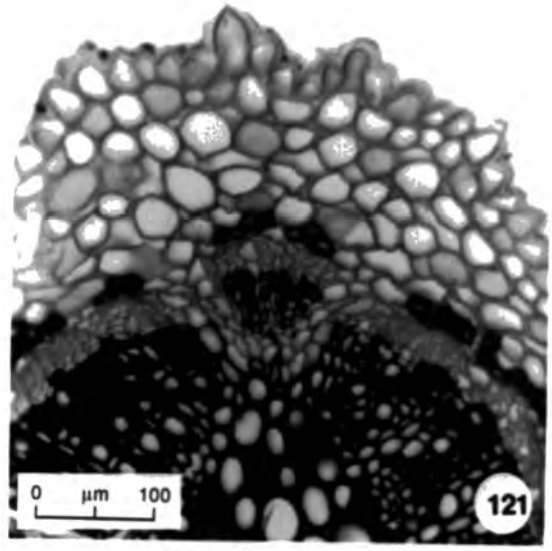

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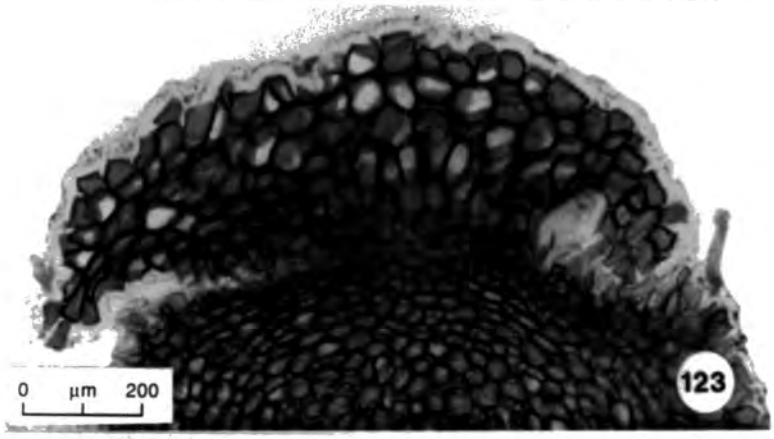

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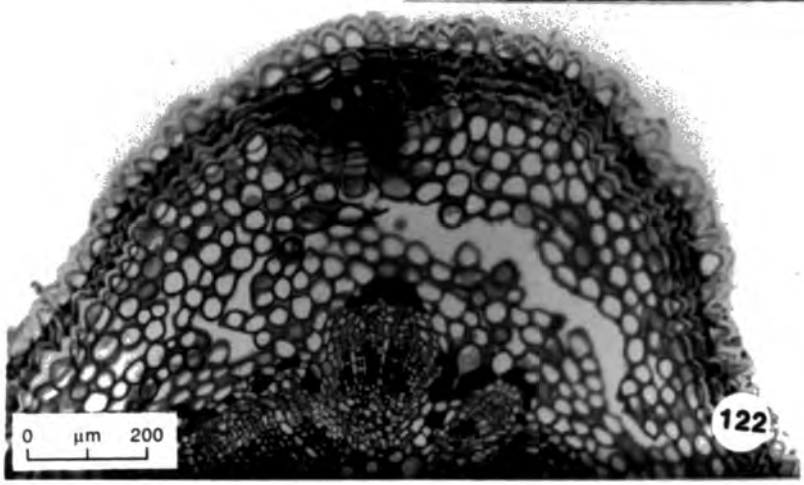

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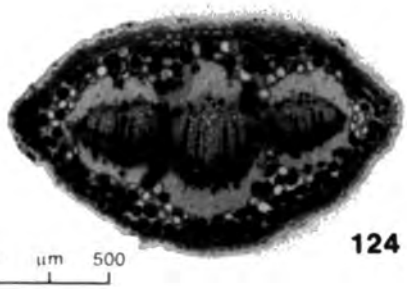

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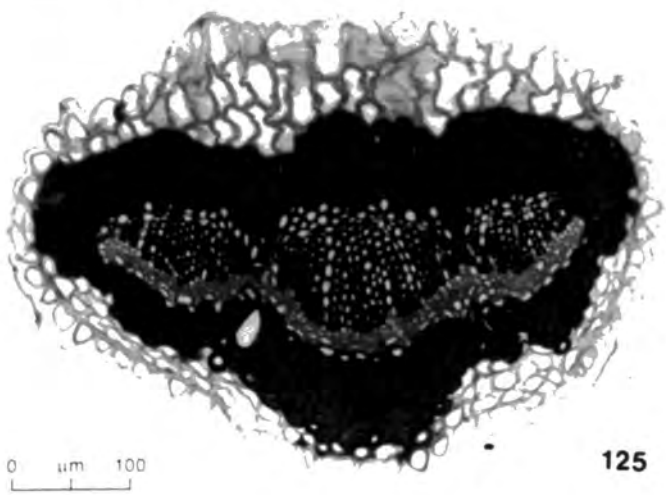

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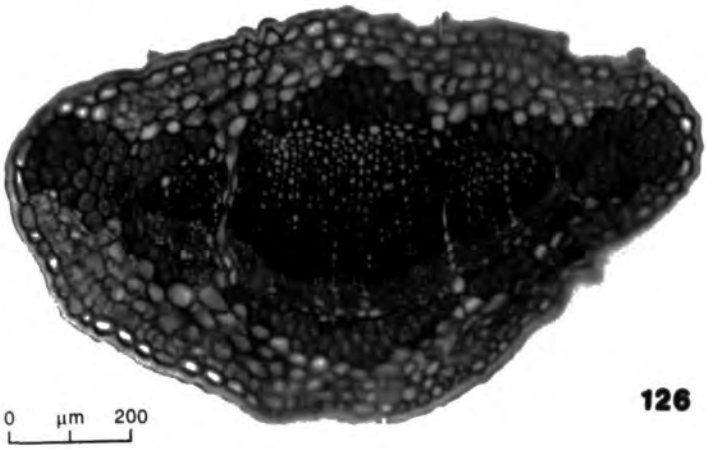
Figs. 126-133. - 126, *P. marginata* (N.S.W. 21275). Leaf base, transverse section. - 127, *P. mollis* (Weston 1267). Leaf base, transverse section. - 128, *P. rufiflora* (Flora Australiensis). Leaf, transverse section. - 129-130, *P. rufiflora* (George 676). - 129, Leaf, transverse section. - 130, Leaf margin, transverse section. - 131-133, *P. laurina* ssp. *laurina* (N.S.W. 20950). - 131, Leaf, transverse section. - 132, Midrib, transverse section. - 133, Sclereid, transverse section.



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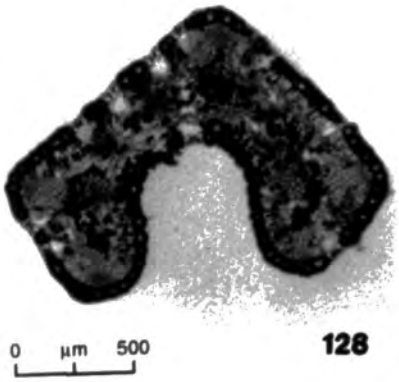

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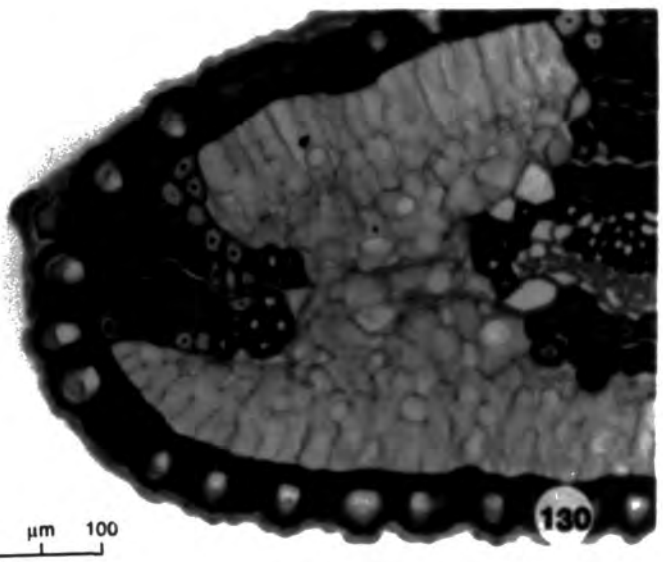

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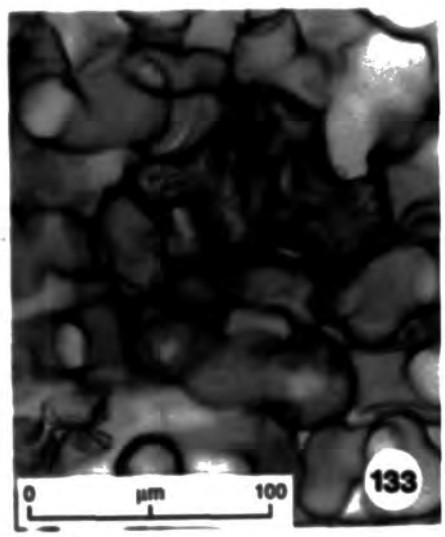

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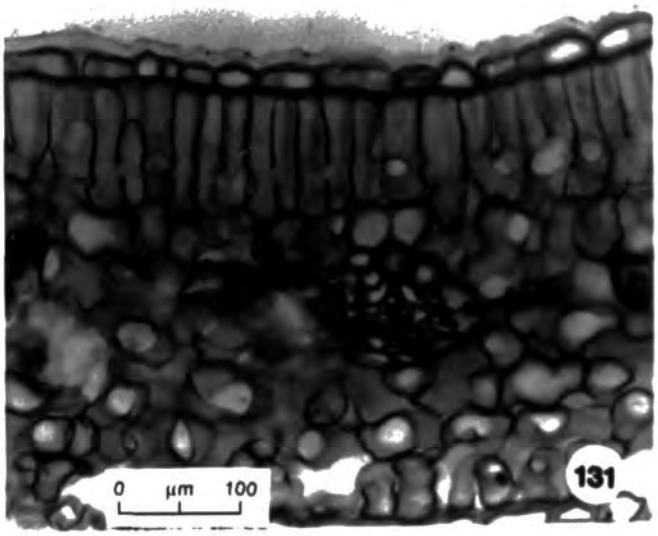

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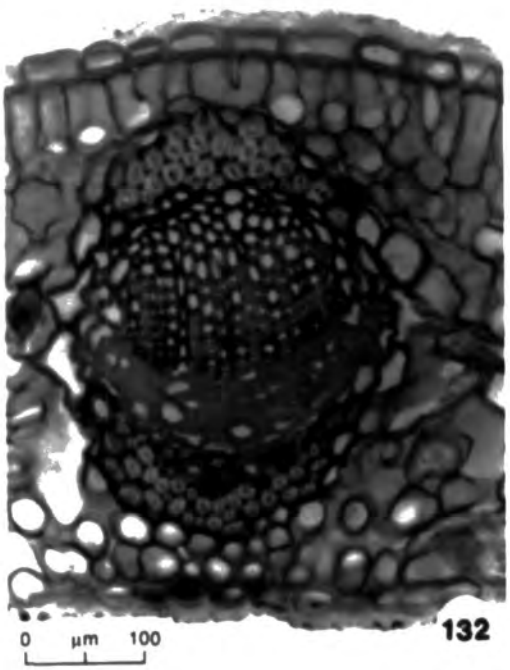

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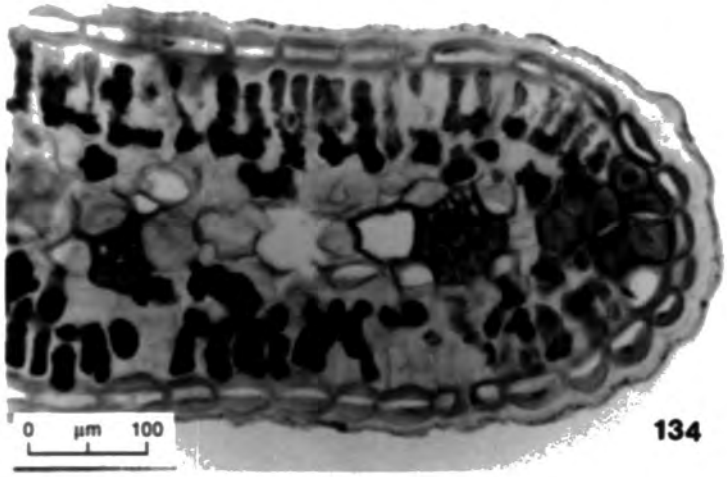
Figs. 134-138. - 134-138, *P. myrtilloides* (Constable 5144). - 134, Leaf margin, transverse section. - 135, Small vascular bundle, transverse section. - 136-137, *P. marginata* (N.S.W. 21275). - 136, Leaf margin, transverse section. - 137, Fibre sclereids, transverse section. - 138, *P. quinquenervis* (Coveny 8338). Tracheary elements, longitudinal section.



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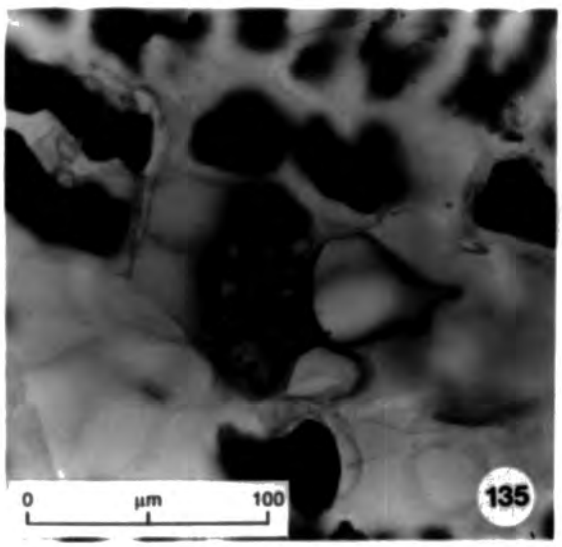

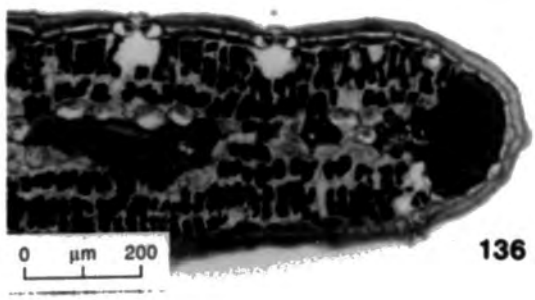

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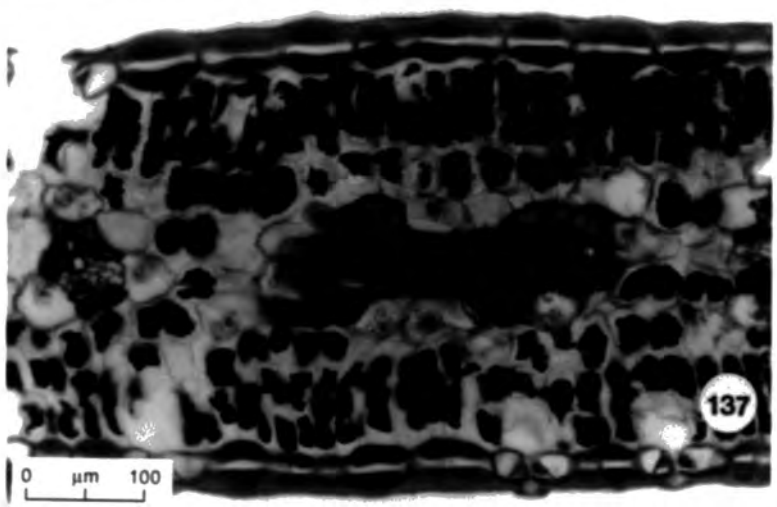
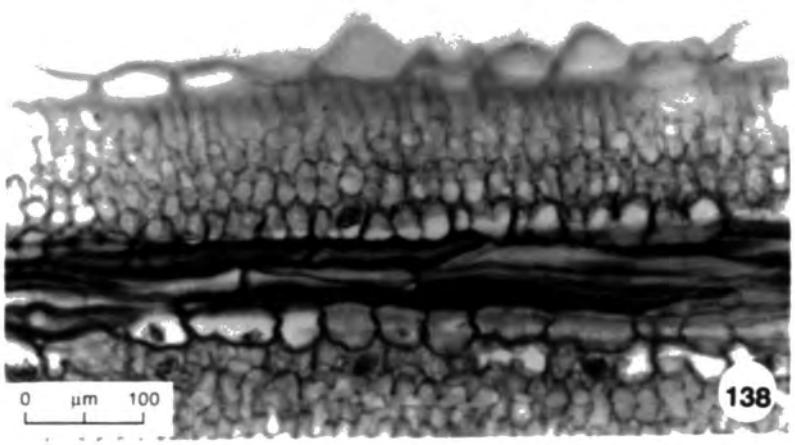
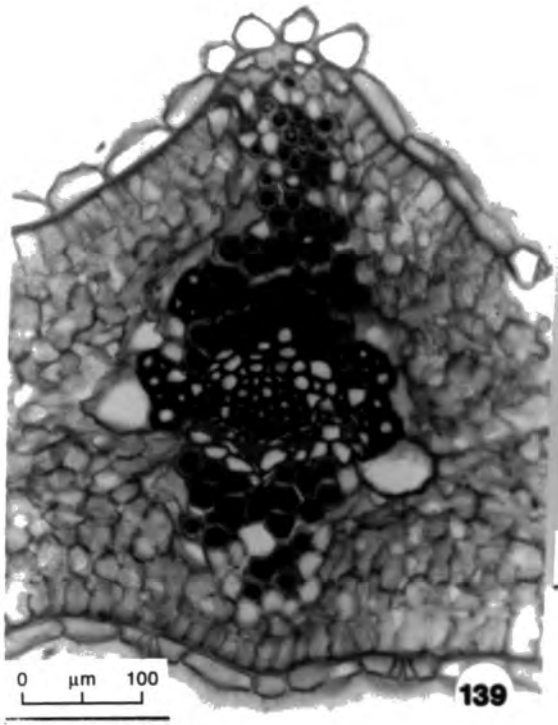




