



A TAXONOMIC REVISION OF *DODONAEA* MILLER (SAPINDACEAE)
IN AUSTRALIA

by

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ABSTRACT

A revision of *Dodonaea* Miller (Sapindaceae) in Australia is presented. The classification proposed contrasts with the only other monographic work on the group by Radlkofer (1933). Sixty one species are placed in seven sections, based largely on fruit characters and leaf type. Seven new species, two subspecies and two varieties are described and several new combinations are made.

Breeding system and floral biology studies indicate the genus to be wind pollinated with high pollen : ovule ratios. Several species are dioecious and many species are shown to be polygamo-dioecious. The evolution of dioecy within the genus is discussed.

Leaf morphological variation in the *D. viscosa* complex (*D. viscosa* Jacq., *D. cuneata* Sm. and *D. angustissima* DC.) is analysed with multivariate numerical techniques. These species are inseparable in all other features. The use of an electronic digitiser in digitising the outlines of leaves and the direct use of these digitised images for calculating leaf parameters by computer is tested. The value of the digitiser for morphological data collection is demonstrated. Discriminant analyses and clustering techniques show the three species to overlap greatly with respect to leaf morphology. *D. cuneata* and *D. angustissima* are reduced to infraspecific level and five other subspecies (ssp. *viscosa*, ssp. *burmanniana* (DC.) West, ssp. *angustifolia* (L.f.) West, ssp. *mucronata* West, ssp. *spatulata* (Sm.) West) are proposed within the polymorphic *D. viscosa*.

The relationships within and the evolution and biogeography of the genus are discussed in relation to its position within Australia and on a world-wide basis. Morphological and fossil evidence suggest Sect. *Dodonaea* to be the most primitive of the genus. Members of this section appear to be relatively conservative and to have changed little morphologically since the Miocene. Several hypotheses concerning the origin of *Dodonaea* are discussed and a case is made for an Australian origin with subsequent spreading through the tropics by long-distance dispersal.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University. To the best of my knowledge and belief this thesis contains no material previously published or written by another person, except where due reference is made in the text.

Judith G. West.

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CHAPTER 1

INTRODUCTION

This revision of *Dodonaea* arose from initial taxonomic and ecological studies in the *D. viscosa* complex. Recent treatments of *Dodonaea* in Australia (e.g. Willis, 1972) or extra-Australian treatments of the *D. viscosa* group (e.g. Sherff 1945, 1947; Brizicky, 1963) have referred to the complex variation within *D. viscosa*. Problems have arisen several times in the application of names to these taxa and others closely related to *D. viscosa*. It was decided to investigate the variation within *D. viscosa* in Australia as part of a revision of the genus so that this group could be better placed in context. The revision is based on a wide range of herbarium material, supplemented by observations, including population studies, of many species in the field and glasshouse.

The only other monograph of *Dodonaea* is that of Radlkofer (1933), whose treatment has formed the basis of relationships between species for the past 40 years. Radlkofer's work suffered from the paucity and inadequacy of the material available to him. In several cases only one or two specimens of each species were studied by him. This resulted in Radlkofer adopting a relatively narrow species concept and in some cases he simply followed previous workers whose concepts were also based on very few collections.

In the last 50 years many more collections of *Dodonaea* have been made and the range of herbarium material available now is far greater than Radlkofer was able to study. Attempts to name these collections have drawn attention to the unsatisfactory nature of his classification.

1.1 MATERIALS AND METHODS

1.11 MORPHOLOGY

The macromorphology of the genus was studied using extensive herbarium collections and fresh material in the field and glasshouse.

Herbarium

Herbarium material from the following Australian herbaria (abbreviated according to Holmgren & Keuken, 1974) were examined and annotated : AD, ADW, BRI, CANB, CBG, MEL, NSW, NT, PERTH, the private herbarium of Mr Cliff Beauglehole of Portland, Victoria (cited as BEUGL). Additional material, including types, was obtained from the following herbaria : B, BM, CGE, CHR, G, K, L, P, U, W.

The types of most validly published names within the genus have been examined. Where the type was not available this is indicated in the taxonomic treatment (Chapter 7) by n.v. (non vidi) after the abbreviation of the relevant herbarium, but no indication is given in those cases in which the type has been examined.