Figs. 139-144. - 139-140, *P. quinquenervis* (Coveny 8338). - 139, Midrib, transverse section. - 140, Leaf margin, transverse section. - 141-142, *P. hakeiformis* (Flora Australiensis). - 141, Leaf, transverse section. - 142, Sclereids, transverse section. - 143-144, *P. falcata* (Speckt 1147). - 143, Midrib, transverse section. - 144, Leaf margin, transverse section.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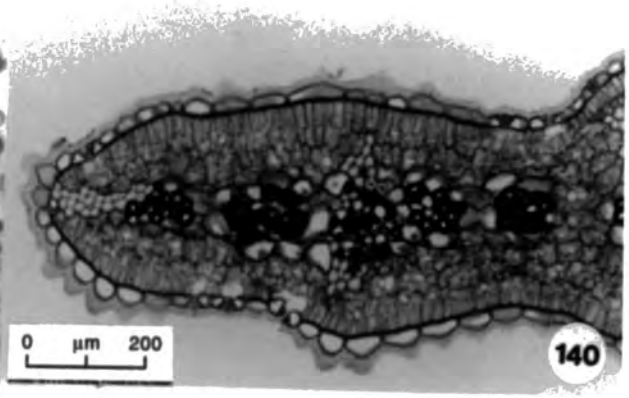
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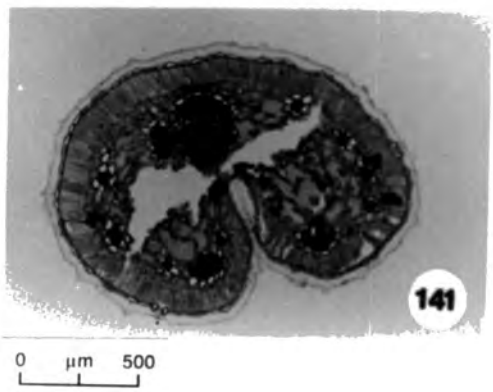
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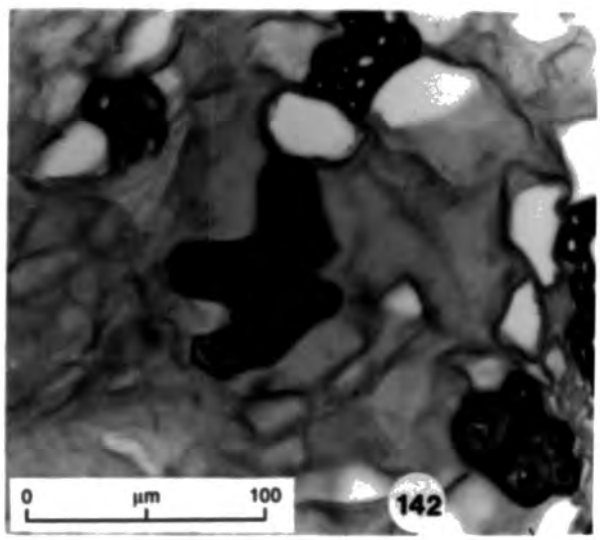
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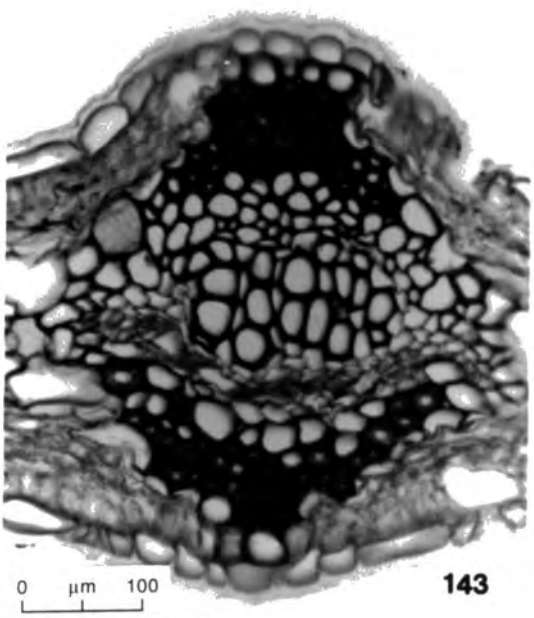
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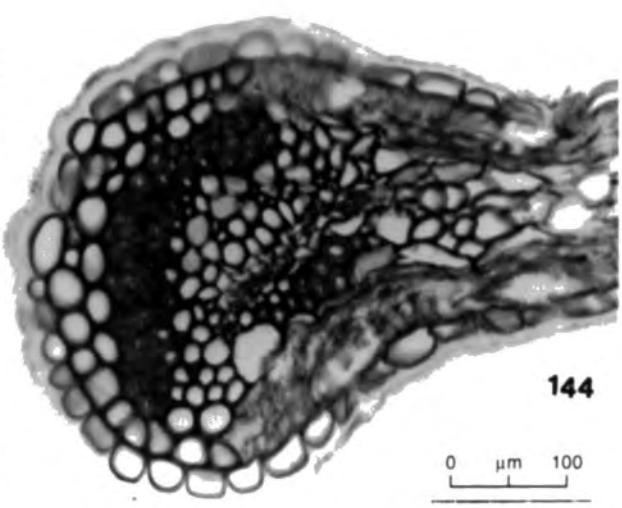
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0 µm 100

Persoonia

Stem (Fig. 120)

Stems included in the stem-node-leaf continuum were 1-2.5 mm in diameter. In some species, these were hairs within the epidermis. Where cork had formed, it was superficial. The unlignified cortex was from 3 to 6, rarely up to 10, cells wide, complementing the size of caps of thick walled fibres where they were associated with vascular bundles. Pericyclic fibres were in a more or less continuous band, often of uniform width. Among the fibres, there were sclereids or lignified parenchyma cells which often, though not necessarily, coincided with medullary rays. Vascular tissues were siphonostelic to weakly siphonostelic. A continuous cambial zone was recognisable. In most specimens, there were interxylary fibres. Pith was weakly lignified.

Nodal anatomy

At the lowest levels, leaf traces were recognised by wider rays bordering them and by their modified xylem which consisted of simple vascular elements and unlignified parenchyma. At higher levels, fibre caps were smaller and fibres were less lignified. Ahead of leaf traces, the cortex was wider. In some specimens, there were occasional sclereids in the nodal region. Where leaf traces were in the cortex, they were without fibre caps.

In 3 specimens of *P. rufiflora* and in *P. gunnii* var. *angustifolia*, nodes had 3 lacunae and 3 traces. In *P. gunnii*, *P. hirsuta* and *P. mollis* there was a single lacuna. At the lowest level, a single leaf trace was recognised (Fig. 121). At higher levels, in *P. gunnii* and *P. mollis*, there were modifications in stelar tissues on either side of the leaf trace and, higher still, a small bundle was outside the stele on either side of the median leaf trace within the same lacuna (Fig. 122). In *P. virgata*, the node was unilacunar; a small part of the stele was associated with the vascular system of the leaf; tissues spread

within the cortex and near the abscission layer. In *P. hirsuta*, the node was unilacunar and there was one trace.

Leaf base

The leaf base was first recognised on the edge of a ridge in the stem formed by cortical parenchyma. At this level, the abscission layer was not well defined; occasionally a small constriction marked the adaxial boundary of the leaf base. At higher levels, the abscission layer was seen in this position (Fig. 123).

In some specimens, tissues in the leaf base and cortex were unlignified.

In one node in *P. gunnii*, at a low level, there was a group of lignified parenchyma cells below the epidermis and cork, opposite the median leaf trace (Fig. 122). At higher levels, the cortex in the region of leaf traces was lignified. Above this, there was unlignified parenchyma within the leaf base; there was a region of lignified parenchyma on the adaxial side of the abscission layer. In a second node, there was no cork formation in the stem; tissues in the nodal region and leaf base were unlignified.

In *P. gunnii* var. *angustifolia*, cortical tissues were lignified outside the leaf traces and cells contained tannin. At higher levels, the leaf base was composed of unlignified parenchyma. On the adaxial side of the abscission layer, cortical tissues were lignified and there were large sclereids.

In *P. mollis*, there was no cork formation in the stem. In one node only, there was some indication of phellogen activity and some lignification of parenchyma cells outside the nodal region. At a higher level, there were lignified cortical cells on the adaxial side of the abscission layer.

In 3 specimens of *P. rufiflora*, there was lignified parenchyma below the epidermis, opposite nodes. There was lignified parenchyma on the adaxial side of the abscission layer and, also in this region, there were regular

cell divisions similar to the early stages in phellogen activity. At higher levels, leaf bases were composed of unlignified parenchyma.

Leaf traces crossed the cortex.

Within the leaf base, fibres were associated with leaf traces. In *P. elliptica*, *P. gunnii* and *P. longifolia*, there were gelatinous fibres.

In most specimens, at higher levels within the leaf base, there were 3 or, occasionally, 4 or 5 vascular bundles. Abaxial and adaxial fibre caps were associated with bundles (Fig. 124). In *P. elliptica*, *P. marginata* and *P. rufiflora*, vascular tissues were merged in a continuous arc (Fig. 125). In *P. elliptica*, abaxial fibres were in a single band; adaxial fibres were in separate groups. In *P. marginata*, there was a separate central group of adaxial fibres. Towards the outside of the vascular arc, adaxial fibres were continuous with a band of abaxial fibres and broad girders extended to each margin (Fig. 126). In *P. rufiflora*, a continuous zone of thick walled fibres surrounded vascular tissues. In *P. hirsuta*, there was one small vascular bundle in the leaf base. At higher levels, there was a small component on each end of the bundle and, above this, there was a small separate group of vascular tissues on one side of the central bundle.

The distal end of the leaf base

Leaf bases were short and, generally, the structure was constant until there were changes associated with the transition from leaf base to leaf.

The transition from leaf base to leaf

Leaf bases were tangentially expanded. There was unlignified parenchyma between vascular bundles. The number of bundles was increased by divisions (Fig. 127). In specimens where, at lower levels, there was an arc of vascular tissues, there were separate bundles in the lower leaf.

Leaf anatomy

In all the specimens the epidermis consisted of a single row of cells. Stomata were paracytic and there was a single subsidiary cell on either side of the guard cells. Stomata occurred on the abaxial and adaxial surfaces except in *P. mollis* where they were on the abaxial surface only. These features will not be described again.

Group 1

P. rufiflora

Outline in transverse section

Three specimens were different.

In the first specimen (J. Drummond Series 6, 176), abaxial and adaxial surfaces were more or less parallel. Margins were reflexed. There was an abaxial and adaxial ridge at the midrib and an adaxial ridge associated with the main vein near each margin.

In a second specimen (Flora Australiensis), the adaxial surface was convex. The reduced abaxial surface was in a deep groove opposite the midrib (Fig. 128).

In the third specimen (George 676) leaves were liner-terete. The reduced abaxial surface was within an abaxial groove (Fig. 129).

Anatomy

J.R. Drummond Series 6, 176

Leaves were isolateral. Hairs rarely occurred. Epidermal cell walls were heavily lignified; on both surfaces, outer walls were cutinised. Surfaces were papillose; papillae were more pronounced on the adaxial surface. Below the adaxial and abaxial epidermis, there was a single row of irregular palisade cells. Arm palisade cells (Esau, 1965) frequently occurred. Abaxial palisade cells were slightly shorter than adaxial cells. Between the

palisade cells there were some 6 rows of spongy mesophyll cells. Major bundles were collateral. Phloem was abaxial. At the midrib, there was a single bundle with well developed abaxial and adaxial caps of thick walled fibres. On the adaxial side, the fibres were below the epidermis, on the abaxial, they were separated from the epidermis by highly modified palisade. At each margin, associated with a small group of vascular tissues, there was an adaxial girder of thick walled fibres below the epidermis (Fig. 130). Close to it, there was a vascular bundle with a well developed cap of thick walled fibres below the adaxial epidermis and abaxial fibres which were within the spongy mesophyll. Lower order bundles which were within the mesophyll had abaxial and adaxial or adaxial fibre caps. In smaller bundles, vascular tissues were not precisely delimited and orientated and fibres were loosely associated with them. Many fibres were gelatinous (Fig. 130) but few gelatinous fibres were associated with the midrib. Some small bundles contained only short, thick walled vascular elements. Similar cells were associated with larger bundles. Bundle sheaths were not an obvious feature but, often, there were large, irregular mesophyll cells near bundles. In these cells and in palisade and spongy mesophyll cells there were occasional druses or rhombic crystals.

The description of J.R. Drummond Series 6, 176 described a second specimen (CSIRO Canberra), but, in all the vascular bundles and in the midrib, there were more gelatinous fibres.

Flora Australiensis

The description of J.R. Drummond Series 6, 176 described this specimen. In all the vascular bundles there were more gelatinous fibres. Abaxial palisade was less well developed. Abaxial palisade and mesophyll cells contained tannin. Inner mesophyll cells were large and thin walled. There were fewer lower order veins.

George 676

The description of J.R. Drummond Series 6, 176 described this specimen. There was spongy mesophyll at the base of the abaxial groove. Abaxial fibres associated with the midrib were within the spongy mesophyll. Lower order veins were few and small and without fibres.

Group 2

P. laurina ssp. *laurina*

Outline in transverse section

Abaxial and adaxial surfaces were parallel. Margins were rounded. In a second specimen (NSW 6247) there was an abaxial ridge over the midrib.

Anatomy

Leaves were dorsiventral. Hairs occurred infrequently and were mostly on the adaxial surface. Over the whole surface, the outer walls of epidermal cells were cutinised. The surface was papillose. Below the adaxial epidermis, there was a single row of palisade cells. Arm palisade cells frequently occurred (Fig. 131). On the abaxial side of the leaf there were some 7 rows of spongy mesophyll. In epidermal and mesophyll cells there were occasional mineral deposits, possibly silica. Major bundles were collateral. Phloem was predominantly abaxial. At the midrib, there was a single vascular bundle with well developed caps of thick walled fibres separated from the abaxial surface by 2 rows of parenchyma and from the adaxial surface by a row of sheath like parenchyma and modified palisade (Fig. 132). At the margins, there was palisade and mesophyll. Lower order veins had abaxial fibre caps which were within the mesophyll and adaxial caps which sometimes extended into the modified palisade. Minor veins which were within the mesophyll had abaxial and adaxial fibres, adaxial

fibres or were without fibres; vascular tissues were not always precisely delimited and orientated. Many large simple vascular elements were associated with vascular bundles, especially with minor bundles. Bundle sheaths were weakly developed. Occasional druses occurred in sheath cells and mesophyll cells. There were large irregular sclereids within the mesophyll (Fig. 133).

P. laurina ssp. *leiogyna*

This specimen was slightly different from *P. laurina* ssp. *laurina*. Epidermal cell walls were weakly lignified. The surface was only weakly papillose. Stomata occurred less frequently on the adaxial surface. On each side of the leaf, only one lower order vein had an adaxial fibre cap which extended into the palisade. Sclereids were not an obvious feature.

Group 3

P. longifolia

Outline in transverse section

Abaxial and adaxial surfaces were parallel. Margins were rounded or slightly pointed. There were pronounced abaxial and adaxial ridges over the midrib and main veins.

Anatomy

Leaves were isolateral to weakly isolateral. There were occasional hairs, mostly towards margins. Epidermal cell walls were weakly lignified; over the whole surface, outer walls were cutinised. The surface was papillose. Below the abaxial and adaxial epidermis there was a single row of palisade cells. Arm palisade cells occurred. Between the palisade cells, there were some 10-12 rows of spongy mesophyll cells. Major bundles were collateral. Phloem was predominantly abaxial. At the midrib, there was a

single bundle with well developed caps of thick walled fibres, separated from the epidermises by a single row of parenchyma. At each margin, palisade was reduced and there was spongy mesophyll or, in some leaves, rounded parenchyma. In some leaves there was a group of fibres towards the margin. Lower order veins which had well developed abaxial and adaxial fibre caps were within the mesophyll, hardly extending into the palisade. Particularly in smaller bundles, vascular tissues were not precisely delimited and orientated. Among vascular bundles, there were groups of fibres only or fibres associated with few xylem elements. There were numerous gelatinous fibres. Simple tracheary elements occurred within bundles or on the edges of bundles. Bundle sheaths were irregular; many contained druses.

In one specimen (CSIRO Canberra 2566) palisade cell walls were weakly lignified and cells contained tannin.

P. elliptica

Outline in transverse section

Abaxial and adaxial surfaces were parallel. Margins were rounded. Slight abaxial and adaxial ridges occurred over main veins.

Anatomy

Generally, the description of *P. longifolia* described this species. There were some differences:-

Hairs occurred and were mostly on the adaxial surface. Both surfaces were weakly papillose. There were some 6-7 rows of spongy mesophyll. There were 1-3 rows of parenchyma between abaxial fibres associated with the midrib and the epidermis. Towards each margin, there was a small group of vascular tissues and, associated with it, there was a well developed group of fibres. Lower order veins extended into the palisade. Some small bundles contained only short, thick walled vascular elements. No groups contained

fibres only. Thick walled, irregular fibre sclereids occurred near vascular bundles and, occasionally, as idioblasts. There were no gelatinous fibres.

Group 4

P. gunnii

Outline in transverse section

Abaxial and adaxial surfaces were parallel. Margins were rounded. There were slight adaxial undulations over main veins.

Anatomy

Generally, the description of *P. longifolia* described this species. There were some differences:-

Hairs rarely occurred. Both surfaces were only weakly papillose. Arm palisade cells rarely occurred. There were 8-9 rows of mesophyll. The midrib and lower order veins were within the mesophyll. At the margins, palisade was continuous; there were no fibres or vascular tissues close to the margin. Throughout the leaf, fibres were few and often gelatinous. There were no groups of fibres only. Bundle sheaths were fairly well developed. Crystals occurred in sheath cells and mesophyll but were rare and weakly developed.

P. gunnii var. *angustifolia*

Outline in transverse section

The abaxial and adaxial surfaces were more or less parallel. Margins were rounded and slightly incurved. Leaves were slightly thicker near main veins.

Anatomy

Generally, the description of *P. longifolia* described this species. There were some differences:-

Leaves were dorsiventral. Hairs occurred on both surfaces and were abundant on the abaxial surface. Below the adaxial surface, there was a single row of palisade cells. Arm palisade cells occurred only rarely. Some palisade and mesophyll cells had weakly lignified walls; some contained tannin. The midrib and lower order veins were within the mesophyll. At each margin palisade was continuous or interrupted by more isodiametric parenchyma cells. There were no groups of fibres only. there were no gelatinous fibres.

Group 5

P. myrtilloides

Outline in transverse section

Abaxial and adaxial surfaces were parallel. Margins were rounded.

Anatomy

Leaves were isolateral. Hairs were few. The outer walls of epidermal cells were weakly cutinised over the whole surface. The surface was weakly papillose. Below the epidermis, there was a single row of palisade cells. Arm palisade cells frequently occurred. Between the palisade, there were 7-8 rows of irregular mesophyll. Palisade and mesophyll cells contained tannin. Major bundles were collateral. Phloem was abaxial. The midrib and lower order veins had abaxial and adaxial fibre caps and were within the mesophyll. At each margin, there was a small group of large, thick walled fibres below the epidermis. In some leaves, there was a small group of vascular tissues associated with the fibres (Fig. 134). Particularly in smaller bundles, vascular tissues were not precisely delimited and orientated.

Associated with minor bundles, there were abaxial and adaxial or adaxial fibres or they were without fibres. Fibres were often large and approaching fibre sclereids (Fig. 135). Large tracheary elements occurred in some bundles but were not an obvious feature. Bundle sheath cells were irregular; many contained druses.

P. marginata

Generally, the description of *P. myrtilloides* described this species. There were some differences:-

Epidermal cell walls were heavily lignified. Over the whole surface, the cuticle was thick and there were few papillae. Mesophyll cells were regular and closely packed. At each margin, immediately below the epidermis there was a large group of fibres which was associated with a small vascular bundle (Fig. 136). Among vascular bundles, there were groups of fibres and fibre sclereids only. Fibre sclereids were associated with small vascular groups or occurred as idioblasts (Fig. 137). Large, simple tracheary elements were associated with some vascular bundles. Some small groups contained only short thick walled vascular elements and fibre sclereids. Bundle sheath cells were large and irregular and contained druses.

In a second specimen (CSIRO: Cunningham), arm palisade cells were few. Mesophyll cells had thin walls and were less regular. At the midrib, fibre caps were separated from the abaxial and adaxial epidermis by modified palisade cells.

P. hirsuta

Outline in transverse section

The adaxial surface was weakly convex and the abaxial weakly concave. Margins were rounded.

Anatomy

Leaves were dorsiventral. Hairs occurred occasionally on both surfaces. Especially on the adaxial surface, the outer walls of epidermal cells were cutinised. Below the adaxial epidermis, there was a single row of palisade cells. Below the abaxial surface, there were some 7 rows of spongy mesophyll. Palisade and mesophyll cells contained tannin. Bundles were few, small and loosely collateral and were within the mesophyll. Phloem was predominantly abaxial. The midrib which was one of 3 larger veins had few abaxial and adaxial fibres. At the margins there was palisade and mesophyll. Towards each margin, there was a bundle; one had abaxial and adaxial fibres, the other had adaxial fibres only. Lower order veins were small vascular strands. Bundle sheath cells contained crystals, generally druses.