In most cases only a selected number of specimens examined during this study are cited under the relevant taxon. In those cases in which less than 20 collections were studied all collections are cited. In all other cases the total number of collections examined for each taxon is given and usually 10 cited specimens have been selected to include the morphological and geographical variation of the taxon. The selected specimen information is given alphabetically by author, under the state or country of collection, in the following order: collector, collector's number, locality (abbreviated if necessary), date, state of specimen, herbarium and herbarium number, which is included only if there is no collector's number. Collections made during this study are

usually given as populations, rather than individuals, and include all numbers collected at that locality. Abbreviations used to indicate the state of development of specimens are as follows:

f.fl. = female flowers

m.fl. = male flowers

bisex.fl. = bisexual flowers

fr. = fruit

st. = sterile

Herbarium sheets containing a specimen in different states of development are indicated by separating the codes by a comma, while a slash indicates the collection includes more than one state of development on different specimens.

The type is cited under each valid name and is not included again in the selected specimens examined. Where lectotypification was necessary, the reasons for the selection of a particular specimen are given after the description of the relevant taxon.

Field and Glasshouse

Populations of approximately 60% of the species were studied in the field during field trips in South Australia, Western Australia, Victoria and New South Wales. Unfortunately it was not possible to do field work in north and western New South Wales, Queensland or in any part of northern Australia. The first sheets (male and female) of all population collections made during this study are housed in AD and the duplicates will be distributed to other herbaria.

Many species were grown in the glasshouse for morphological and breeding system studies. Germination tests were carried out for all species of which seed could be obtained. In total I was able to examine live material, propagated either from seed or cuttings, of 41 species (67%).

Cuticle Preparations

Cuticles were isolated from the leaves, leaflets or fruits of several species in order to examine the major indumentum types within the genus. Either dried or fresh material was heated in Schulz's solution or H_2O_2 until the cuticle separated from the rest of the leaf. After washing and neutralising the preparations the cuticles were stained in crystal violet and mounted in phenol glycerine jelly. (See Chapter 3, p.15 for details of the technique).

Floral Vascular Anatomy

The patterns of vascular strands in flowers of *D. viscosa* ssp. *cuneata* and ssp. *spatulata*, *D. humilis* and *D. baueri* were studied using serial paraffin sectioning techniques. Fresh material preserved in formalin-acetic acid-ethanol (F.A.A.) for at least 24 hours was dehydrated using a tertiary butyl alcohol (T.B.A.) series, embedded in paraffin, sectioned at 10μ , and stained in safranin-fast green according to Johansen (1940). Sections were mounted in Xam and photographed.

Chromosome Number

Chromosome numbers were determined for as many Australian *Dodonaea* taxa as possible. All determinations were made from bud material from plants in the field and from glasshouse-grown plants. Following bud fixation in 3 parts 70% alcohol and 1 part glacial acetic acid, pollen mother cell squashes were prepared by the iron aceto-carmin method of Radford et al. (1974, p. 254). Voucher specimens of populations for which chromosome counts were obtained are housed in AD. The collection numbers corresponding to these specimens are given following each species description (Chapter 7) and in table 3.1.

1.12 DISTRIBUTION

Distribution data given for each taxon in the formal taxonomic treatment (Chapter 7) were obtained from previous herbarium collections as well as those populations sampled during this project. A distribution map is included for each taxon recognised here.

1.13 ECOLOGY

The ecological notes included with each taxon provides a summary of the available data. This has been obtained from the rare, usually brief, notes on herbarium sheets and from my field observations. Any literature or research in progress relating to ecology of a particular taxon, such as response to fire or grazing, is included in that section.

1.14 BREEDING SYSTEMS

Reproductive strategies and population dynamics were studied in several species and in *D. viscosa* in particular. These included field and glasshouse studies involving self compatibility tests, flowering sequences, pollination mechanisms, tests for apomixis, forms of dioecy and seed viability and longevity. Sex ratio counts were made on field populations for most species collected and detailed long term population studies were carried out for several species occurring in South Australia. Chapter 4 includes discussion on breeding systems within the genus.

1.15 NUMERICAL TAXONOMY

A numerical taxonomic analysis of vegetative features was carried out on the *D. viscosa* complex. This involved development of a new technique in recording leaf data through the use of an electronic

digitiser. The data were comparatively analysed using principal components analysis, discriminant analysis and cluster analysis. Results and discussion of this analysis are contained in Chapter 6.

CHAPTER 2

TAXONOMIC HISTORY OF DODONAEA

At the time of Miller's (1754) description of *Dodonaea* the species now known as *Dodonaea viscosa* was under cultivation in Europe under various names including *Dodonaea*, *Triopteris* and *Staphylodendron*. The combination of the type species, *D. viscosa* was first validly published by Jacquin (1760). This was based on an illustration of material collected in Jamaica by Sloane and published 35 years earlier (Sloane, 1725).

During the latter half of the eighteenth century several new species were described and Smith (1809) was the first to attempt to distinguish between a number of species. He recognised *D. viscosa*, *D. spatulata*, *D. angustifolia*, *D. cuneata*, *D. eriocarpa*, *D. triquetra* and *D. pinnata*; the first four species are here regarded as being conspecific.

Humboldt, Bonpland and Kunth (1822) placed *Dodonaea* and *Llagunoa* in Section *Dodonaeaceae* of the family *Sapindaceae*. This was followed by de Candolle (1824), who added *Koelreuteria* and *Alectryon* to his tribe *Dodonaeaceae* and recognised 17 species of *Dodonaea*.

Miquel (1844) was the first to describe any infrageneric categories within *Dodonaea* when he recognised the simple-leaved Section *Eu-Dodonaea* and placed the pinnate-leaved species *D. hirtella* (= *D. boroniaefolia*) in Section *Remberta*.

Bentham and Hooker (1862) divided the family *Sapindaceae* into five suborders. They classified *Dodonaea* in suborder *Dodonaeae* with the genera *Distichostemon*, *Alectryon*, *Pteroxylon*, *Alvaradoa* and *Aitonia*.

Bentham (1863) in his *Flora Australiensis* presented the first comprehensive key and natural classification for *Dodonaea* in Australia. His treatment recognised 39 species in five series, the delimitation of which was largely based on capsule and leaf characters. Bentham separated the pinnate-leaved species (Series *Pinnatae*) from those with simple leaves. In this latter group he defined four new series based primarily on capsule appendages, i.e. Series *Cyclopterae* (= *Dodonaea*), *Platypterae*, *Cornutae* and *Apterae*. It is evident that Bentham recognised the parallels between the simple and compound-leaved groups by also delimiting the species within series *Pinnatae* primarily on capsule characters. Apart from the reclassification of a small number of species and the placement of those published since 1863 it is Bentham's system which bears most resemblance to the classification of *Dodonaea* proposed here.

During the period from 1855 to 1875 Ferdinand von Mueller made a significant contribution to the taxonomy of *Dodonaea* in describing 17 new species. Mueller did not put forward any overall classification of the genus himself, but in *Fragmenta Phytographiae Australiae* (1875) and his *Census of Australian Plants* (1882, 1889) it is clear that he adopted Bentham's (1863) system.

In Engler and Prantl's *Die natürlichen Pflanzenfamilien* (1895) Radlkofer placed *Dodonaea*, together with *Distichostemon*, *Diplopeltis* and *Loxodiscus*, in the subfamily Dyssapindaceae and tribe Dodonaeae. This classification is still accepted today by most Sapindaceae workers (e.g. Muller & Leenhouts, 1976).

Radlkofer's (1900) contribution of Sapindaceae for *Flora Brasiliensis* presents an exceptionally thorough treatment of *Dodonaea viscosa*, the

only species of the genus represented in Brazil. He accepted Bentham's (1863) three varieties and further subdivided var. *vulgaris* Benth. into three forms, f. *repanda* (Schum. et Thonn.) Radlk., f. *schiedeana* (Schltdl.) Radlk. and f. *burmanniana* (DC.) Radlk.