P. mollis

Outline in transverse sections

Abaxial and adaxial surfaces were more or less parallel. Margins were rounded.

Anatomy

Leaves were dorsiventral to weakly isolateral. Hairs occurred on both surfaces. Epidermal cells were lignified; especially on the adaxial surface, the outer walls were cutinised. The adaxial surface was papillose. Stomata occurred on the abaxial surface only. Below the adaxial epidermis, there was a single row of palisade; arm palisade cells occurred. Below the abaxial epidermal, there were some 7 rows of spongy mesophyll. In the outermost row, cells were more upright and arm cells occurred. Palisade and mesophyll cells contained tannin. Bundles were collateral. Phloem was abaxial. All the bundles were within the mesophyll. The midrib which was

larger than other bundles had abaxial and adaxial fibre caps. On one side of the leaf, there were 3 smaller bundles with similar structure and, on the other side, there were 2. At the margins, there was palisade and mesophyll. Lower order veins had abaxial and adaxial fibres, adaxial fibres or were without fibres. Bundle sheaths were well developed; cells contained crystals. Associated with some bundles, there were large, irregular fibre sclereids.

Group 6

P. quinquenervis

Outline in transverse section

Abaxial and adaxial surfaces were more or less parallel. Margins were slightly pointed. There were abaxial and adaxial ridges over main veins.

Anatomy

Leaves were isolateral. Hairs were few. On both surfaces the outer walls of epidermal cells were heavily cutinised. Surfaces were papillose. Below the abaxial and adaxial epidermis, there was a single row of palisade. Arm palisade cells frequently occurred. Between the palisade, there were some eleven or twelve rows of spongy mesophyll. Vascular bundles were loosely collateral; in many, tissues were not precisely delimited and orientated. Especially in main bundles, phloem was predominantly abaxial. Larger bundles were tangentially spread and, on the edges, there were numerous simple, thick walled tracheary elements. Similar cells comprised small bundles (Fig. 138). At the midrib, there were abaxial and adaxial fibre caps associated with a tangentially extended bundle. On the adaxial side, fibres were below the epidermis, on the abaxial side, they were within the modified palisade. Some fibres were unlignified, possibly gelatinous (Fig. 139). On either side of the leaf, 2 bundles were similar in structure but

smaller and within the modified palisade. Other lower order bundles were similar in structure but fibre caps were less well developed. Near each margin, there was a group of tracheary elements. A narrow girder of unlignified fibres associated with them reached the epidermis (Fig. 140). Sheath like cells were associated with bundles but did not always surround them. There were numerous crystals in these cells and in palisade and mesophyll (Fig. 138).

P. hakeiformis

Outline in transverse section

Leaves were nearly terete with a deep abaxial groove.

Anatomy (Fig. 141)

Leaves were nearly terete. There were occasional hairs over the whole surface. The outer walls of epidermal cells were heavily cutinised; the cuticle penetrated between anticlinal walls. The surface of the leaf was papillose. Stomata were over the whole surface, including the abaxial groove. Below the epidermis, there was a single row of tall, narrow, irregular palisade cells. Within the abaxial groove and in the centre of the leaf there was spongy mesophyll. The midrib which was towards the adaxial side of the leaf, within the mesophyll, had abaxial and adaxial fibre caps. On either side of the abaxial groove, there was a bundle in which tissues were not well delimited and orientated; there was a fibre cap associated with the xylem. Minor bundles contained only simple tracheary elements and there were numerous similar cells on the edges of the 3 main bundles. Sheath cells were associated with major and minor veins but did not always surround them. Crystals occurred in sheath cells. Large irregular fibre sclereids were associated with vascular bundles or occurred as idioblasts (Fig. 142).

Group 7.

P. falcata

Outline in transverse section

Abaxial and adaxial surfaces were more or less parallel. Margins were rounded and bulbous. There were abaxial ridges and less well developed adaxial ridges over major veins.

Anatomy

Leaves were isolateral. Hairs were few. The outer wall of epidermal cells were cutinised; cuticle penetrated between anticlinal walls. The surface was weakly papillose. Below the abaxial and adaxial epidermis, there was a single row of palisade cells. Between the palisade there were some 5 or 6 rows of closely packed mesophyll cells. Palisade and outer mesophyll cells contained tannin. In the centre of the leaf there were 4 or 5 rows of large thin walled cells. Vascular bundles were loosely collateral. Phloem was predominantly abaxial. Especially in smaller bundles, tissues were not precisely delimited and orientated. The vascular bundle at the midrib had abaxial and adaxial caps of thick walled fibres separated from the epidermises by 1 or 2 rows of parenchyma. Vascular tissues were laterally spread and there were vascular elements on the abaxial side of the phloem and on the edges of the complex (Fig. 143). At each margin, there was a spread group of vascular tissues and, around the margins, there were thick walled fibres separated from the epidermis by 2 rows of parenchyma (Fig. 144). Lower order veins which had abaxial and adaxial fibre caps were within the central mesophyll. Many minor veins contained only large simple tracheary elements.

P. saundersiana

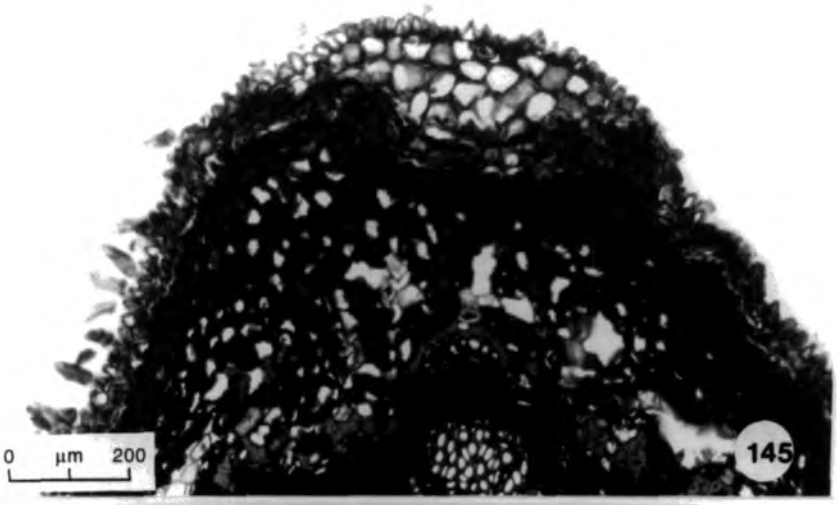
Outline in transverse section

There were pronounced abaxial and adaxial ridges over main bundles. Margins were slightly extended and rounded.

Anatomy

Leaves were isolateral. Hairs were not an obvious feature. The outer walls of epidermal cells were heavily cutinised. Both surfaces were papillose. Epidermal cells contained occasional druses and numerous rhombic crystals, many of which were twinned. Below the abaxial and adaxial epidermis there was a single row of palisade cells. Arm cells frequently occurred . In grooves, palisade cells were shorter. Between the palisade, there were some 6 rows of spongy mesophyll. Palisade and mesophyll cells contained numerous, mostly rhombic, crystals. Major bundles were collateral. Phloem was abaxial. In each ridge, there was a vascular bundle with well developed abaxial and adaxial fibre caps which were within the spongy mesophyll. The midrib was the largest of 5 bundles. At the margins, palisade was continuous. Either side of the midrib, there were one, or occasionally two, minor bundles. Each bundle had a few abaxial and adaxial fibres, xylem was scattered and simple tracheary elements occurred on the edges of the complex. Bundle sheaths were well developed; sheath cells contained crystals, mostly druses.

Figs. 145-150. - *Garnieria spathulaefolia* (Herb. mus. Paris, 278). - 145, Leaf base, transverse section. - 146, Leaf base, transverse section. - 147, Bundle sheath cells in lower leaf. - 148, Midrib, transverse section. - 149, Leaf margin, transverse section. - 150, Minor bundle, transverse section.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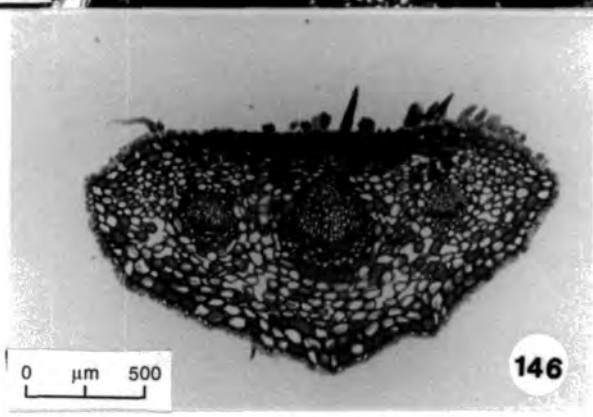
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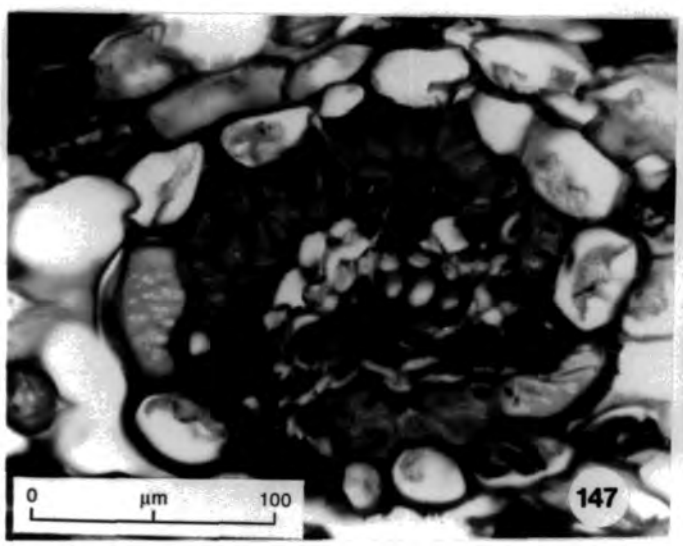
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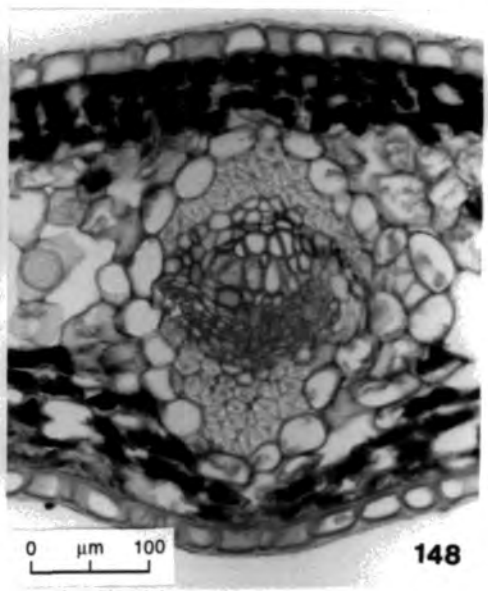
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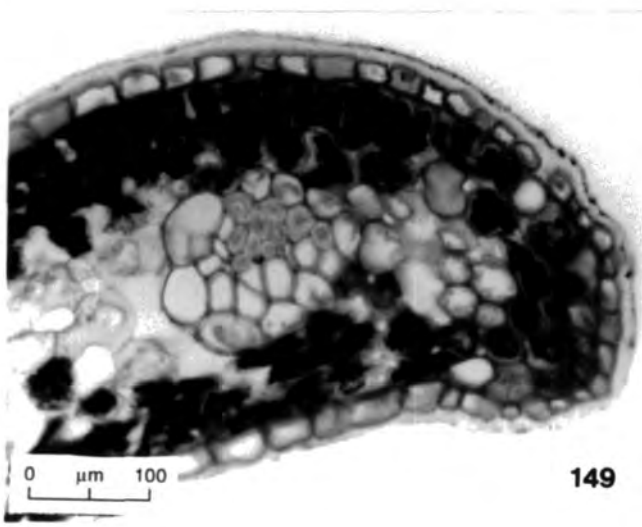
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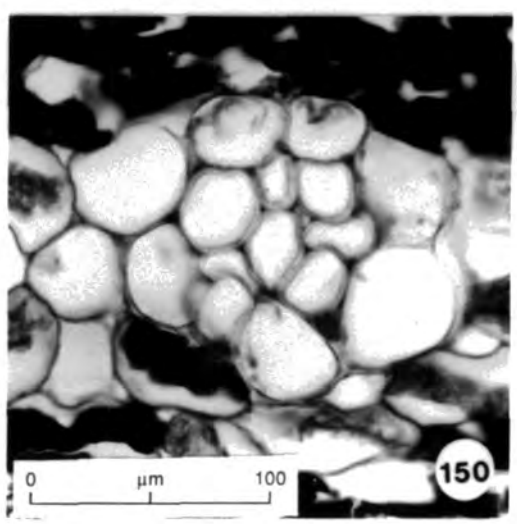
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150

Garnieria

Garnieria spathulifolia

Stem

The stem included in the stem-node-leaf continuum was 2.5 mm in diameter. Cork was superficial. The cortex was some 9 cells wide. Among the unlignified parenchyma, there were some lignified and heavily pitted cells. Particularly in the outer layers, many cells contained tannin. There were small caps of thick walled fibres associated with vascular bundles. Among the pericyclic fibres, there were lignified parenchyma cells which often, though not necessarily, coincided with rays. Vascular tissues were eustelic to siphonostelic. A continuous cambial zone was recognisable. Interxylary fibre groups were small. Pith was lignified and included heavily lignified parenchyma cells and sclereids.

Nodal anatomy

At the lowest levels, leaf traces were recognised by their modified xylem which consisted of simple vascular elements and unlignified parenchyma. Changes in the xylem were seen, on either side of the median leaf trace, in a wide arc of siphonostelic vascular tissues. The cortex was enlarged opposite the median leaf trace. In the lateral position, on one side of the stem, a single bundle had modified xylem; on the other side, changes were seen in 2 closely associated bundles. At the level where they were outside the stele, each lateral trace was a single small bundle. There were occasional sclereids in the cortex and pith. At higher levels, fibre caps associated with leaf traces dispersed. Three supradjacent nodes had 3 lacunae and 3 traces and their structure was similar.

Leaf base

At the lowest levels, the leaf base was first seen as a group of large, mostly lignified parenchyma cells outside the cork and cortex (Fig. 145). At higher levels, there was a zone of lignified cortical cells which contained tannin on the adaxial side of the leaf base which was composed of unlignified parenchyma. Leaf traces crossed the cortex. They were without fibre caps. Just above the level at which traces were within the leaf base, there were a few fibre cells on the abaxial side of each of them. At a higher level, there were a few adaxial fibres associated with each trace (Fig. 146).

The distal end of the leafbase

Abaxial and adaxial fibre caps were larger at higher levels. Three bundles were continuous throughout the leafbase. There was a small component on each edge of the central bundle.

The transition from leaf base to leaf

The leaf was tangentially extended. Small groups of vascular tissues, seen as components of the central bundle at lower levels, were separate bundles. Bundle sheaths were well developed. Some sheath cells were lignified and heavily pitted (Fig. 147). At higher levels, the structure was similar, the leaf was further extended and there were more vascular bundles.

Leaf anatomy

Leaves were dorsiventral. There were occasional hairs on the abaxial surface. On both surfaces, the epidermis consisted of a single row of cells with weakly cutinised outer walls. Around margins, the cuticle was slightly thicker. Stomata which were restricted to the abaxial surface were paracytic and had a single subsidiary cell on either side of the guard cells. Below the adaxial epidermis, there was a single row of irregular palisade cells; arm

cells regularly occurred. Palisade cells contained tannin. Below the abaxial epidermis, there were 3-4 rows of mesophyll cells which contained tannin. In the centre of the leaf, there were some 5 rows of large, rounded mesophyll cells. Main bundles were collateral, phloem was abaxial. The midrib which had an abaxial and adaxial fibre cap was within the mesophyll (Fig. 148). The midrib was distinguished only by its position; there were 3 other bundles of similar size and structure. At the margins, palisade and mesophyll were modified and there were rounded parenchyma cells, many of which contained tannin (Fig. 149). Lower order bundles which were of various sizes had abaxial and adaxial fibres, adaxial fibres or were without fibres. Many fibres were gelatinous (Fig. 149). Some minor bundles contained only large tracheary elements (Fig. 150). Bundle sheaths were well developed around bundles of all sizes.

DISCUSSION

Infrageneric classification in the Grevilleeae

Grevillea

The genus showed great diversity among more than 250 species. Among the 71 specimens of 43 species examined, there was anatomical diversity.

In most species in Groups 1 and 2 and in some species from Groups 7, 9, 13, 19 and 21, towards the margins of leaves, there were vascular bundles, often two bundles, with well developed adaxial fibre caps, separated from the epidermis by a single row of parenchyma cells or by modified palisade cells. At the margins, there was palisade and mesophyll or adaxial palisade extended around the margins (e.g. Figs. 33, 63).

In Group 1, tissue patterns at the margins showed some plasticity even within species and within specimens. Three species, *G. ramosissima*, *G. laurifolia* and *G. repens*, lacked bundles towards the margins; at the margin, thick walled fibres associated with a small vascular bundle were separated from the epidermis by a single row of parenchyma. In *G. ramosissima*, close to the margin, there was another bundle with a well developed adaxial fibre cap; this might be accepted within the range of variability of the feature. In *G. laurifolia* and *G. repens*, there were no other bundles towards the margin. In *G. repens*, on either side of the leaf, between the midrib and the margin, there was one bundle of similar structure and extent to the midrib and, in *G. laurifolia*, there were 2. All lower order veins were within the mesophyll.

In *G. laurifolia*, at the distal end of the petiole, there was an arc of 7 large bundles of more or less equal size.

On anatomical evidence, it was possible to suggest that *G. laurifolia* and, perhaps, *G. repens* did not belong in this Group.

In Group 2, As in Group 1, tissue patterns at the margins showed plasticity (Table 6).

The range of variation among specimens of *G. victoriae* might illustrate the variability of the character (Figs. 30, 31, 32). Conversely, if, as taxonomists think, *G. victoriae* is a complex of taxa (R.O. Makinson, pers. comm.), diversity might reflect this situation.

Within *G. speciosa*, differences were not associated with different subspecies.

In *G. mucronulata* and *G. occidentalis*, there were no bundles towards margins. In *G. mucronulata*, across the leaf, there were many bundles with well developed adaxial fibre caps which extended into the modified palisade. In *G. occidentalis*, most lower order veins were within the mesophyll. If, in the opinion of taxonomists, these species are best placed in Group 2, their anatomical characteristics are at the extreme of a range.

Within Group 2, there were pronounced anatomical similarities among 3 species. The only specimen of *G. sparsiflora* examined conformed to the pattern of the group. In *G. acuaria*, there was within species variation in tissue patterns at the margins of leaves (Figs. 35, 36). In *G. pauciflora* groups of fibres towards each margin were not associated with vascular bundles (Fig. 37). In the 3 species, on the adaxial side of the leaf, there were many fibre groups which were not associated with vascular tissues (Fig. 36). Affinities between *G. acuaria* and *G. sparsiflora* were supported by early phellogen activity (Fig. 2) and the development of several rows of cork in stems of narrow diameter. The grouping of *G. sparsiflora*, *G. acuaria* and *G. pauciflora* was further supported by the sharing of a similar nodal structure in which, within a single leaf gap, 3 leaf traces alternated with 2 smaller bundles associated with the vascular supply to the axillary bud (Fig. 8). Although, in *G. australis* and *G. australis* var. *montana*, nodes had 3 lacunae

Table 9 . Grevillea, Group 7.
Tissue patterns in midribs, margins and major veins in 4 species

Species	Midrib	Margin	Lower order veins
G. robusta	There was a small bundle on either side of a large central bundle. Bundles were separated by lignified parenchyma. Fibre caps were weakly defined. Towards the adaxial side, there was a group of fibres separated from the epidermis by parenchyma. On the abaxial side, a more or less continuous zone of fibres was separated from the epidermis by some 4 rows of parenchyma.	Palisade and mesophyll.	On one side of the leaflet, there were 2 bundles with well developed abaxial and adaxial fibre caps which extended nearly to the epidermis and, on the other, there were 3.
G. meisneri	There was a small bundle on either side of a large central bundle. Bundles were separated by lignified parenchyma. Occasional large sclereids occurred among parenchyma. On the adaxial side, within the parenchyma, there was a small group of fibres. On the abaxial side, there was a band of fibres separated from the epidermis by some 4 rows of lignified parenchyma.	A fibre cap associated with a small bundle was separated from the epidermis by 2-3 rows of large lignified parenchyma cells.	On either side of the leaf, there were 2 or 3 bundles with well developed fibre caps separated from the adaxial epidermis by a single row of large, upright parenchyma cells and from the abaxial by 2-3 rows of lignified parenchyma.

G. papuana	There was a single large bundle. A tangentially extended fibre cap was separated from the abaxial epidermis by some 5 rows of lignified parenchyma. Adaxial fibres were mixed with lignified parenchyma; there were 2-3 rows of lignified parenchyma below the epidermis. On each side of the complex, there was a small vascular bundle.	A tangentially extended band of fibres associated with a small vascular bundle was separated from the epidermis by 3 rows of small parenchyma cells which had lignified walls and contained tannin.	On either side of the leaf, there were several (>10) bundles which, with their associated tissues, spanned the thickness of the leaf and were separated from the epidermises by lignified parenchyma. Often, this parenchyma was extended tangentially and, particularly on the edges of groups, was large and well pitted.
G. glauca	There was a tangentially spread complex which included 3 bundles. Between the bundles, there was lignified parenchyma. Each bundle had a well developed abaxial and adaxial cap of fibres. Around the complex, there was a single row of sheath like cells which contained silica bodies. A row of unlignified parenchyma or, in places, modified palisade cells separated these tissues from the epidermises.	There was a weakly developed vascular bundle separated from the epidermis by some 2 rows of unlignified parenchyma.	On either side of the leaf, there were 6 to 9 bundles with well developed abaxial and adaxial fibre caps most of which were separated from the epidermises by heavily modified palisade and surrounding sheath cells which often contained silica.

and 3 traces, these taxa shared some leaf characters with *G. sparsiflora*, *G. acuaria* and *G. pauciflora*. At the margins, *G. australis* conformed to the general description of Group 2 but, in addition, there was a group of fibres which was not associated with a vascular bundle (Fig. 33). In *G. australis* var. *montana*, all the vascular bundles were within the central mesophyll and, near the inner boundary of the palisade, there were small fibre groups. At the midrib, in *G. australis*, *G. australis* var. *montana*, *G. acuaria*, *G. sparsiflora* and *G. pauciflora*, there was a small vascular bundle and fibre caps were weakly developed (Figs. 27, 28 29). There were additional adaxial palisade layers in *G. australis*, *G. australis* var. *montana* and *G. sparsiflora* and some development of *abaxial palisade* in *G. pauciflora* and *G. acuaria* and *G. sparsiflora*. Anatomical evidence supported the grouping of *G. acuaria*, *G. pauciflora* and *G. sparsiflora* within Group 2 and suggested that *G. australis* and *G. australis* var. *montana* might be included with them.

In *G. striata* in Group 7, towards each margin, there were two bundles with well developed adaxial caps of thick walled fibres. In *G. brachystachya*, at the margin, there was a vascular bundle with a well developed fibre cap and, between the margin and the midrib, there were 4 bundles with well developed adaxial caps of thick walled fibres. Both species were dorsiventral. Subepidermal lignified parenchyma was well developed. In *G. brachystachya* there were 1-4 rows below the adaxial epidermis and, in *G. striata*, there were 4. In *G. striata* there were fibres among the lignified parenchyma. Around margins in *G. brachystachya*, a single row of lignified parenchyma was continuous; in *G. striata*, 1-3 rows were continuous.

In 4 other species from Group 7, towards the margins, bundles with well developed adaxial fibre caps were not an obvious feature (e.g. Fig. 43). Characteristics at the midribs and margins and features of lower order veins are summarised in Table 9.

At the margins, in *G. robusta*, there was palisade and mesophyll. Among the other species, there was greater development of parenchyma at the margins. At the midrib, in *G. robusta*, *G. papuana* and *G. meisneri*, lignified parenchyma was well developed. In *G. glauca*, abaxial and adaxial fibre caps were separated from the epidermises by a single row of sheath like cells which contained silica bodies and a row of parenchyma or modified palisade cells. In *G. papuana* and *G. glauca*, tissues at the midrib were tangentially extended and, in *G. glauca*, the midrib complex included 3 vascular bundles. Lower order veins extended almost to the epidermises and, in *G. papuana* and *G. glauca*, they were numerous. In *G. papuana* subepidermal parenchyma associated with lower order veins was tangentially extended. In 3 of the 4 species, leaves were dorsiventral and there was a single row of adaxial palisade cells. In *G. glauca*, leaves were isolateral.

Although there were differences in tissue patterns, it was possible to see the 4 species as a series and to include *G. brachystachya* and *G. striata* within the series. Only the position of *G. glauca* seemed open to question on the grounds of its isolateral leaf structure and the occurrence of silica in bundle sheath cells.

Three species from Group 9 were described. In *G. paniculata*, towards each margin, there were 3 bundles with well developed adaxial fibre caps separated from the epidermis by a single row of parenchyma cells. Between the midrib and the margin, there was a slightly smaller bundle with fibres separated from the adaxial epidermis by modified palisade cells. The midrib was radially elongated. Towards the abaxial side there was a large bundle and, adaxial to it, there were 2 radial files of small bundles and vascular strands. Species in Group 1 uniformly had a complex of 3-5 bundles at the midrib and, in some specimens, there were peripheral bundles. In *G. pteridifolia*, the midrib was radially elongated.

Tissue patterns at the midrib and margins in *G. paniculata* resembled those in species from Group 1 more than those in the other species from Group 9.

In Group 13, only *G. patentiloba* was examined. Around margins, there was palisade and, near each margin, there were 2 vascular bundles with well developed adaxial caps of thick walled fibres separated from the epidermis by a single row of parenchyma. Within the midrib and in a second vein with similar structure, there were 3 vascular bundles separated by lignified parenchyma and fibres and, associated with each complex, there were large abaxial and adaxial fibre caps separated from the epidermises by 1-3 rows of parenchyma. Crystals occurred in epidermal and mesophyll cells (Fig. 62).

In the 3 taxa from Group 19, towards each margin, there were vascular bundles with well developed adaxial fibre caps which were separated from the epidermis by a single row of parenchyma. In *G. hakeoides* subsp. *commutata*, there were 3 bundles of similar structure (Fig. 66) and, in *G. diversifolia*, there were 2. In *G. hakeoides*, leaves were smaller and linear-terete; on either side of the midrib, there were 2 bundles with well developed adaxial fibre caps (Fig. 64).

In the 3 taxa, there were well developed abaxial and adaxial caps of thick walled fibres associated with the midrib and, on the edges of the complex, there were smaller bundles. In *G. diversifolia* some epidermal cells contained small acicular crystals.

In *G. diversifolia*, the single row of lignified parenchyma cells which separated fibre caps from the adaxial epidermises was extended laterally beyond bundles (Figs. 67, 68) and, sometimes, merged with similar cells to form a sub-epidermal row. Some groups of similar parenchyma occurred where there was no vascular bundle (Fig. 69). Subepidermal lignified parenchyma was not a characteristic of the other taxa from Group 19 which

Table 10.

Anatomical characteristics in 5 species of *Grevillea*

Species	Palisade	Arm cells in palisade	Pits in projections in anticlinal walls	Central mesophyll	Lower order veins
G. pulchella	Weakly developed second row	None seen	Occurred	Long axes parallel to the leaf surface	Well developed fibre caps
G. trifida	1 row	Occasional	None seen	5 rows of spongy mesophyll	Within mesophyll
G. vestita	1 row. Some abaxial palisade	None seen	None seen	5 rows of spongy mesophyll	1 vein of approximately the same abaxial/adaxial extent as the midrib on each side of the leaf
G. mucronulata	1 row	None seen	None seen	4-7 rows of spongy mesophyll	1 or 2 veins of approximately the same abaxial/adaxial extent as the midrib on either side of the leaf
G. occidentalis	1 row	None seen	Occurred	4-7 rows of spongy mesophyll	Within the mesophyll

were examined. Considering only anatomical features, it might be suggested that *G. diversifolia* should be grouped with species from Group 7 although, *G. diversifolia* is not obviously misplaced in Group 19.

In Group 21, species were of unassigned affinities.

In *G. bracteosa*, at each margin, there was a vascular bundle with a well developed fibre cap separated from the epidermis by a single row of parenchyma cells and, near the margin, there were 2 bundles with well developed adaxial caps of thick walled fibres separated from the epidermis by a single row of parenchyma. At the midrib, there were well developed abaxial and adaxial fibre caps and, on the edges of the complex, there were several small vascular groups. In epidermal cells, there were occasional acicular crystals and druses.

In Group 9, *G. paniculata* has been considered. In *G. trifida* and *G. vestita*, towards each margin, there were no bundles with well developed adaxial fibre caps. *G. pulchella*, from Group 5, also lacked these features. In a comparison, *G. mucronulata* and *G. occidentalis* from Group 2 were included with these 3 species. In all five species, leaves were dorsiventral. At the midrib, in all the species, there was a single large vascular bundle with well developed abaxial and adaxial fibre caps separated from the epidermis by 1-3 rows of parenchyma. At the margins, there were palisade and mesophyll cells or, in *G. trifida*, continuous palisade.

Within this group, there were more similarities than the species shared with taxa from other Groups but the similarities were often in minor characters or in the absence of features (Table 10). It would be necessary to have more positive evidence to make a good case for suggesting new relationships.

With one exception, all the species discussed so far had dorsiventral leaves or, if there was some abaxial palisade, it was weakly developed. The position of the exception, *G. glauca*, has been questioned. Other species of

Grevillea examined had isolateral or linear terete leaves. None had bundles with well developed abaxial caps of thick walled fibres towards the margins.

In Group 8, 3 species, *G. pyramidalis*, *G. mimosoides* and *G. dimidiata* shared exceptional characters (Figs. 19 and 48-55). Leaves, or leaflets, were isolateral. Leaf bases were radially extended and leaf blades were laterally flattened. In leaves, the main vascular bundles were in a double row; phloem was towards the palisade. At margins palisade was continuous or was interrupted by rounded parenchyma cells. At the 2 margins, the arrangement of vascular bundles was different. Around the periphery of the central parenchyma, there were small bundles and vascular strands. Stomata occurred on both surfaces. In *G. pyramidalis*, they were paracytic and there was a single subsidiary cell on either side of the guard cells. In *G. mimosoides* and *G. dimidiata*, some stomata had 2 parallel subsidiary cells on one or both sides of the guard cells (e.g. Figs. 56 and 58). All 3 species had druses and acicular crystals in epidermal cells; prismatic and rhombic crystals occurred and, sometimes, they were twinned. This strong suite of characters argued very well for close relationships among the 3 species. In *G. nematophylla* leaves were linear-terete. Although there were only small changes in dimensions in the transition to the leaf, there was radial elongation of the leaf base. In leaves, the midrib was towards the abaxial side of the leaf and, on either side of it, were 3 main veins in a radial file (Fig. 21). *G. nematophylla* should be grouped with *G. pyramidalis*, *G. mimosoides* and *G. dimidiata*.

Among other taxa from Group 8 which were examined, 2 had isolateral leaves and 2 linear-terete leaves. In *G. polybotrya*, on each side of the leaf, there was a weakly developed second row of palisade cells and, between the palisade, there were some 4 rows of more or less rectangular mesophyll cells. In *G. integrifolia* (Tindale 207 and Maslin), there were 2 rows of palisade cells on either side of the leaf and, between them, 3-4 rows

of mesophyll cells similar in shape and orientation to palisade cells. In both species, stomata occurred on both surfaces of the leaf. At margins, there was continuous palisade in *G. polybotrya* and mesophyll in *G. integrifolia*. In both species, the midrib was distinguished only by its position. Vascular bundles were within the mesophyll in *G. polybotrya* and within the palisade in *G. integrifolia*. Similarities supported the close positions of these species.

G. biformis (*G. integrifolia* ssp. *biformis*) was very similar to *G. didymobotrya* (Fig. 18). The only remarkable difference between them was the occurrence of silica bodies in bundle sheath cells in *G. biformis*. The only other species examined which had similar silica bodies in bundle sheaths was *G. glauca* which was the only species with isolateral leaves in Group 7. Like *G. polybotrya*, between the abaxial and adaxial palisade, *G. glauca* had 4 rows of rectangular mesophyll cells with their long axes parallel to the surface of the leaf.

On anatomical grounds, *G. glauca* might have been better placed in Group 8 or similarities might point to connections between the two Groups. It would be useful to make a more complete investigation of this part of the genus.

In *G. wickhamii*, *G. insignis* and *G. heliosperma*, leaves were isolateral. In *G. insignis* and *G. heliosperma*, stomata were on the abaxial surface and, in *G. wickhamii*, they were on both surfaces. In one specimen of *G. wickhamii* (Latz 7160), there were 2 inverted bundles towards the adaxial side of the midrib (Fig. 59) and, in the other (Carolin 6200), there was an inverted bundle and one double bundle with phloem on either side of the xylem.

In *G. wickhamii* and *G. heliosperma*, in many vascular bundles, xylem was well developed on the abaxial side of the phloem (Fig. 72).

In one specimen of *G. wickhamii* (Latz 7160), there were 2 bundles of similar abaxial-adaxial extent to the midrib on either side of the leaf and, in

the other (Carolin 6200), there were 6. In *G. insignis*, there were 2 or 3 bundles of similar extent on either side of the leaf and, in *G. heliosperma*, there were 7 or 8.

In all three species, there were crystals, particularly druses, in epidermal cells and occasionally, in mesophyll cells.

For *G. heliosperma*, affinities were undecided. The unusual distribution of the xylem in this species and in *G. wickhamii* suggested that further investigation of other species in Group 11 might show that *G. heliosperma* shared characters with this group. The study of more species in Group 12 might show whether similarities among *G. wickhamii*, *G. insignis* and *G. heliosperma* were significant.

The occurrence of sclereids in *Grevillea*

Sclereids occurred in the cortex of *G. glauca* and *G. mimosoides* and were well developed in the cortex of *G. meisneri*, *G. striata* and *G. nematophylla*. In most specimens, there were no sclereids in the cortex.

In *G. glauca*, *G. meisneri*, *G. didymobotrya*, *G. striata* and *G. insignis*, large, well developed sclereids in the pith were an obvious feature. In *G. meisneri*, *G. brachystachya*, *G. glauca*, *G. striata*, *G. pyramidalis*, *G. mimosoides* and *G. dimidiata*, there were large sclereids in leaf bases. In all the specimens from Groups 7 and 8 in which a complete node was examined, there was a band of lignified parenchyma and/or sclereids, sometimes mixed with fibres on the adaxial side of the abscission layer. This character was also seen in *G. insignis* as well as *G. sparsiflora*, *G. acuaria* and *G. pauciflora*.

Tissue patterns in the distal end of the petiole

In *G. insignis*, *G. glauca*, *G. papuana* and *G. striata*, as well as in *G. laurifolia* and *G. victoriae*, there were between 7 and 10 large vascular

bundles of more or less the same size in the distal end of the leaf base (Fig. 11). In one specimen of *G. mimosoides* (Evans 3356) there were 9 bundles and, in a second specimen (CSIRO 4843), there were 16. In one specimen of *G. dimidiata* (Perry 2073), there was an arc of 20 bundles in the leaf base and, in a second (H1193/77 154) there were 8. There were also many bundles in *G. pyramidalis* where changes were associated with the separation of the rachillae.

These additional similarities supported the suggestion that more species from Groups 7 and 8 should be studied to show whether anatomical features give indications of relationships within and between Groups.

The taxonomic ranks of specimens described

Among the specimens studied, the ranks of several taxa have been discussed by taxonomists.

Grevillea speciosa

Two of the specimens in the Kew Herbarium for which material was sampled were named *G. punicea* R.Br. and *G. punicea* R.Br. var. *crassifolia* A.A. Hamilt. *G. punicea* R.Br. is a straight nomenclatural synonym of *G. speciosa* (Knight) McGillivray, s. str. and *G. punicea* R.Br. var. *crassifolia* A.A. Hamilt. is a synonym of *G. speciosa* (Knight) McGillivray, s. str. The *crassifolia* entity belongs to the type subspecies sensu McGillivray. The type of the variety was from the extreme north of the range and does represent a leaf morphotype population. It is not clear whether the species, in the narrow sense, should be formally subdivided further; the leaf morphology is very variable (R.O. Makinson, pers. comm., 1996).

G. oleoides and *G. dimorpha* were reduced to subspecies within a broad *G. speciosa* by McGillivray (1993). For these taxa, the nomenclature of McGillivray was used in this project (Appendix 1) although Makinson (pers. comm., loc. cit.) favours reinstating them at the specific rank.

Table 11.

Tissue pattern at the margins in *G. speciosa*

G. speciosa ssp. *dimorpha*. Ashby B	There were 2 bundles with well developed adaxial fibre caps at the margin. Between the margin and the midrib, there were 3 large, similar bundles on one side of the leaf and 4 on the other.
G. speciosa ssp. *dimorpha*. Ashby A	There were 3 bundles with well developed adaxial fibre caps towards each margin.
G. speciosa ssp. *oleoides*. Sikes 101	There were 2 bundles with well developed adaxial fibre caps towards each margin and a third between the margin and midrib.
G. speciosa s.str. collected as *G. punicea* V-468	
G. speciosa ssp. *oleoides* H973/80 460	These specimens conformed to the general description.
G. speciosa s.str. collected as *G. punicea* var. *crassifolia* NSW 19368	

Six specimens from the complex were examined. There were some anatomical differences but these were not correlated with subspecies. In 4 specimens, there was some palisade tissue on the abaxial side of the midrib; the exceptions were the specimen collected as *G. punicea* R.Br. var. *crassifolia* A.A. Hamilt. (N.S.W. 19368) and one specimen of *G. speciosa* (Knight) McGillivray ssp. *oleoides* (Sieber ex Schultes et Schultes f.) McGillivray (Kew no. H973/80 460).

There were differences in tissue patterns at the margins among the six specimens (Table 11).

These are taxa which need further consideration.

G. speciosa and its subspecies are still the subject of discussion among taxonomists.

The anatomical character states which differ among these specimens need careful evaluation.

G. integrifolia

In the Kew Herbarium, specimens of *G. integrifolia* (Endl.) Meisn. and *G. biformis* Meisn. were retained at specific rank.

McGillivray (1993) reduced *G. biformis* Meisn. to *G. integrifolia* subsp. *biformis*. Olde and Marriott (1994, 1995) reinstated *G. biformis* at specific rank and recognised 2 subspecies (Olde and Marriott, 1994); the segregate being subsp. *cymbiformis* P.M. Olde and N.R. Marriott. This entity was referred to a population of *G. integrifolia* unassigned to subspecies by McGillivray (1993). In the opinion of Makinson (pers. comm., loc. cit.), it is likely that *G. biformis* will be retained at species rank.