Several new species were described in the first 30 years of this century, but the genus was not treated as a whole until Radlkofer's (1933) monograph in *Das Pflanzenreich*. The classification proposed by Radlkofer contrasts with that of Bentham (1863), the only other work providing analysis of the whole genus. Radlkofer (1933) maintained his tribe Dodonaeae (Radlkofer, 1895) containing *Loxodiscus*, *Diplopeltis*, *Dodonaea* and *Distichostemon* within subfamily Dyssapindaceae. He recognised 52 species of *Dodonaea* from Australia. His classification is primarily based on fruit and seed characters, while leaf characters, including the presence of simple or compound leaves, are regarded as being of less importance. Within each of the three series (i.e. *Cyclopterae* (= *Dodonaea*), *Platypterae* and *Aphanopterae*) the species were grouped into two subseries on seed and fruit characters, so that Subseries *Oospermae* and Subseries *Inappendiculatae* contain both simple- and compound-leaved species. Despite the small number of specimens seen by Radlkofer (in several species less than five) his delimitation of species proved satisfactory in most cases and it is his work that has formed the basis of *Dodonaea* taxonomy to this time.

Sherff (1945,1947) contributed to the taxonomy of *Dodonaea* in attempting to update Radlkofer's nomenclature relating to *D. viscosa* Jacq. Bentham (1863) and Radlkofer (1933) had both recognised the polymorphism and taxonomic problems of the *D. viscosa* complex. Sherff (1945) further complicated the nomenclature of this complex when he

reduced var. *angustifolia* (L.f.) Benth. to a form of var. *linearis* Harv. & Sond. (apparently assuming incorrectly that the two varieties were based on the same type) and var. *spatulata* (Sm.) Benth. to a form of var. *arborescens* (Hook.) Sherff. In the Hawaiian species, *D. eriocarpa* Sm., Sherff (1945) described 18 varieties and 12 forms.

The recently produced regional Australian floras such as Black (1952), Blackall & Grieve (1956), Curtis (1956), Burbidge & Gray (1970), Beadle et al. (1972) and Willis (1972) have mostly followed Radlkofer's (1933) system in their treatments of *Dodonaea*. Willis (1972) and Beadle et al. (1972) both drew attention to the problems in the taxonomy of the *D. viscosa* complex (including *D. angustissima* and *D. cuneata*) through polymorphism and possible hybridisation.

In comparing the macromorphology and pollen morphology in relation to the taxonomy and the phylogenetic relationships of Sapindaceae, Muller & Leenhouts (1976) agree with Radlkofer's (1933) groupings into the two subfamilies and a number of tribes. They do, however, deviate from his ideas on the evolutionary and phylogenetic relationships between the genera and tribes. Because Muller & Leenhouts regarded morphological specialisations and elaborations as derived and Radlkofer believed them to be the more primitive, the phylogenetic scheme proposed by Muller & Leenhouts for the family is basically the reverse of Radlkofer's.

Lippold (1978) dealt with the genus in the Americas and recognised five species, *D. arizonica* A. Nelson, *D. bialata* H.B.&K, *D. elaeagnoides* Rudolphi ex Ledebour, *D. linearifolia* Linden ex Turcz. and *D. viscosa* Jacq. He combined *D. viscosa* Jacq. var. *angustifolia* Benth (p.p.), *D. viscosa* var. *vulgaris* Benth. f. *schiedeana* (Schltdl.) Radlk. and f. *burmanniana* (DC.) Radlk. (p.p.), var. *linearis* f. *angustifolia* (L.f.) Sherf

under the name *D. bialata* H.B.&K. Lippold believed *D. viscosa* var. *angustifolia* Benth. to be in part synonymous with *D. linearifolia* Linden ex Turcz. He placed the material recognised by Radlkofer and Sherff as *D. viscosa* Jacq. var. *vulgaris* Benth. f. *repanda* (Schumm. et Thonn.) Radlk. and (in part) f. *burmanniana* (DC.) Radlk. under the name *D. viscosa* Jacq. and that previously known as *D. viscosa* var. *spatulata* (Sm.) Benth. he classified as *D. elaeagnoides* Rudolphi ex Ledebour.

Apart from different classificatory schemes within the genus, most of the changes occurring in the taxonomic history of *Dodonaea* have revolved around the *D. viscosa* complex both within and beyond Australia. In many cases the species concept has become so narrow and the characters of the taxa have overlapped so much that it has been virtually impossible for subsequent workers to reorganise the complex from descriptions and keys. A major contribution to the difficulties within the *D. viscosa* complex is the fact that previous workers, including Lippold (1978), have based their classifications on herbarium material only. Little field experience, and certainly not on a population basis, has been included in their work.

CHAPTER 3

MORPHOLOGICAL CHARACTERS AND THEIR TAXONOMIC USEFULNESS

Within *Dodonaea* there is little morphological variation in flowers but considerable variation in fruits, seeds and vegetative parts. This is not unusual in a genus of this size. In addition, the anemophilous nature of *Dodonaea* means flower structure is more likely to be consistent than if species were reliant on specific pollinators for successful pollination, e.g. *Eremophila*, *Euphrasia*.

This chapter includes a discussion of those characters which have been found useful in this and other taxonomic treatments of *Dodonaea*. Each feature is assessed on the nature and significance of its variability, and consideration is given to the usefulness of each character at different levels of classification.

The various morphological features of the taxa have been studied primarily from herbarium material and supplemented where possible with fresh or alcohol preserved specimens. As many taxa as possible were propagated from seed or cuttings. This living material was used for morphological studies for 41 species (67%). For each taxon measurements or observations have been made for each character on a selected 15 to 20 specimens. Apart from the typical form of each taxon attempts were made to incorporate the morphological range, with particular emphasis on any ecologically or geographically induced variation. The measurements are recorded by giving the range in which 80% of the total sample of measurements falls, and either side of that in round brackets the full range is given.

It has been necessary to measure and describe some parts, e.g. capsules and anthers, by analysing their component features. The particular method used is described or illustrated under the relevant organ.

In general, descriptive terminology employed in this thesis follows Jackson (1928) and Stearn (1973), but in some cases where these works appear inadequate Lawrence (1951) and Radford et al. (1974) have been used. Inflorescence terminology follows that of Briggs & Johnson (1979).

3.1 HABIT

All species of *Dodonaea* are evergreen woody perennials. Most are erect, multistemmed shrubs of 1-2m in height, but there is considerable variation in size. *D. humifusa* and *D. procumbens* are prostrate shrubs less than 10cm high and with stems rooting at the nodes, while *D. viscosa* can be a single-stemmed tree to 10m high.

Widespread species vary extensively in size and shape over the different habitat types in which they occur. For instance, *D. viscosa* in the mountain ranges of arid Central Australia exhibits the habit of a small shrub, whereas on the east coast of Australia and in New Guinea this species is a small tree. *D. hexandra* which is usually a small, erect shrub of semi-arid mallee scrub can assume the form of a prostrate or spreading shrub to 1.5m diameter in more lush conditions.

Some species have a characteristic habit which can be readily used in the field for identification, e.g. *D. caespitosa*, and *D. viscosa* ssp. *angustissima*.

3.2 ROOT SYSTEM

The root system of *Dodonaea* is composed of a single main taproot branched laterally into secondary axes, which are themselves branched many times laterally. In prostrate species (*D. humifusa*, *D. procumbens*) adventitious roots sometimes develop from the nodes of branches.

The main taproot and lateral root system is already well developed in seedlings of 5 months.

3.3 BRANCHLETS

Branchlets vary greatly in shape between species, and this feature can be useful in a diagnostic sense at the species level. The branchlets range from terete or subterete, through angular or flattened, to ribbed and winged. *D. truncatiales* has distinctive ribbed branchlets, while those of *D. camfieldii* are winged. Branchlet colour is a distinguishing and consistent character in some species, e.g. red in *D. caespitosa* and light orange in *D. coriacea*.

The branchlets of most species are viscous and are covered with sessile or verruculose glands. In some taxa the branchlets can be covered in the resin secreted by these glands. *D. rhombifolia* has white, viscous branchlets resulting from resin secretion. The types of indumentum found on vegetative parts are discussed in the next section. Rarely, the branchlet indumentum is arranged in a particular manner, e.g. in *D. hackettiana* the dense villous indumentum forms longitudinal rows along the branches.