In the opinion of Makinson, one specimen of *G. integrifolia* (H973/80 288) is *G. biformis* subsp. *biformis*, sensu Olde and Marriott. *G. integrifolia*, Tindale 207 and Maslin, is not either subspecies of *G. biformis* but is *G. shuttleworthiana* Meisn. synonym *G. integrifolia* subsp. *shuttleworthiana* (Meisn.) McGillivray and probably *G. shuttleworthiana* subsp. *obovata* (G.

Bentham) P.M. Olde and N.R. Marriott for which the basionym is *G. integrifolia* var. *obovata* Benth.

In 3 of the 4 specimens from this complex which were examined, (N.S.W. 119161, Strid 20757 and Kew no. H973/80 288), the anatomy was similar. Leaves were linear-terete. Vascular bundles were within the central mesophyll (Fig. 18). At the centre of the abaxial side of the leaf, there was a large bundle which was continuous with the median leaf trace (Figs. 15-18). At the centre of the adaxial side there were 2 small bundles with phloem which, by comparison with other bundles in the leaf, were turned through ninety degrees. It was possible to consider the structure as a flat leaf in which the adaxial surface was reduced but characters which were useful in comparison with *G. integrifolia* which had broad leaves were few.

In *G. integrifolia*, leaves were isolateral and stomata were on both surfaces but characters on the adaxial side of the leaf were not seen in the terete leaf. In *G. integrifolia* the dimensions and orientation of the central mesophyll were similar to palisade cells. This might be considered to be a significant character state. In *G. biformis*, central mesophyll was homogeneous. In *G. biformis*, there were large silica bodies in bundle sheath cells but silica was not seen in *G. integrifolia*.

Anatomically, there is probably no reason to suggest that *G. biformis* and *G. integrifolia* are more closely related to each other than they are to other species.

G. hakeoides

McGillivray (1993) reduced *G. commutata* to *G. hakeoides* subsp. *commutata* (F. Muell.) McGillivray. The taxon was reinstated at specific rank by Olde and Marriott (1995).

Leaves of *G. hakeoides* have been described as linear-terete (Bentham, 1870; McGillivray, 1993). On either side of the midrib, there

was a deep groove in which stomata and hairs were concentrated. In the grooves, there was spongy mesophyll below the epidermis. The grooves might be considered to be the reduced abaxial surface (Fig. 64). On either side of the midrib, there were 2 bundles with well developed adaxial fibre caps. This tissue pattern might be considered to be a reduced form of the pattern seen in many species of *Grevillea*, particularly in Groups 1 and 2 (sensu McGillivray, 1993).

In *G. hakeoides* ssp. *commutata*, leaves were broad and margins recurved. Towards each margin there were 3 vascular bundles with well developed adaxial fibre caps (Fig. 66).

Whilst the leaf anatomy of the 2 taxa could be usefully compared with each other and with tissue patterns seen in many other species of *Grevillea*, there were no anatomical characters which suggested that they were more closely related to each other than to other taxa within the genus.

Table 12.
Summary of anatomical features in broad leaves of *Hakea* species

	Midrib		Margins	Crystals	Sclereids	Central mesophyll	Peripheral bundles	Bundle sheaths	Palisade
	Abaxial side	Adaxial side							
Sub-division 2	Parenchyma and fibres	Parenchyma and fibres. Not applicable in *H. sulcata* which is almost terete.	Parenchyma and fibres. Not applicable in *H. sulcata* which is almost terete.	Present.	Irregular and mostly in central mesophyll. But: Columnar in *H. falcata*. Absent in *H. undulata, H. elliptica, H. sulcata.*	2-4 rows of unlignified cells. But: Lignified in *H. falcata* and *H. sulcata*. Weakly lignified in *H. undulata*. Orientated parallel to leaf surface in *H. elliptica.*	Small bundles occasionally associated with main veins.	Weakly developed. But: Absent in *H. sulcata*. A continuous row of morphologically distinct cells surrounds the central mesophyll in *H. falcata.*	2 rows. But: 1 row in *H. ambigua, H. undulata, H. elliptica.*
H. trineura	Parenchyma and fibres.	Parenchyma and fibres.	Palisade.	Present.	Columnar across entire thickness of leaf.	6-7 rows of unlignified cells.	Not an obvious feature.	Well developed.	1 row. Abaxial palisade shorter and wider than adaxial.
H. salicifolia var. *salicifolia.*	Modified palisade.	Modified palisade.	Palisade.	Absent.	Columnar, intruding into central mesophyll.	5-6 rows of unlignified cells. Inner layers orientated parallel to leaf surface.	Associated with large vascular bundles.	Well developed.	1 row.
H. florulenta.	Weakly lignified parenchyma.								

Sub-division 3 trifurcata group and species of uncertain affinity.	Modified palisade. But: Parenchyma and fibres in *H. eriantha.*	Modified palisade. But: Parenchyma and fibres in *H. eriantha* except in specimen R.B.G. Sydney 13385 which has modified palisade.	Palisade.	Absent.	Columnar intruding into central mesophyll.	2-4 rows of unlignified cells orientated parallel to the leaf surface.	Associated with large vascular bundles.	Well developed. Some merging to enclose more than one bundle but this is rare in *H. eriantha.*	2 rows. But: Inner row weakly developed in *H. lasiantha.*
Sub-division 3 obliqua group.	Bundles within central mesophyll.	Bundles within central mesophyll.	Palisade.	Absent.	Columnar across palisade.	Lignified at the centre to non-lignified at periphery.	Well developed around central mesophyll.	Not an obvious feature.	2 rows.
H. arborescens H. persiehana.	Bundles within central mesophyll.	Bundles within central mesophyll.	Palisade.	Absent.	Columnar across palisade.	Lignified at the centre to non-lignified at periphery.	Well developed around central mesophyll.	Not an obvious feature.	1 row.

Hakea

A major revision of *Hakea* was undertaken by Drs W.R. Barker, R.M. Barker and L. Haegi at the Botanic Gardens of Adelaide and State Herbarium. Their preliminary classification has been used in this project.

Terete leaves occurred in 2 of the 3 subdivisions. Differences among shapes in transverse sections did not appear to have consistent taxonomic significance. In all the corkwoods examined, there were 2-3 uninterrupted rows of heavily pitted, lignified cells at the periphery of the central parenchyma (Fig. 92). There are twelve species of corkwood. When more have been examined the feature might be found to have taxonomic value. Generally, tissue patterns in terete leaves showed little variation. The examination of other characters, for example, those of the leaf surface, might give more information about these species.

Among broad leaved species, leaf anatomy showed less diversity than in *Grevillea*. Using 4 characters, tissue patterns at the midrib and margins, the form and distribution of sclereids and the presence or absence of crystals, it was possible to arrange broad leaved species of *Hakea* in 3 categories (Table 12). One corresponded to the second subdivision studied in Adelaide, the others were typified by the Obliqua and Trifurcata groups of subdivision 3. The leaf anatomy of *H. arborescens* and *H. persiehana* conformed exactly to that of the Obliqua group. *H. salicifolia* var. *salicifolia* and *H. florulenta* from subdivision 1 were similar to the Trifurcata group. *H. trineura* was labelled *sedis incertae*. The extent of the midrib (Fig. 94) and the abundant crystals suggested affinities with subdivision 2 but tissue patterns at the margins (Fig. 95) did not support the relationship. Large columnar sclereids which crossed the whole thickness of the leaf were unique among the species examined (Fig. 93). The species might have a position between subdivision 2 and the Trifurcata group of subdivision 3,

perhaps nearer to subdivision 2. When more species have been examined its natural position might become clearer.

As well as the characters which defined the 3 main categories, others were of taxonomic interest (Table 12) and suggested affinities beyond main groupings. Among the 45 species examined, only *H. undulata*, *H. sulcata* and *H. elliptica* lacked sclereids. These species were from subdivision 2. *H. elliptica* and *H. undulata*, as well as *H. ambigua*, were unlike other species in the subdivision in having only one row of palisade cells. In *H. elliptica*, central mesophyll cells were orientated parallel to the leaf surface, a feature found in the Trifurcata group of subdivision 3. In subdivision 2, *H. falcata* was exceptional in having columnar sclereids which crossed the palisade; this form and distribution was found in subdivision 3. When more species have been described, it is possible that more diversity will be found within the genus and that relationships between species and subdivisions will become clearer.

Within the Obliqua group of subdivision 3, there were differences among species particularly in the arrangement and orientation of vascular bundles. In *H. brownii* and *H. baxteri*, there were inverted bundles towards the adaxial side of the leaf (Fig. 107). In *H. pandanicarpa* and *H. pandanicarpa* ssp. *crassifolia* there was a double row of oppositely orientated main bundles and, at the leaf margins, tissue patterns were different (Figs. 102-104). These features, seen in the leaf, were directly related to the structure of the node. In *Hakea* there was more variation in tissue patterns in nodes and leaf bases than in *Grevillea*.

In *H. pandanicarpa* and *H. pandanicarpa* ssp. *crassifolia*, in the transition from leaf base to leaf, extension was in the radial plane and the leaf blade was laterally flattened (Fig. 84). The median leaf trace was at one margin and, at the other, there were smaller bundles. At a low level, a main branch of the median leaf trace followed a direct course to the leaf tip, more

or less in the position of a midrib. *H. clavata* had oval terete leaves and, in this species also, the leaf base was radially extended (Fig. 85).

The nodal anatomy of *H. brownii* and *H. baxteri* showed variation (Table 7) but, in all the specimens, small stelar bundles near the median position were continuous with adaxial inverted bundles in the leaf base and leaf (Figs. 86 and 87).

In 37 specimens studied there were 3 nodes and 3 lacunae. Different numbers of traces were seen in ten specimens (Table 7). Variation within species made it impossible to suggest taxonomic significance for these characteristics. If data were collected for more species and many specimens, some features might be shown to be stable. An unvarying occurrence of 3 lacunae and 3 traces or a stable continuity between stelar bundles and inverted vascular groups in the leaf suggested themselves but, on limited evidence, this was only speculation. In many specimens, small groups of vascular tissues, separated from the stele or leaf trace or differentiated among cortical tissues, formed ephemeral or persistent bundles associated with leaf traces. The occurrence of these bundles varied among species, within species and within specimen and could not be considered as characters of taxonomic significance.

Especially towards the adaxial side of the leaf base, inversely orientated vascular bundles occurred in some specimens with or without inverted bundles in the leaf (Table 7). Perhaps it is difficult to believe that the inverted bundles in *H. brownii* and *H. laurina* (Fig. 81) happened by chance but it will be necessary to examine more specimens before suggesting taxonomic or phylogenetic significance.

Most species had short leaf bases and, at the distal end, the structure remained stable for only a short length before there was expansion into the leaf blade. In the most simple arrangement of tissues, there were 3 main vascular bundles. In some specimens there was a small bundle between the

lateral bundle and the central bundle and/or a small bundle outside the lateral bundle towards the margin. In some species there was an arc of more than 5 large bundles of more or less equal size (Fig. 82). If this is found to be a stable character, it might have taxonomic value.

Finschia

It was not possible to obtain material to compare species within the genus.

Grevilleeae

In the opinion of some taxonomists, accepting *Grevillea robusta* as basal in *Grevillea*, *Finschia* is primitive within the tribe. Anatomically, it is different from *Grevillea*. In the single specimen for which nodal material was available for examination, the node had a complicated structure which involved 7 stelar bundles, 2 lateral and 5 in the median position. In *Grevillea*, only 2 species, *G. glauca* and *G. insignis* had more than 3 lacunae and 3 traces at the node. Only one specimen of each species was examined so that it was not certain whether this was a recurring character. Additional leaf traces at the node occurred more often in *Hakea* (Table 7) but there was within species variation. It would seem that the multilacunate state is apomorphic in the Grevilleeae. This poses problems about the position of *Finschia* which is almost certainly primitive.

Within the petiole of *Finschia*, there was a ring of vascular bundles which included inverted bundles. Inversely orientated bundles persisted in the midrib of the leaf. Only one species of *Grevillea*, *G. wickhamii*, had inverted bundles in the midrib and this species had isolateral leaves, an apomorphic character in *Grevillea* which was not found in *Finschia*.

The laterally spread tissues in the midrib and the abundance of parenchyma and weak development of fibres in this region as well as tissue

patterns at margins and the dorsiventral form of the leaf, all of which were found in species in group 7 would support the taxonomists view that species in this group probably have a close relationship with *Finschia* (Figs. 38, 41, 43, 115, 118 and 116).

Among species of *Hakea*, no dorsiventral leaves were found and stomata consistently occurred on both surfaces, were paracytic and had 2 subsidiary cells on either side of the guard cells. Within the tribe, these were apomorphic character states. Leaves in *Grevillea* were predominantly dorsiventral or weakly isolateral; stomata were variously distributed, were paracytic and, generally, had a single subsidiary cell on either side of the guard cells. Species in Group 8, a single species from Group 11 and from Group 12 and *G. heliosperma* which was of uncertain affinities, as well as *G. glauca* from Group 9 were isolateral and, therefore, probably derived species and, perhaps, more closely related to *Hakea*.

The marked similarities among 4 species of *Grevillea*, *G. pyramidalis*, *G. dimidiata*, *G. mimosoides* and *G. nematophylla*, from Group 8, and *Hakea pandanicarpa*, *H. pandanicarpa* ssp. *crassifolia* and *H. clavata* from subdivision 3, Obliqua group, in *Hakea* suggested affinities between these groups of species from the 2 genera.

Infrageneric classification of Persooniinae

Persoonia

Species of *Persoonia* have been placed in four unequal subdivisions by Weston (pers. comm., 1987, based on unpublished data in Weston, 1983). Subdivisions were divided into smaller groups. In this work, species were first considered in these groups.

Group 1.

In the listings of Weston, *P. rufiflora* and 2 proposed new species which had affinities with *P. rufiflora* were in the first subdivision which corresponded to group 1. Three specimens of *P. rufiflora* have been studied. In the three samples, leaf shapes in transverse sections were different. In one (J.R. Drummond Series 6, 176) leaves were flat, only the margins were reflexed. In 2 other specimens, the abaxial surface was reduced and was within an abaxial groove (Figs. 128, 129).

At the microscopic level, the description of the leaf anatomy in one specimen (J.R. Drummond, Series 6, 176) described the other 2; minor differences in the frequency of gelatinous fibres or the development of palisade tissues were of little or no taxonomic significance.

Group 2.

In group 2, there were 3 species. Three subspecies of *P. laurina* were recognised. Three samples of 2 subspecies were examined.

The description of the leaf anatomy of *P. laurina* ssp. *laurina*, collected by Weston in the Blue Mountains, described both specimens of this taxon. The single specimen of *P. laurina* ssp. *leiogyna* was similar although epidermal cells were weakly lignified, stomata were less frequent on the adaxial surface and sclereids were not an obvious feature.

Group 3.

In group 3, there were 2 species both of which have been examined. The description of the leaf anatomy of *P. longifolia* based on samples from the TYPE specimen (Bentham, 1870), described the second specimen (CSIR 2566). With some differences, it also described *P. elliptica*. There were no groups of fibres only within the mesophyll and no gelatinous fibres; irregular fibre sclereids occurred near vascular bundles and, occasionally, as idioblasts. The similarities among these specimens supports a relationship between these species.

In most species of *Persoonia*, in the leaf base, there was an arc of separate bundles. In *P. elliptica*, vascular tissues were in a continuous arc. It is necessary to examine more specimens to show whether the feature is consistent and unique to *P. elliptica* in this group.

Group 4.

In group 4, there were 3 species. *P. gunnii* and *P. gunnii* var. *angustifolia* were studied.

Generally, the leaf anatomy of *P. gunnii* was described by the description of *G. longifolia* but the midrib was within the mesophyll and, throughout the leaf, fibres were few and, often, gelatinous. There were no groups of fibres only.

The description of *G. longifolia* described *P. gunnii* var. *angustifolia* but, in this taxon, leaves were dorsiventral whereas in *P. longifolia*, *P. elliptica* and *P. gunnii* they were weakly isolateral or isolateral. In *P. gunnii* var. *angustifolia*, the midrib and lower order veins were within the mesophyll. At the margins, palisade was continuous or interrupted by more isodiametric cells. There were no groups of fibres only within the mesophyll and no gelatinous fibres.

Nodal anatomy was different in *P. gunnii* and *P. gunnii* var. *angustifolia*. In *P. gunnii* var. *angustifolia*, nodes had 3 lacunae and 3 traces. In *P. gunnii* there was a single lacuna and 3 traces. This is a marked difference and if, when more specimens are examined, it is found to be consistent, could well be grounds for separating the taxa.

Groups 2, 3 and 4 were in the second subdivision proposed by Weston. The similarities in leaf anatomy among the groups supported the larger subdivision.

Group 5.

Group 5 which included 33 species corresponded to subdivision 3. Four species were examined.

With some modifications, the description of *P. myrtilloides* described the leaf anatomy of *P. marginata*. *P. marginata* had heavily lignified epidermal cell walls. In *P. myrtilloides*, large fibres or fibre sclereids were associated with minor bundles. In *P. marginata*, within the mesophyll there were groups of fibres and fibre sclereids only and fibre sclereids occurred as idioblasts (Fig. 137). In *P. myrtilloides* spongy mesophyll was irregular. In one specimen of *P. marginata*, mesophyll cells were regular and closely packed but in a second specimen cells had thin walls and were less regular.

Two species from the group were different from *P. myrtilloides* and *P. marginata*. In *P. hirsuta* leaves were dorsiventral, in *P. myrtilloides* and *P. marginata* they were isolateral. In *P. hirsuta*, at margins, there was palisade and mesophyll, in *P. myrtilloides* and *P. marginata* there was a group of thick walled fibres below the epidermis (Figs. 134 and 136). Fibres and fibre tracheids were not a feature in *P. hirsuta*.

In *P. mollis* leaves were dorsiventral to weakly isolateral. This species was unique among the species of *Persoonia* examined in having stomata on the abaxial surface only. At the margins, there was palisade and mesophyll.

P. hirsuta was different from *P. mollis*. Leaves were dorsiventral in *P. hirsuta* and dorsiventral to weakly isolateral in *P. mollis*. *P. mollis* was unique among the species of *Persoonia* examined in having stomata on the abaxial surface only; stomata were on both surfaces in *P. hirsuta*. Epidermal cells were weakly lignified in *P. hirsuta* but unlignified in *P. mollis*. In both species, the midrib was within the mesophyll. In *P. hirsuta*, it was distinguished only by its position; adaxial and abaxial fibre caps were weakly developed. In *P. mollis*, the midrib was larger and had abaxial and adaxial fibre caps. Fibre sclereids were associated with vascular bundles in *P. mollis*.

In the leaf base, there were separate bundles in *P. myrtilloides*, *P. mollis* and *P. hirsuta* but, in *P. marginata*, vascular tissues were merged in an arc. In *P. marginata* there was a separate central bundle of adaxial fibres. Towards the outside of the vascular arc, adaxial fibres were continuous with a band of abaxial fibres and broad girders extended to the margins (Fig. 126).

Among the 4 species in this small sample from Group 5, there was considerable diversity of structure.

Group 6.