3.4 INDUMENTUM (excluding sepals)

Very few species of *Dodonaea* are entirely glabrous, although several have indumentum on the sepals only. (The calyx indumentum is discussed in

the section on sepals). The distribution, composition and density of the indumentum on the branchlets, leaves, pedicels, sepals, androecium and gynoecium, capsules and seedlings are important diagnostic characters at the specific and infraspecific levels.

A brief survey of the major indumentum types within the genus was carried out using cuticle preparations. Dried or fresh leaves, leaflets or part thereof, or capsules in the case of *D. humilis*, were placed in Schulz's solution (1:1, HNO_3 :HCl) and heated in a water bath for 15-60 minutes, depending on the fragility of the material. As the cuticle began to separate from the rest of the leaf the material was removed from Schulz's solution, washed thoroughly, neutralised with a dilute ammonia solution and washed again. The cuticles were stained in crystal violet (safranin can be used as a temporary stain) and mounted on slides in phenol glycerine jelly.

This method is successful for those species in which a flat section of leaf greater than ca. 5mm square is available. However, in cases in which only a small leaflet could be used it proved difficult to obtain a flat preparation large enough to show clearly (by photographs) the hair arrangements.

Delicate material, such as *D. humilis* capsules yielded intact cuticle preparations using a more gentle method of heating in H_2O_2 instead of Schulz's solution. This technique is essentially the same as that described above except that the neutralisation step is not required.

Glandular hairs are rare (found only in *D. humilis* and *D. glandulosa*), but eglandular ones are common. The simple hairs are single-celled usually with a bulbous base, and differ from species to species mainly in length, thickness, shape (straight or curved) and density.

The range of simple hairs in the genus is shown in figures 3.1 to 3.4. Some species (e.g. *D. multijuga*, fig.3.1) have falcate hairs; those of *D. triangularis* (fig.3.2) and *D. hirsuta* (fig.3.3) are narrow and attenuate towards the tip and in others, such as *D. rupicola* (fig.3.4) they are longer and soft.

The glandular hairs of *D. humilis* (figs.3.5 & 3.6) and *D. glandulosa* (figs.3.7 & 3.8) are composed of a multicellular stalk supporting the globose, multicellular gland. *D. humilis* is glabrous apart from these glandular hairs on the capsule. In *D. glandulosa* the vegetative parts and fruit have an indumentum of simple and glandular hairs, which are shorter than in *D. humilis*.

The viscous nature of most species is a common feature in the genus and is usually associated with the presence of sessile glands (figs.3.9 & 3.10). These are multicellular, hemispherical, peltate, resin-secreting glands which are responsible for the sticky nature of the plant or particular organ. The multicellular head of the gland may be supported on a 2-3-celled stalk or sessile. These glands appear to be sessile unless sectioned microscopically and they are described as such in the species descriptions to differentiate them from the stalked glandular trichomes described above. The developmental stages of such glands were described and illustrated by Collins (1920). These sessile glands appear to vary throughout the genus in density only. In characteristically viscous species (e.g. *D. viscosa*, *D. baueri*, *D. petiolaris*) they are common, while in some species with dense indumentum (e.g. *D. rupicola*) sessile glands are rare. *D. amblyophylla*, *D. bursariifolia* (fig.3.11), *D. lanceolata* and *D. triquetra* lack sessile glands.

In some taxa (e.g. *D. tepperi*, *D. coriacea*) rigid, flask-shaped glands protrude above the leaf surface resembling very small papillae or warts. These have been termed 'verruculose glands' to distinguish them from the more common sessile glands. The cuticle preparations of *D. ericoides* (fig.3.12) and *D. tepperi* (fig.3.13) illustrate these single-celled glands. They resemble the lageniform trichomes described by Payne (1978). The presence of sessile or verruculose glands is characteristic of particular species.

D. boroniaefolia and *D. multijuga* have a small number of large sunken glands near the margin of the upper leaflet surface and on the veins below. These glands are sunken below the leaf surface and are visible to the naked eye.