In group 6, 2 species, *P. quinquenervis* and *P. hakeiformis* were examined. Leaves of *P. quinquenervis* were isolateral and those of *P. hakeiformis* were linear-terete. In *P. quinquenervis*, the bundle at the midrib was tangentially spread and abaxial and adaxial fibres associated with it were tangentially extended. On the adaxial side fibres were below the epidermis, on the abaxial side they were within the modified palisade. Some fibres were unlignified, possibly gelatinous (Fig. 139). In *P. hakeoides*, the midrib with its associated abaxial and adaxial fibre caps was within the mesophyll (Fig. 141). In *P. quinquenervis*, towards each margin, there was a group of tracheary elements. A narrow girder of unlignified fibres associated with

them reached the epidermis (Fig. 140). In *P. hakeoides*, on either side of the abaxial groove, vascular tissues were not well delimited and orientated; fibres were associated with the xylem. Large irregular sclereids were associated with vascular bundles in *P. hakeoides*. In *P. quinquenervis*, some fibres were unlignified, probably gelatinous. Even, allowing for modifications associated with the terete leaf form, these species were very different.

Group 7.

In group 7, 2 species, *P. falcata* and *P. saundersiana* were examined. both species had isolateral leaves. In *P. falcata*, in 4 or 5 rows of central mesophyll, cells were large and thin walled. In *P. saundersiana* mesophyll was spongy. In *P. falcata*, in the midrib, vascular tissues were laterally spread and there were tracheary elements on either side of the phloem (Fig. 143). Abaxial and adaxial caps of thick walled fibres were separated from the epidermis by 1-2 rows of parenchyma. In *P. saundersiana* the midrib was the largest of 5 large bundles which coincided with pronounced abaxial and adaxial ridges; well developed abaxial and adaxial fibre caps were within the mesophyll. At the margins, palisade was continuous but in *P. falcata*, at each margin, there was a spread group of vascular tissues and, around the margins, there were thick walled fibres separated from the epidermis by 2 rows of parenchyma (Fig. 144). No crystals were seen in *P. falcata* but crystals were numerous in *P. saundersiana*.

The leaf anatomy of the 2 species was very different.

Groups 6 and 7 were in subdivision 4 which contained 35 species, 14 of which were new species. Although the sample was small, there was great diversity among species.

In groups 2, 3 and 4 similarities supported the larger subdivision proposed by Weston. In group 5 which corresponded to subdivision 3 and

in groups 6 and 7 from subdivision 4, there was great diversity of leaf structure. With such a small sample of species from the genus, it was not reasonable to suggest other groupings.

Persooniinae

Within the subtribe, there are 4 genera, *Persoonia*, *Toronia*, formerly *P. toru* Cunn., *Acidonia*, formerly *P.* sect. *acrantha* Benth. and *Garnieria*.

It has not been possible to obtain information about the relationship of *Garnieria spathulifolia* to *Persoonia*. Leaves were dorsiventral. Stomata were restricted to the abaxial surface whereas, in *Persoonia*, only *P. mollis* showed a similar distribution, all the other specimens examined had stomata on both surfaces. Palisade cells were irregular and contained arm cells. Central mesophyll cells were rounded. The only other specimen which had 2 types of mesophyll cells was *P. falcata* but, in that species, leaves were isolateral. The midrib was within the mesophyll and distinguished only by its position. At margins, palisade and mesophyll were modified and there were rounded parenchyma cells, many of which contained tannin. No sclereids or crystals were seen. Many fibres were gelatinous.

Although *Garnieria* shared some leaf characters with species of *Persoonia*, none was very like it.

Characters and character states

The discussion of anatomy in five genera of the Proteaceae has been based on observations. The validity of characters was not discussed and there has been no attempt to establish character states. Stevens (1991) has said that the step in cladistic analysis which has received least attention is the delimitation of character states. He added that, usually, there was little justification for their delimitation. The establishment of character states for the anatomical features described in the course of this work and the

difficulties associated with defining them are illustrated by a consideration of nodal anatomy and isolateral leaves.

Nodal Anatomy

At different taxonomic levels, nodal characteristics have been found to be significant by, among others, Sinnott (1914), Bailey and Howard (1941), Singh (1972) and Baas (1975).

Sinnott (1914) found *Ilex* to be a genus with both unilacunar and trilacunar nodes and this was confirmed by Baas (1975) who added three forms to the known range of structures in the genus, describing species in which lateral traces entered the stele at much lower levels than the median trace, several traces departed from the median leaf gap and lateral traces supplied the stipules only. The last condition was similar to that described in some taxa in the Euphorbiaceae (Singh, 1972). Bailey and Howard (1941) found that within the Icacinoideae, some genera had trilacunar nodes and others unilacunar. Within the Icacineae, there were genera in each category. Trilacunar Icacineae were erect. In the Iodeae, Sarcostigmateae and Phytocrenae, most of which were climbers, nodes were only unilacunar. Genera in the Icacineae with unilacunar nodes were taken to represent a transitional stage between the trilacunar Icacineae and other tribes.

Larson (1984) has said that the number of gaps at each node varied greatly among plants of a species and nodes on a plant. He suggested that the number of leaf gaps usually increased with size and age. Having examined five hundred nodes from positions in sun and shade and from vigorous and short shoots, Howard (1979) found no significant variation in any instance. Sinnott (1914) reported a stable rather than a variable situation and suggested that the three lacunae, three trace condition was the most prevalent in *Hakea*. In this study, nodes were examined in:

41 specimens of 25 species of *Grevillea* and in 5 subspecies of 4 of these species.

47 specimens of 31 species of *Hakea*.

8 specimens of 5 species of *Persoonia* and in 1 variety of 1 of these species.

1 specimen of *Finschia chloroxantha*.

1 specimen of *Garnieria spathulifolia*.

In *Grevillea sparsiflora*, *G. acuaria* and *G. pauciflora*, within a single gap, 2 small bundles, associated with the vascular supply to the axillary bud, alternated with 3 leaf traces (Fig. 8). In each specimen, several nodes were similar. Three specimens of *G. acuaria* were examined. The three species shared other anatomical features and are regarded as a natural group by taxonomists. It is suggested that this form of nodal structure might be established as a character state in the Grevilleeae.

In 37 specimens of 24 species of *Hakea* and 39 specimens of 23 species of *Grevillea*, nodes had three lacunae and three traces. The three lacunar, three trace condition has been recognised in *Hakea* (Sinnott, 1914; Howard, 1979) and in Proteaceae by Venkata-Rao (1971). Although its stability can be only hypothetical, it should be a second character state in Grevilleeae.

In a single specimen of *G. insignis* there were four lacunae and four traces. In *G. glauca*, in the position of each lateral trace, xylem was modified in two adjacent stelar bundles which combined to form one trace before leaving the stele. In a second node, there were two bundles in each lateral position. On one side, tissues combined outside the stele, within the cortex. On the other, bundles were separate to the leaf base.

Different numbers of traces were seen in ten specimens of *Hakea* (Table 7). In second specimens of *H. trineura* and *H. elliptica*, nodes had

three lacunae and three traces. In two specimens of *H. brownii* and *H. platysperma*, there were additional traces but their distribution was different.

Because, there was variation within species, the taxonomic value of these observations must be questioned but, if many specimens were studied and only some species exhibited variability, would this variability be admissible as a character state for taxonomic analysis?

Too few specimens of *Persoonia* were studied for useful comparisons of nodal anatomy. The occurrence of unilacunar nodes and nodes with a single lacuna and three traces, as well as trilacunar nodes with three traces showed diversity in this character in this genus.

The phylogenetic significance of nodal characteristics has been considered by many authors (e.g. Sinnott, 1914; Swamy and Bailey, 1949; Marsden and Bailey, 1955; Takhtajan, 1969; Venkata-Rao, 1971). The development of cladistic methodology has resulted in an increased interest in characters and character states and their plesiomorphic or apomorphic status.

In *Finschia chloroxantha*, stelar bundles on either side of the median leaf trace contributed to the vascularisation of the leaf base. Outside the stele, their orientation was changed and, in the midrib, they were inverted. Accepting *Grevillea robusta* as basal in *Grevillea*, taxonomists consider *Finschia* to be primitive within the Grevilleeae. It might be reasonable to propose the hypothesis that, in the node, in Grevilleeae, in the plesiomorphic condition, there were three traces within the median leaf gap and that the three lacunar, three trace node was achieved by a loss of traces or a fusing of tissues. In *Finschia*, in the lateral position, the fusing of stelar bundles within the stele or outside it, might support this argument and, even, offer evidence for the occurrence of extra bundles in the lateral positions in a multi lacunar node in primitive Grevilleeae.

Using the reasoning of Sinnott (1914), the hypothesis could be extended to suggest that unilacunar nodes were developed from the

trilacunar type by the elimination of two gaps or by the closing together of those which were originally separate.

These proposals might seem plausible until it is remembered that *Hakea* is derived in the Grevilleeae and nodes in *Hakea* showed more variation and more specimens had extra nodal bundles. There were no species of *Hakea* with unilacunar nodes.

In many taxa, the nodal structure of cotyledons is different from that of mature foliage leaves (e.g. Bailey, 1956; Dickison, 1969; Sugiyama, 1976). Neubauer (1991) has described the vascularisation of cotyledons in 45 species of the Proteaceae including six species of *Grevillea* and nine species of *Hakea*. In all the species, the two cotyledons were supplied by six bundles. Two traces from a single lacuna were associated with each cotyledon and there were two split laterals. Variations in nodal structure have been reported in seedling leaves (e.g. Sugiyama, 1976; Swamy and Bailey, 1949; Slade, 1952). Many species in the Proteaceae have morphologically distinct juvenile leaves. Studies of seedlings might provide useful information for defining and ordering character states.

Until more species and more specimens have been studied and suitable out groups considered, it is not possible to order character states in the nodal characteristics of the Grevilleeae.

Leaf traces often branched near the abscission layer or within the leaf base. Hare (1944) suggested that the apparent complexity of many petioles was due to the presence of additional minor vascular strands supplementing those of the main system. The network of dividing and merging vascular tissues in the lower leaf base was rarely symmetrical and there were differences within specimens and species. It must follow that these features had no taxonomic value.

At higher levels, the pattern of vascularisation was more stable. In some species, there were inversely orientated vascular bundles. Some

occurred in only a small part of the leaf base. Others persisted at higher levels and, in some cases, were a conspicuous feature in the leaf.

In *Finschia chloroxantha* inversely orientated bundles which were continuous with stelar bundles in the node were seen in the petiole and, particularly in one specimen (NGF 10358), in the midrib. In the second specimen (NGF 9123) adaxial vascular tissues in the midrib were more diffuse (Figs. 111, 114, 115, 118).

In *Hakea brownii* and *H. baxteri*, small bundles which separated from the stele in the median position, above the leaf trace, were continuous between the stem and the leaf where they were inverted and towards the adaxial side.

Probably the inverted bundles in *Finschia chloroxantha*, *Hakea brownii* and *H. baxteri* are established features and have taxonomic significance.

In *Grevillea pyramidalis*, *G. dimidiata* and *G. mimosoides* and in *Hakea pandanicarpa* and *H. pandanicarpa* ssp. *crassifolia* nodes had three lacunae and three traces. Changes in the orientation of vascular tissues which were seen towards the distal end of the leaf base were associated with changes in the distribution of vascular bundles in the radially elongated leaf base and laterally flattened leaf blade. The feature was similar in the five taxa and, when additional specimens were available for examination, it showed no within species variation.

In *Grevillea wickhamii*, inverted bundles were seen in the upper part of the petiole and were continuous between the petiole and the midrib.

In another eight species of *Hakea* and three species of *Grevillea* inverted bundles occurred in only a small part of the leaf base, especially towards the adaxial side. Where specimens were available for examination, the feature showed no within species variation. Particularly when bundles

were numerous, for example in *Hakea laurina* and *H. hookeriana*, it was difficult to believe that they occurred by chance.

In studying the node and leaf base, it was necessary to consider the three dimensional structure. Traces which left the stele at different levels and inverted bundles which occurred in different parts of the leaf base might have been overlooked in a single section.

Even though the whole structure was studied, it was described at four arbitrary levels, at the node, in the leaf base, at the distal end of the leaf base and at the level of transition from leaf base to leaf. In setting character states for analysis, the same structure might be given significance as a feature in the node, petiole and leaf. Eventually, it might be better to consider character states which describe the continuum.

Petiole anatomy, based on descriptions of the distal region has been found to be reliable (e.g. Hare, 1944; Metcalfe and Chalk, 1950; Stern *et al.*, 1970).

In *Persoonia elliptica*, *P. marginata* and *P. rufiflora*, vascular tissues were in a continuous arc (Fig. 125) and there was merging of fibres associated with them (Figs. 125, 126). In *P. hirsuta* there was a single vascular bundle and, on one side of it, there was a separate group of vascular tissues. In other species of *Persoonia*, in *Garnieria spathulifolia* and in most species of *Grevillea* and *Hakea*, there was an arc of three main bundles, sometimes with an additional small bundle between the central bundle and the lateral bundle and/or a small bundle outside the lateral bundle towards the margin. The structure at the distal end of the petiole was not useful in distinguishing genera or, in most cases, species.

In some species of *Hakea* and *Grevillea* there was an arc of more than five large bundles of similar size (Fig. 82). There was variation within species and overlap among species but, in both genera, it was possible to

define two character states to separate these species and those with the more usual pattern of tissues in the distal end of the petiole.

In *G. pyramidalis*, *G. mimosoides*, *G. dimidiata*, *G. nematophyll*, *Hakea pandanicarpa*, *H. pandanicarpa* ssp. *crassifolia* and *H. clavata* the transition from leaf base to leaf blade was exceptional. The extension of the leaf base was in the radial plane and the leaf blade was laterally flattened (Figs. 19, 84). This distinguished these taxa within each genus and pointed to a relationship between the genera.

Isolateral leaves

In *Persoonia*, *Hakea* and *Grevillea* some leaves were isolateral. McGillivray (1993) described species of *Grevillea* which had unifacial leaves. He suggested that the bulk of the leaf tissue was derived from the midrib and that the leaf blade was reduced to a small extension on the adaxial side of the midrib. He added that, although the leaves and lobes of *G. nematophylla* were usually rounded in transverse section, their structure was homologous to the unifacial pattern. The leaves which McGillivray described as unifacial are those in which there was a radial extension of the leaf base in the transition to the laterally flattened leaf blade. In the specimens examined, there were no noticeable extensions on the edges of the adaxial side of the leaf base which remained almost unchanged or, even, was slightly compressed (Fig. 19). In essence, McGillivray's interpretation of the structure was correct but he did not comment on dimensional changes or the lateral flattening of the leaf blade. The structure of the leaf was isolateral (sensu Metcalfe and Chalk, 1950; Esau, 1965). At the margins, tissue patterns were different. At one, there was a single large bundle which was continuous with the median leaf trace, at the other, there were small bundles. Palisade was well developed on both sides of the leaf. Within the central parenchyma, the main vascular bundles were in a double row.

Phloem was towards the palisade (Figs. 50-55). *G. nematophylla* was similar in structure but there were only small changes in the dimensions of the leaf bases in the transition to the linear-terete leaves (Fig. 21).

Plants with unifacial leaves (sensu McGillivray, 1993) were grouped together in Group 8 in the classification proposed by McGilivray (1993). Among other taxa from this group which were examined, two had isolateral leaves and two linear terete leaves. In *G. biformis* which was reduced by McGillivray to *G. integrifolia* ssp. *biformis*, the adaxial surface did not expand during transition from the leaf base to leaf. There were increases in leaf tissues and in the number of vascular bundles and, at a short distance above the base, the leaf was rounded and ridged. Opposite a large central vascular bundle which was continuous with the median leaf trace, a small part of the leaf represented the adaxial surface. On either side of it, there was a small bundle in which tissues were turned through ninety degrees. At lower levels, these bundles were the lateral bundles in the leaf base (Figs. 15-18). Superficially, these leaves were very different from the species with radially extended leaf bases but it could be argued that differences are only spatial and that the structures are homologous.

The structure of *G. didymobotrya* was similar to *G. biformis*. *G. integrifolia* and *G. polybotrya*, *G. glauca*, *G. wickhamii*, *G. insignis* and *G. heliosperma* were broad leaved species with isolateral leaves. In these taxa, patterns of expansion in the leaf base or the arrangement of tissues within the leaf gave no information about the derivation of the leaf form.

In *Hakea*, all the species had isolateral leaves. *H. pandanicarpa* and *H. pandanicarpa* ssp. *crassifolia* were similar to the unifacial leaves described by McGillivray. In the taxonomic groupings proposed by Barker, Barker and Haegi (Barker, 1990), the species were placed in the Obliqua Group of Subdivision 3 of the genus. This Group and *H. arborea* and *H.*

persiehana had many features in common with each other and with some species in Group 8 of *Grevillea*.

Broad leaved species in Subsection 2 of the genus *Hakea* shared anatomical characteristics which illustrated the close relationships among them and distinguished them from Groups in Subdivision 3 but, at present, there is no anatomical basis on which to judge relationships between the two Groups or, even, the homology of the leaf structures of the species within them.

In *Hakea*, there are may species with terete leaves. Some terete leaves have a flattened or grooved abaxial surface (Fig. 91). This form might suggest that the abaxial surface has been reduced. If this is so, the leaves illustrate another route for the development of terete leaves.

Three specimens of *Persoonia rufiflora* were studied and, in transverse sections, leaf shapes were different. The changes in the leaf shape were associated with a reduction in the abaxial surface (Figs. 128, 129). One species of *Persoonia* examined had nearly terete leaves in which there was a deep abaxial groove (Fig. 41). This structure suggested that the abaxial surface had been greatly reduced in the formation of a terete leaf.

Many species of *Persoonia* had flat isolateral leaves and, as in many other taxa, it was not possible to trace the development of the form.

It is possible that studies of juvenile leaves will help to solve some of these problems. It might be necessary to study the ontogeny of the leaves to obtain more information. Until it is possible to decide whether the leaves in the different taxa are homologous, it will be difficult to establish character states and any comparison can only be tentative.

In systematic anatomy and in cladistic analyses characters are compared. A consideration of isolateral and terete leaves in the Proteaceae has shown that it is not always easy to be certain that structures are homologous.

When character states are established, they should be discrete. It is not difficult to recognise isolateral or dorsiventral leaves but when is a leaf weakly isolateral or weakly dorsiventral? Many authors have reported variations in palisade amounts particularly in conditions of sun and shade or in extreme climates (Turner, 1995; Shields, 1950 and 1951; Transeau, 1904). In some taxa, the number of rows of palisade cells might appear to be significant but this character state can be unstable. Among several of the specimens examined, there was within species variation. Stevens (1991) has said that qualitative characters are essentially quantitative and anatomists know that character states are not always easy to define.

Absence of evidence is not evidence of absence and more attention should be given to present or absent character states. In the Princes Risborough punched card key for wood identification (Brazier and Franklin, 1961), crystals cannot be used as a negative character and, probably, all anatomists should be similarly cautious. Whilst crystals in the leaves in Subsection 2 of *Hakea* were well developed and an obvious feature, in *Grevillea*, crystals were extremely small and weakly birefringent. Silica posed similar difficulties and it was not possible to decide whether small mineral deposits in *Persoonia laurina* were silica. The development of ergastic materials and, also, of sclereids can be affected by the environment and the age of the plant. Whilst large columnar sclereids and sclereids in the central mesophyll were well developed in the leaves of *Hakea*, in *Grevillea* only occasional palisade cells branched at their limits and had thick, well pitted walls. If this feature regularly occurred, it would have taxonomic value. Simple isodiametric sclereids in the cortex or pith seemed to be a particularly unreliable feature; there was within species variation among three specimens of *G. sericea* (Figs. 5 and 6). Character states which describe sclereids are difficult to define. An absence of sclereids cannot be safely used and although much has been written about these cells (e.g. Das, 1977;

Rao, 1991) there is still controversy about an appropriate terminology (Baas, 1993).

When character states are difficult to define, there is a temptation to add more to describe intermediate states, but some useful programs, especially those which have been written for nucleotide sequencing, will accept only four character states.

Many of the difficulties experienced in establishing character states for the taxa to be analysed will occur again in describing out groups. In studying the node-leaf continuum in the traditional way, features were described at several levels. Three different views of the same structure were three characters which, in analysis, gave nodal anatomy added weight.

Even more difficulties are encountered when character states must be polarised. This was true of many character states among the taxa examined and was well illustrated by a consideration of nodal anatomy. If the pleiomorpohic or apomorphic status of character states cannot be decided, analyses can be made with unordered data.

Like the tissues in many small vascular bundles in the Proteaceae, character states are not always precisely delimited and orientated.

Many of the Proteaceae are strongly xeromorphic. Fahn and Cutler (1992) listed 18 xeromorphic characters and, based on a sample of 71 species known to grow in arid and semi arid conditions, calculated the percentage of species possessing each feature. Of the 18 characters, 15 occurred in the species studied and 9 were among 25 characters used in a preliminary cladistic analysis of the Grevilleeae. Results showed a high degree of homoplasy which might be associated with xeromorphy within the tribe.

The increased interest in cladistic methodology has encouraged more careful consideration of features evaluated in taxonomy and systematic anatomy. There would be an advantage in compiling a handbook for

characters and character states on the stem-node-leaf continuum. Stevens (1991) has suggested that explicit justification for the delimitation of character states should be given as a matter of course in all phylogenetic studies.

SUMMARY

The anatomy of leaves has been described in 91 species in the Grevilleeae and 15 species in Persooniinae and the stem-node-leaf continuum in 57 species in the Grevilleeae and 6 species in the Persooniinae.

Reliable descriptions are necessary before taxa can be compared. Anatomical features have been discussed in the context of taxonomic relationships in genera and at a higher level.

Characters and character states have been critically considered. It has been possible to offer guidance to taxonomists particularly concerning the homology of leaf forms.

A preliminary cladistic analysis has been made.

CONCLUSIONS

A major reason for undertaking this work was to provide anatomical descriptions of species in the Grevilleeae and Persooniinae. This has been done.

These data might be used for further analyses of relationships within the Proteaceae but, before these are begun, careful evaluation of characters and character states is necessary.

It was hoped that the results of this work would be useful to taxonomists revising genera. An excellent collaboration has developed between Durham and Australian botanists.

In *Hakea*, anatomical features closely support the groupings proposed by Barker, Barker and Haegi (Barker, 1990).

In *Grevillea*, anatomical characteristics support several natural groups established by McGillivray (1993) and Makinson. Among more than 250 species there is great diversity in external morphology and in anatomical characters within the genus. Much work remains to be done and our collaboration will be enthusiastically continued.

In *Persoonia* more species and specimens must be examined.

"There is a life time's work in the anatomy of the Proteaceae"
(Dr. A.S. George, personal communication to Dr. D.F. Cutler,
October, 1987).

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Appendix 1
Specimens examined.

1: STEM 2: NODE 3: LEAF BASE 4: CENTRE LEAF 5: LEAF MARGIN 6: LEAF TIP

Species	Collector	Location	Regions examined
		GREVILLEEAE	
		Grevillea	
		Group 1	
Group 1.1			
G. pteridifolia Knight	R.F. Thorne & W.T. James 21170	Some miles West of Mareeba	4, 5,6
	Hoogland 8487	3 miles East of Mareeba, Atherton Table-Lands, Cook District	4,5,6
	H.S. McKee 9237	5 miles North West of Dimbulah	4,5,6,
G. banksii R.Br.	N.H. Speck 1726	14.3 miles North of Toorilla Homestead, Port Curtis District, Queensland	4,5,6
Group 1.2			
1.2.1.1. *G. laurifolia* Sieb.	E.F. Constable N.S.W. 5273	Blackheath	3,4,5,6
1.2.1.5 *G. ilicifolia* (R.Br.) R.Br. *G. repens* F. Muel. ex Meisn.	Melville 1096 Foreman 1901	Big Desert	4,5,6 3,4,5,6

1.2.2 *G. ramosissima* Meisn.	McGillivray 3150 & Coveny	Eastern side of Worrumba Range N.S.W. North East of Grenfell. Alt. 600 m.	1,2,3,4,5,6
		Group 2	
Group 2.1			
2.1.1.1.1 *G. mucronulata* R. Br.	T. & J. Whaite 3358	Holbrook Castle. 5 miles South of Holbrook	1,2,3,4,5,6
	Coveny 9514	Woronora Dam catchment area. 6.5 miles North North West of Darkes Forest	1,2,3,4,5,6
2.1.1.2 *G. saccata* Benth.	Holotype. Kew. Kew negative 223b		1,2,3,4,5,6
	McGillivray 3277 & George	18 km. from Dandaragan on road to Badgingarra	1,2,3,4,5,6
2.1.2 *G. occidentalis* R. Br.	Flora Australiensis Drummond 270		1,2,3,4,5,6
	Kew no. H973/80 434	Western Australia	1,2,3,4,5,6
G. buxifolia (Sm.) R. Br.	L.A.S. Johnson & E.F. Constable. Nat. Herb. N.S.W. 48295	South of Putty (at 55 miles by road from Windsor)	1,2,3,4,5,6

2.2.1.1			
G. victoriae F. Muell.	Herb. Chas. Walker		3,4,5,6
	P. Darbyshire 70	Between Bull's Head and Mount Franklin, Brindabella Range	3,4,5,6
	C.J. Everist	Myall Park, 4 miles North West of Glenmorgan	3,4,5,6
2.2.1.2			
**G. speciosa* (Knight) McGillivray s. str. collected as *G. punicea* R. Br.	Flora Australiensis		3,4,5,6
collected as *G. punicea* R. Br. var. *crassifolia* A.A. Hamilt.	E.F. Constable Nat. Herb. N.S.W. 19368	Mangrove Mountain. West of Gosford, N.S.W.	1,2,3,4,5,6
**G. speciosa* (Knight) McGillivray ssp. *dimorpha* (F. Muell.) McGillivray	Cultivated by E. Ashby	Blackwood, S. Australia B	3,4,5,6
	Cultivated by E. Ashby	Blackwood, S. Australia A	1,2,3,4,5,6
**G. speciosa* (Knight) McGillivray ssp. *oleoides* (Sieber ex Schultes et Schultes f.) McGillivray	F.H. Sikes 1905 No. 101 Kew no. H973/80 460		1,2,3,4,5,6 3,4,5,6
G. sericea (Sm.) R. Br.	L.A.S. Johnson Nat. Herb. N.S.W. 17828	Howel's Mountain, South West of Singleton, N.S.W.	1,2,3,4,5,6
	E.F. Constable Nat. Herb. N.S.W. 18628	Berowra (Hornsby to Hawkesbury River, N.S.W.	1,2,3,4,5,6
	C.E. Hubbard Flora of N.S.W. 8504	National Park, Near Sydney	1,2,3,4,5,6

G. linearifolia (Cav.) Druse	L.A.S. Johnson Nat. Herb. N.S.W. 18004	Silent Grove to Torrington, N.S.W.	3,4,5,6
	Tindale 2027 Nat. Herb. N.S.W.	Angourie	3,4,5,6,
	Rodway Flora of N.S.W.	Cambewarre near Nowra, N.S.W.	1,2,3,4,5,6
G. australis R. Br.	A. Strid 22016	Victorian Alps. south West side of Mt. Hotham	1,2,3,4,5,6
G. australis R. Br. var. *montana* Hook f.	T.E. Burns 5302/9013. Kew no. H973/80 146. Flora of Tasmania	Plateau of Mt. Barrow	1,2,3,4,5,6
2.2.2. *G. sparsiflora* F. Muell.	L.A.S. Johnson 2151	Coast near Baxter memorial. 42 km by road South, South East of Caiguna, W.A.	1,2,3,4,5,6
G. acuaria F. Muell. ex. Benth.	D.F. Blaxell DFB/W75/45	159 km. East of Hyden	1,2,3,4,5,6
	Melville & George 71.442	52.3 miles East of Norseman on Nullarbor Road	1,2,3,4,5,6
	M.D. Tindale 3756	12.3 miles East of Lake Grace Post Office on road to Newdegate	1,2,3,4,5,6
G. pauciflora R. Br. ssp. *pauciflora*	A.S. George 13107	Turn off of Memory Cove from road to Spalding Cove, South of Port Lincoln, S.A.	1,2,3,4,5,6

		Group 5	
G. pulchella (R. Br.) Meisn.	W.V. Fitzgerald Nat. Herb. N.S.W. 27001	Marbellup, Western Australia	1,2,3,4,5,6
		Group 7	
G. robusta A. Cunn.	C.E. Hubbard 5416	University grounds, Brisbane	3,4,5,6
G. meisneri Montr.	Vieillard 3092	New Caledonia	3,4,5,6
G. brachystachya Meisn.	Drummond II 319	Swan River	1,2,3,4,5,6
G. *papuana Meisn.*	Henty. Isgar & Galore NGF 38967	Oksapmin, Telefomin subdist. West Sepik District, TNG	3,4,5,6
G. glauca Knight	S.T. Blake 9497	Mareeba 16° 5' S 145° 2' E	1,2,3,4,5,6
G. striata R. Br.	Flora Australiensis		3,4,5,6
	Helen Lee	20 km South of Clifton Hills H.S. Budsville Track, S.A.	1,2,3,4,5,6
		Group 8	
G. nematophylla F. Muell.	N. Forde 411	15 miles South of Emu, S.A.	1,2,3,4,5,6
	D.E. Simon 2701. ADW No. 26518	30 miles North West of Kenmore Park Station, near Ernabella, S.A.	1,2,3,4,5,6

G. polybotrya Meisn.	Pritzel. Kew no. H973/80 243	Between Moore and Murchison Rivers	1,2,3,4,5,6
**G. integrifolia* (Endl.) Meisn.	Kew no. H973/80 288		1,2,3,4,5,6
	Tindale 207 & Maslin Nat. Herb. N.S.W. 119109	7 miles East of Newdegate on the highway to Lake King, W.A.	1,2,3,4,5,6
**G. biformis* Meisn.	W.A. Tindale 28 & Bennett Nat. Herb. N.S.W. 119161	35.5 miles South East of Kalgoorlie on the road to Coolgardie, W.A.	3,4,5,6
	A. Strid 20757	Kalbarri National Park c. 8 km. North East of Kalbarri Lat. 27° 41' S, Long 114° 31' E	3,4,5,6
G. didymobotrya Meisn.	Strid 21056	35.5 km. from Ravensthorpe on road to Lake King	1,2,3,4,5,6
	Kelso 206	Bullabulling, Coolgardie District	1,2,3,4,5,6
G. pyramidalis A. Cunn. ex R. Br.	McGillivray 3867	24 km. East from Gibb River Station-Drysdale River Station. Lat. 6° 05' S, Long. 126° 45' E	3,4,5,6
	McGillivray 3769	1.7 miles South of Cockatoo Springs on the road from Kununurra. Lat. 15° 57' S, Long. 128° 57' E.	3,4,5,6
G. mimosoides R. Br.	Evans 3356	Stuart Highway, Tindal turn-off. N.T. Herbarium, Darwin	3,4,5,6
	N.H. Speck. CSIRO Canberra 4843	60 miles South of Kaumburo Mission, W.A.	1,2,3,4,5,6

G. dimidiata F. Muell.	R. Helms. Kew no. H1173/77 154	East Kimberley District	3,4,5,6
	R.A. Perry 2073. CSIRO Canberra	40 miles South West of Birrimbah Out Station N.T.	3,4,5,6
		Group 9	
G. trifida Meisn.	Dr A. Morrison. Herb. Hort. Reg. Bot. Edin. Kew no. H973/80 233	Margaret River, W.A.	1,2,3,4,5,6
G. vestita (Endl.) Meisn.	Nat. Herb. N.S.W. 17890	Dripstone (cultivated)	4,5,6
G. paniculata Meisn.	E. Pritzel. Plantae Australis occidentalis. Kew no. H973/30 311	District of Victoria VIII	4,5,6
		Group 11	
G. wickhamii Meisn.	Carolin 6200	South end of Schwerin Mural Crescent	3,4,5,6
	Latz 7160	Cox River	3,4,5,6
		Group 12	
G. insignis Kippist ex. Meisn.	A.S. George 343	Newdegate	1,2,3,4,5,6
		Group 13	
G. patentiloba F. Muell.	Melville & George 71.273	6 miles East of Ravensthorpe on Esperance Road	4,5

Group 19

G. hakeoides Meisn.	Flora Australiensis. Kew no. H973/80 187		1,2,3,4,5,6
	Alex Morrison. Flora of Western Australia	Ebbans Wall. Epsom	4,5,6
**G. hakeoides* subsp. *commutata* (F. Muell.) McGillivray	A. Strid. Flora Western Australia no. 20747.	Kalbarri National Park. Lat. 27° 45' S. Long. 114° 08' E	1,2,3,4,5,6
	McGillivray 3329 & George	6 km. North of Binnu (at 371 mile peg) North West Coastal Highway. Lat. 28° 00' S. Long. 114° 40' E.	1,2,3,4,5,6
G. diversifolia Meisn.	Alex. Morrison. No. 8532 24/12/98	Midland Junction, Swan River	1,2,3
	Kew no. H973/80 175		4,5

Group 21

G. heliosperma R. Br.	McGillivray & Dunlop 3914	31.5 km. by road North of Cooper Creek on the road from Denpelli to Morganella	4
	McGillivray 3891	1.5 km. North West of Maggie Creek on the road from Kununurra to Wyndham	4,5,6
	S. T. Blake 16979	Near Beatrice Hill	4,5,6

G. bracteosa Meisn.	Drummond. Flora Australiensis. Kew no. H/973/80 197	1,2,3,4,5,6

*These species are the subject of some controversy among taxonomists. They have been considered in the discussion.

Species	Collector	Location	Regions examined
		Hakea	
		Subdivision 1 (W.R. Barker)	
Needlewoods			
Group A			
H. lissosperma R. Br.	N.T. Burbridge 3255	Lake Dobson, Tasmania.	4, 5
H. "Wallum" W.R.Barker	WRB 5626		4, 5, 6
Group B			
H. leucoptera R.Br.	WRB 5083		1, 2, 3, 4, 5
	Lee	South Australia, 17 km E of Cameron's	1, 2, 3, 4, 5
	Lee	Corner, Sturt National Park, N.S.W.	1, 2, 3, 4, 5
H. tephrosperma R.Br.	Pickard 1251 & Campbell	33.8 km E of Roto	1, 2, 3, 4, 5
	Constable. Nat. Herb., N.W.S. 39956.	Willow Point, 55 mls. N. of Wentworth	1, 4, 5
	WRB 5693		3, 4, 5
Group C			
H. nodosa R.Br.	Lee	Nr Penola, South Australia	1, 2, 3, 4, 5) 4 collections,
	Lee	Grampians	1, 2, 3, 4, 5) North, South, East, West

Group E			
H. macraeana F.Muell.	WRB 5682		1, 3, 4, 5, 6
H. "Dorrigo" W.R.Barker	WRB 5634		1, 3, 4, 5, 6
H. sericea H.A.Schroder	WRB 5686		4, 5, 6
Group G			
H. bakeriana F.Muell. & Maiden	WRB 5658		4, 5
Corkwoods			
H. ivoryi F.M.Bailey	WRB 5589		3, 4, 5, 6
	WRB 5590		1, 2, 3, 4, 5, 6
H. suberea S.Moore	Nelson 1507	Stuart Highway, 52 miles N. of Alice Springs	4, 5
H. fraseri R.Br.	WRB 5597		1, 3, 4, 5, 6
Arborescens-salicifolia Group			
H. arborescens R.Br.	WRB 5543		1, 2, 3, 4, 5, 6
	R.H. Cambage 3931	Normanton, Gulf of Carpentaria, Queensland	1, 2, 3, 4, 5
H. persiehana F.Muell.	WRB 5565		1, 2, 3, 4, 5, 6

H. salicifolia (Vent.) B.L.Burtt var *salicifolia*	WRB 5638		1, 2, 3, 4, 5, 6
	WRB 5687		1, 3, 4, 5
	c/Stuart/Mueller. Kew No: H1128/86 317	New England	1, 2, 3, 4, 5
H. florulenta Meisn.	WRB 5629		3, 4, 5, 6
Sedus incertae			
H. trineura F.Muell.	WRB 5654		1, 2, 3, 4, 5, 6
	WRB 5653		1, 2, 3, 4, 5, 6

Subdivison 2 (L. Haegi)

Laurina Group			
H. laurina R.Br.	WRB 5082		1, 3, 4, 5
Undulata Group			
H. undulata R.Br.	R. Coveny 8025	Parkerville, W.A.	4, 5
	R.B.G. Sydney 853783	Sydney Botanic Gardens	4, 5, 6
H. neurophylla Meisn.	Cranbourne Gdns.	Cranbourne Gardens., Royal Botanic Gardens, Melbourne	3, 4, 5, 6

H. loranthifolia Meisn.	S. Patrick 120	Clackline to Toodyay Road, 10.5 km N. of junction with Great Eastern Highway	1, 2, 3, 4, 5, 6
	Drummond. Kew no. H1128/86 448	Swan River	1, 2, 3, 4, 5, 6
H. elliptica (J.E. Smith) R.Br.	R. Brown. Iter. Australiensis 1802-5. No. 3367. Kew no. H1128/86 421	No information	1, 2, 3, 4, 5, 6
	J. Backhouse. Kew no. H1128/86 422	King George's Sound	1, 2, 3, 4, 5, 6
H. ambigua Meisn.	Kew no. H1128/86 500	No information	1, 2, 3, 4, 5, 6
H. falcata R.Br.	Drummond Ser. 15. Kew no. H1128/86 462	Swan River	1, 2, 3, 4, 5, 6
H. dactyloides Cav.	E.F. Constable. Nat. Herb., N.S.W. 32128	Green Cape, Disaster Bay	3, 4, 5
	E.F. Constable. Nat. Herb., N.S.W. 32129	Green Cape, Disaster Bay	4, 5
	WRB 5630		2, 3, 4, 5, 6
	WRB 5617		1, 2, 3, 4, 5, 6
	WRB 5665		3, 4, 5
	WRB 5627		1, 3, 4, 5
	WRB 5661		3, 4, 5

Ulcinia Group

H. muelleriana J. M. Black	Lee	Nr Penola, South Australia	1, 2, 3, 4, 5. 4 collections North, South, East, West
H. plurinervia F.Muell. ex . Benth.	R.W. Johnson 825	18 miles from Cracow, Taroom - Cracow Road	3, 4, 5
	L.J. Brass 33659	Atherton, Queensland	
Sulcata Group			
H. sulcata R.Br.	Coveny 8106	Boundary Road, Wattle Grove, W.A.	4, 5

Subdivision 3 (R.M. Barker)

Trifurcata Group			
H. lasiantha R.Br.	Drummond. Kew no. H1128/86 90	No locality	3, 4, 5
	Kew no. H1128/86 94. No name	King George's Sound	3, 4, 5
	Herbarium Hookerianum. Kew no. H1128/86 92	King George's Sound	1, 2, 3, 4, 5, 6
	Melville 4443	Many Peaks, W.A.	3, 4, 5
Microcarpa Group			
H. microcarpa R.Br.	WRB 5615		1, 2, 3, 4, 5, 6
H. clavata Labill.	Melville & George 71.324	Mount Le Grand, Cape Le Grand National Park	4, 5

	Strid 22500	Cape Le Grand National Park, by Thistle Cove	1, 2, 3, 4, 5, 6
Species of Uncertain Affinity			
H. linearis R.Br.	Drummond 335	S.W. Australia	1, 2, 3, 4, 5
	E. Pritzer	S.W. Plantagenent	3, 4, 5
H. eriantha R.Br.	P.R.H. St. John	Mueller River, Victoria	1, 3, 4, 5
	R.T. Baker	Monga	3, 4, 5
	T. James 513 & Taylor	Nungatta Mountain ca. 48 km SWW of Eden	1, 3, 4, 5
	WRB 5623		1, 2, 3, 4, 5, 6
	R.B.G. Sydney 13385	R.B.G. Sydney	1, 2, 3, 4, 5, 6
Rostrata Group			
H. rostrata F.Muell.	WRB 5488		1, 2, 3, 4, 5, 6
Verrucosa Group			
H. verrucosa F.Muell.	WRB 5093		1, 2, 3, 4, 5, 6
Obliqua Group			
H. obliqua R.Br.	WRB 5430		1, 2, 3, 4, 5, 6

H. baxteri R.Br.	Cunningham. Kew no. H1128/86 696	King George's Sound	1, 2, 3, 4, 5, 6
	Melville & George 71.114	Stirling Range N.P. North end of Red Gun Pass.	1, 2, 3, 4, 5, 6
H. brownii Meisn.	Drummond 4th coll. 296.	Swan River	1, 2, 3, 4, 5, 6
	Kew no. H1128/86 30 Kew no. H1128/86 59		1, 2, 3, 4, 5, 6
H. ceratophylla R.Br.	Cunningham 19073	Western Australia	4, 5
	W.H. Harvey. Kew no. H1128/86 120	King George's Sound	3, 4, 5
	Strid 21634	Bow River, S.W. Western Australia	1, 2, 3, 4, 5, 6
H. flabellifolia Meisn.	Drummond. Kew no. H1128/86 695	Murchison Rivers, Western Australia	1, 2, 3, 4, 5, 6
H. hookeriana Meisn.	Drummond. Kew no. H1128/86 699	S.W. Australia	1, 2, 3, 4, 5, 6
H. pandanicarpa R.Br.	Orchard 1536	Western Australia, Nr. Western border of Shire of Esperance.	1, 2, 3, 4, 5, 6
	J. M. Brown 102	Dragon Rock, Notare Reserve	1, 2, 3, 4, 5, 6
ssp. *crassifolia* (Meisn.) R.M. Barker	Drummond 293. Kew no. H1128/86 24	Swan River	1, 2, 3, 4, 5, 6
	Floral Australiensis named by Mr. Bentham. Kew no. H1128/86 25	S.W. Australia	1, 2, 3, 4, 5
H. platysperma Hook.	Melville 148	Western Australia, Bronti, 242 miles E. of Perth	1, 2, 3, 4, 5, 6
	Drummond. Kew no. H1128/86 70	Swan River	1, 2, 3, 4, 5, 6

H. adnata R.Br.	Cunningham. Kew no. H1128/86 29	King George's Sound	1, 2, 3, 4, 5, 6
H. orthorrhyncha F.Muell.	WRB 5451		1, 2, 3, 4, 5, 6

Species	Collector	Location	Regions examined
		Finschia	
F. chloroxantha Diels.	E. Grey & K.J. White. NGF 10358	Department of Agriculture, Oriomo River, Western District, TNG.	3,4,5,
	J.J. Havel. NGF 9123	Bulolo, Morobe District. Lat. 7° 10' S. Long 146° 40' E.	1,2,3,4,5,
F. rufa Warb.	Department of Forests. Lae Lae 59040	South of Manumum Village, Central District. Subdistrict Port Moresby. Lat. 9° 05' S. Long 147° 34' E.	Only a small piece from the margin of one leaf was available for examination.

Species	Collector	Location	Regions examined
		PERSOONIINAE	
		Persoonia	
		Group 1	
P. rufiflora Meisn.	Drummond 1853	Between Moore and Murchison Rivers, Western Australia	1,2,3,4,5
	Drummond Ser. 6 176	Swan River	1,2,3,4,5
	Drummond 1853	Between Moore and Murchison Rivers, Western Australia	1,2,3,4,5
		Group 2	
P. laurina Pers. subsp. *laurina*	J.L. Boorman, N.S.W. 20950	Excelsior *ca.* 25 miles South of Rylstone	3,4,5
P. laurina subsp. *leiogyna* L. Johnson & P. Weston subsp. nov.	Nat. Herb. NSW 6247 E.F. Constable	Mount Colong *ca.* 40 miles South South East of Jenolan Caves	1,3,4,5
		Group 3	
P. longifolia R. Br.	Drummond TYPE.	No loc.	3,4,5
	N.T. Burbige CSIRO 2566	Near Greenbushes, Western Australia	3,4,5

P. elliptica R. Br.	No coll.	Wilson's inlet, Oldfield, Western Australia	3,4,5
	No coll.	Ironstone - Darling Range, Parkerville, near Perth	1,4,5
		Group 4	
P. gunnii Hook f. var. *gunnii*	Lord Talbot de Malahide	Tasmania, Rosès Tier	1,2,3,4,5
P. gunnii Hook f. var. *angustifolia* Benth.	Herb. Hookerianum	Milligan. Gordon River	1,2,3,4,5
		Group 5	
P. myrtilloides Sieber. ex Schultes & Schultes, f., subsp. *myrtilloides*	Constable 5144 N.S.W. 96146	Green Gully, Glen Davis, *c.* 25 miles North of Lithgow	1,3,4,5
P. marginata A. Cunn. ex R.Br.	J.L. Boorman, N.S.W. 21275	Caper Tee	3,4,5
	Cunningham Kew neg. 2074	Cudgegong River	3,4,5
P. hirsuta Pers.	Blakely & Shiress, N.S.W. 20893	Maroota, North East of Windsor	1,2,3,4,5
P. mollis R.Br.	Weston 1267	Blue Mountains	1,2,3,4,5
		Group 6	
P. quinquenervis Hook.	Drummond, Kew neg. 2065	Swan River	3,4,5
P. hakeiformis Meisn.	Drummond, Kew Neg. 2047	South West Australia	3,4,5

P. falcata R.Br.	Specht 1147	Northern Territory. Oenpelli	3,4,5
P. saundersiana Kippist. Kipp. ex Meisn.	F.H. Vachell, N.S.W. 38550	Kellerberrin	3,4,5

Garnieria

G. spathulifolia (Brongn. & Gris) Brongn. & Gris	Herb. mus. Paris 278	No loc.	1,2,3,4,5

Appendix II.

Cladistic analysis

Using 25 characters (Table A1), a matrix was compiled for 78 taxa (Table A2). Running unordered, in Hennig '86 using the mhennig algorithm, this yielded a tree of length 142 with a consistency index (CI) of 35, on a scale of 100, and a retention index (RI) of 79. This indicated a high degree of homoplasy for the limited set of characters used. The consensus tree obtained (Fig. A1) showed a moderate degree of structure with many clades unresolved.

One of the most highly resolved groups indicated a close relationship between *Grevillea paniculata* and *G. patentiloba*.

Taxonomists would not agree with the separation of *G. paniculata* from *G. vestita*. They believe that the 2 species are closely related and place both in the highly distinctive section Manglesia (sensu Bentham 1870). Anatomically, *G. paniculata* was unlike *G. vestita*. Towards margins, *G. paniculata* had vascular bundles with well developed adaxial fibre caps but these were absent in *G. vestita* which had a secondary vein of similar abaxial/adaxial extent to the midrib on either side of the leaf. Also, *G. paniculata* had druses and acicular crystals in epidermal and mesophyll cells whilst none was seen in *G. vestita*. The form of the midrib and the distribution of the stomata were different in the 2 species. In *G. vestita* there were xylem elements on both sides of the phloem. These differences were recorded in columns 6, 10, 14, 16, 19 and 22 of the data matrix.

G. bracteosa was of unassigned affinities and had anatomical features in common with *G. paniculata*.

In *G. patentiloba*, the midrib and arrangement of tissues in the leaf were very different from *G. paniculata* and *G. bracteosa*. It has been suggested that the character state which described the midrib as a complex,

including more than a single bundle, contained too many different structures. The distribution was reasonable in the first 3 groups of *Grevillea* but, in the rest of the table, it was diffuse (C.J. Humphries, pers. comm., 1996).

G. sparsiflora and *G. acuaria* were well resolved and form a natural group but the separation of *G. pauciflora* is not agreed by taxonomists. On the anatomical evidence also, one would have expected a close relationship to have been shown. All 3 species share a distinct nodal structure which is unique among the species of *Grevillea* studied. An examination of the matrix showed which character states had influenced the position of these taxa and, as in other cases, there was much to be learned about anatomical features which are proposed for cladistic analysis.

Most species in Group 1 of *Grevillea* were grouped together in the consensus tree but were unresolved. *G. laurifolia* was artificially basal with *Finschia*. Taxonomists think that *G. laurifolia* is rightly placed in Group 1 but there were definite anatomical differences.

G. mimosoides, *G. pyramidalis* and *G. dimidiata* was a highly resolved natural group in which anatomical characters supported taxonomic opinions. The proximity of *G. nematophylla* and *Hakea clavata* is also supported by anatomical descriptions but the distancing of *H. pandanicarpa* and *H. pandanicarpa* ssp. *crassifolia* is surprising and data should be checked.

Among species of *Hakea*, there is a lack of resolution which reflects the anatomical similarities in the main Subdivisions as defined by Barker, Barker and Haegi (Barker, 1990). The occurrence of many terete leaved species in *Hakea* gave some difficulty in choosing characters for cladistic analysis.

The matrix constructed for this analysis contained far too many taxa for 25 characters. Either more characters must be evaluated or smaller groups must be studied.

From a consideration of the characters and character states used in describing leaf anatomy and in constructing a matrix and, particularly, considering those which separated *G. vestita* and *G. paniculata*, it was clear that much needed to be done in evaluating anatomical features and their variability if they were to be used in cladistic analysis.

Anatomists have lagged behind taxonomists in applying cladistic methodology, perhaps because many problems have to be solved. Cladists have much to discuss with anatomists. Anatomists have much to discuss with taxonomists and cladists.

Table A1.

Characters used in Cladistic Analysis of the Grevilleeae.

NODE

1. Nodal structure

    0: One lacuna, 3 traces.
    1: 3 lacunae, 3 traces.
    2: More than 3 lacunae and 3 traces.
    3: Structure in *Finschia*. 2 lateral leaf traces, one median leaf trace plus 4 minor bundles within the median gap.

LEAFBASE

2. Petiole or leaf base. Inverted bundles

    0: Present.
    1: Absent.

3. Vascular bundles in the distal end of the leaf base

    0: An arc of 3 main bundles, often with additional small bundles at the margins or on either side of the central bundle.
    1: An arc of 7 or more large bundles, more or less equal in size.
    2: Structure in *Finschia*. An abaxial arc of small bundles and adaxial inverted bundles.

4. Transition from leaf base to leaf blade

    0: Tangential extension.
    1: Radial extension; leaf blade laterally flattened.

LEAF

5. Leaf form

    0: Dorsiventral or weakly isolateral.
    1: Isolateral, including terete leaves.

6. Midrib

    0: Single large bundle.
    1: Complex including more than a single large bundle.

7. Abaxial fibres associated with the midrib

0: Within the mesophyll.
1: Separated from the epidermis by modified palisade or mesophyll cells.
2: Separated from the epidermis by 1-4 rows of parenchyma.
3: Separated from the epidermis by more than 4 rows of parenchyma.

8. Adaxial fibres associated with the midrib

0: Within the mesophyll.
1: Separated from the epidermis by modified palisade or mesophyll cells.
2: Separated from the epidermis by 1-4 rows of parenchyma.
3: Separated from the epidermis by more than 4 rows of parenchyma.

9. Tissue patterns at leaf margins

0: Fibres associated with a single vascular bundle close to the margin separated from the epidermis by 1-3 rows of parenchyma.
1: Palisade continuous around the margin.
2: Palisade and mesophyll tissues at the margin.
3: Rounded parenchyma cells, sometimes including fibres.

10. The occurrence of vascular bundles with well developed adaxial fibre caps separated from the epidermis by a single row of parenchyma or modified palisade

0: 1 or more bundles towards margins.
1: Several bundles between the margin and midrib.
2: Absent.

11. Adaxial palisade

0: One row.
1: More than one row.

12. Abaxial palisade

0: One row.
1: More than one row.
2: Absent or weakly developed.

13. Central mesophyll

0: Spongy.

1: Round to angular; square or rectangular.
2: Of similar shape and orientation to the palisade cells.
3: Orientated with their long axes at right angles to the leaf surface.

14. Lower order veins

0: Of similar abaxial/adaxial extent to the midrib.
1: Adaxial fibre caps extending into the modified palisade.
2: Within the mesophyll.

15. Sclereids

0: Large irregular sclereids mainly in the mesophyll, sometimes spreading into the palisade.
1: Columnar sclereids which branch and spread at their limits and cross the palisade.
2: As 1 but penetrating into the inner mesophyll where they are closely associated with vascular bundles.
3: Absent or of another form.

16. Crystals

0: Present.
1: Absent.

17. Silica bodies

0: Present.
1: Absent.

18. Stomata

0: Paracytic with a single subsidiary cell on either side of the guard cells.
1: Type 0 and 2.
2: Paracytic with 2 subsidiary cells on either side of the guard cells.

19. Distribution of stomata

0: On abaxial surface.
1: On abaxial and adaxial surfaces.
2: In abaxial grooves.

20. Subepidermal lignified parenchyma

0: Absent.
1: Present.

21. Inverted bundles in the midrib

0: Present.
1: Absent.
2: Amphivasal bundles towards the adaxial side.

22. Xylem on both sides of phloem in vascular bundles

0: Present.
1: Absent.

STEM

23. Early phellogen activity

0: Present.
1: Absent.

LEAF

24. Adaxial fibre groups not associated with vascular bundles

0: Present.
1: Absent.

25. Shape of leaf margin (Mcgillivray 1993)

0: Flat or slightly recurved.
1: Smoothly revolute.
2: Once refracted.
3: Twice refracted.

Table A2.

Data matrix for cladistic analysis of the Grevilleeae:

G. pteridifolia	ptef	11000122200201411000111 1
G. banksii	bank	11000122200201411000111 0
G. laurifolia	laur	10100122021200411000111 0
G. ilicifolia	ilic	11000122201201411000111 0
G. repens	repe	11000122020200411000111 0
G. ramosissima	rams	11000122000201411000111 0
G. mucronulata	mucr	11000022112201411000111 1
G. saccata	sacc	11000022100201411000111 0
G. occidentalis	occd	11000022220202411000111 0
G. buxifolia	buxf	11000022200201411000111 0
G. victoriae	vict	11100022221201411000111 0
G. speciosa	spec	11000022110201411000111 0
G. sericea	serc	11000022100201411000111 0
G. linearifolia	linf	11000022100201411000111 2
G. australis	aust	11000002102102411000111 01
G. australis var. *montana*	aumt	11000000121202411000111 01
G. sparsiflora	spar	01000020201202411000110 01
G. acuaria	acur	01000020100202411000110 01
G. pauciflora	pauc	010000?212020241100011101
G. pulchella	pucc	11000020221201411000111 0
G. robusta	robs	11000123220201411000111 0
G. meisneri	meis	10000123020200411000111 0
G. brachystachya	brch	11000022021201411011111 1
G. papuana	papn	11100033020210411001111 0
G. glauca	glac	21101122020030410010111 0
G. striata	strt	11100022101200411021111 00
G. nematophylla	nemt	11011000021212401000111 ?
G. polybotrya	plbt	11001000120012411010111 0
G. integrifolia	int	11001000221122411 0?011110
G. biformis	bifm	11001000120?124100?01111?
G. didymohotrya	didy	11001020120?124110?01111?
G. pyramidalis	pyrm	10111000131112401010111 ?
G. mimosoides	mims	10111000131112401110111 ?
G. dimidiata	dimd	10111000131112401110111 ?
G. trifida	trif	11000022120202411020111 0
G. paniculata	panl	11000122200202401020111 2
G. vestita	vest	11000022220200411000101 0
G. wickhamii	wick	10001122120001401010001 0
G. insignis	insg	20101122020000401000211 0
G. patentiloba	patn	11000122101202401000111 2
G. hakeoides	hakd	11001022103?0241100011111
G. hakeoides var. *commutata*	comm	11000022100202411000111 1

G. diversifolia	divf	11000022100202401001111 10
G. heliosperma	hels	11001023120030401000101 10
G. bracteosa	brct	11000022000102401000111 12
F. chloroxantha	fins	30200133321200411000011 10
H. arborescens	arbo	11?01000120012111210111 1?
H. persiehana	pers	11?01000120012111210111 1?
H. salicifolia	sali	11?01011120032211010111 1?
H. florulenta	flor	11?01021120032211210111 1?
H. trineura	trin	?1?01022020012301210111 1?
H. laurina	laur	10?01022021112001210111 1?
H. undulata	undu	11?01022020012401210111 1?
H. neurophylla	neur	11?01022021123001210111 1?
H. loranthifolia	lora	10?01022021112001210111 1?
H. elliptica	elli	?1?01022020032401210111 1?
H. ambigua	ambi	11?01022020012001210111 1?
H. falcata	falc	10?01022021112101210111 1?
H. dactyloides	dact	11?01022021112001210111 1?
H. muelleriana	muel	11?01022021112001210111 1?
H. pleurninervia	pleu	11?01022021112001210111 1?
H. sulcata	sulc	11?0102??2111240121011 11?
H. lasiantha	lasi	11?01011211122112101111?
H. microcarpa	micr	11?0? ? ? ? ? ? ? ? ? ? ? ? ?101111?
H. clavata	clav	11?1? ? ? ? ? ? ? ? ? ? ? ? ?101111?
H. linearis	line	10?01011211122112101111?
H. eriantha	eria	10?01022121122112101111?
H. rostrata	rost	11?0? ? ? ? ? ? ? ? ? ? ? ? ?101111?
H. verrucosa	verr	11?0? ? ? ? ? ? ? ? ? ? ? ? ?101111?
H. obliqua	obli	?1?01000121112112101111?
H. baxteri	baxt	?0?01000121112112101111?
H. brownii	brow	?0?01000121112112101111?
H. ceratophylla	cera	10?01000121112112101111?
H. flabellifolia	flab	?1?01000121112112101111?
H. hookeriana	hook	10?01000121112112101111?
H. pandanicarpa	pand	10?11000121112112101111?
H. pandanicarpa ssp. *crassifolia*	cras	10?11000121112112101111?
H. platysperma	plat	?1?01000121112112101111?
H. adnata	adna	11?01000121112112101111?
H. orthorrhyncha	orth	11?01000121112112101111?

Appendix III. Recipes

Formalin-Acetic-Alcohol (FAA)

Methanol, formaldehyde and glacial acetic acid were combined in the following proportions:

60% methanol	850 ml.
Commercial formaldehyde solution (40%)	100 ml.
Glacial acetic acid	50 ml.

Safranin

1 g. of safranin was dissolved in 100 ml. 50% methanol at room temperature and filtered.

Alcian Blue

1 g. of Alcian Blue was dissolved in 100 ml. distilled water at room temperature and filtered. To prevent the growth of microorganisms a crystal of thymol was added.

Phloroglucinol

1 g. of phloroglucinol was dissolved in 100 ml. of 95 per cent alcohol.

Ferric chloride

1 g. of ferric chloride was dissolved in 100 ml. of 0.1 N hydrochloric acid.