In this treatment the sessile and verruculose glands are described separately from the indumentum of eglandular and glandular hairs.

3.5 LEAVES

Dodonaea shows a large amount of leaf variation and leaf characters are important in distinguishing taxa at all levels. The main characters involved are overall size and shape, shape of the apex and base, variations in the margin, arrangement and types of glands and indumentum as described in the previous section, and petiole characters.

Mature plants of Sections I to IV (39 species) have mainly simple leaves, while those of Sections V to VII (22 species) have compound leaves. One species, *D. heteromorpha* (Section *Dodonaea*), produces some irregularly pinnate leaves, but most plants are predominantly simple-leaved. Those possessing compound leaves always have simple leaves subtending the branchlets.

In general, the pinnate-leaved species show less intraspecific variation in leaf characters than do the simple-leaved taxa. Some of the latter group exhibit broad variation within the species. In some cases it is possible to recognise consistent forms at an infraspecific level using these leaf characters, e.g. in *D. viscosa* and *D. sinuolata*, but in other species such as *D. triangularis* and *D. pinifolia*, the variation seems to be continuous with no natural breaks occurring.

Leaves are arranged spirally, or scattered and in one species, *D. ericoides*, they are opposite. In some species (e.g. *D. caespitosa*) the internodes are very short and the leaves appear to be clustered at the nodes and in *D. filiformis* the leaves are so close to each other that they overlap and obscure the branches.

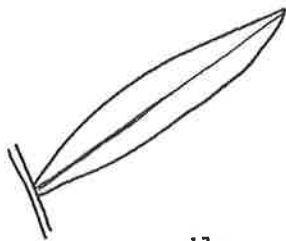
There is considerable variation in the shape of leaves and leaflets, not only within species, but also on individual plants. Combinations of component characters of leaf shape provide useful distinguishing features at the specific and infraspecific levels. Leaf shape variation in *D. viscosa* was analysed numerically (Chapter 6) and plots of the leaves included in that multivariate analysis are given in Appendix B. Closely related species groups within the sections proposed here exhibit very similar leaf shapes, but the total variation within each section is considerable. Leaf silhouettes showing the typical form and some of the range of leaves are illustrated for each taxon (Chapter 7).

Leaves or leaflets of the majority of species are broadest in the distal $\frac{1}{3}$ of the leaf and fall within the oblanceolate, obovate or angular-obovate shape categories. A small number of species have subfiliform or terete leaves, e.g. *D. filifolia* and *D. rigida* of Section *Dodonaea* and *D. stenozyga* of Sect. *Pinnatae*, while others, such as most

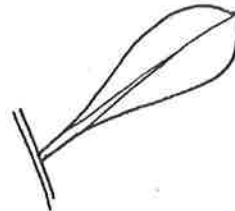
species of Sect. *Cornutae*, have strongly revolute leaves giving a filiform appearance.

Many species have irregularly lobed or toothed apices and several produce teeth irregularly above the middle of the leaf. Although non-entire leaves are common, very few taxa (*D. serratifolia*, *D. ptarmicaefolia* and *D. lobulata*) are regularly toothed or lobed.

Leaf bases are generally attenuate with some tapering to a petiole while others are sessile. *D. camfieldii* is the only species with decurrent leaf bases. The length and shape of the petiole, as well as the type of indumentum, are useful taxonomic characters at specific and infraspecific levels. Because of the attenuate base of many leaves it is often difficult to decide if the leaf has a petiole or not. For the purposes of this revision a petiole exists from that point at which the width of the lamina on either side of the midrib is less than the width of the midrib, as shown below.



sessile



petiolate

As might be expected, most of the narrow-leaved species are sessile, while the broader leaves are often petiolate. All pinnate-leaved species are petiolate and in *D. stenozyga* the petiole often functions as the rachis with only two terminal leaflets present.

Some variation has been observed in tertiary and higher order venation patterns of the basic eucamptodromous system. Leaf clearing of

a range of species may reveal useful diagnostic characters and may locate specific links between the pinnate and simple-leaved groups.

The largest-leaved species are usually in tropical areas and the smallest leaved ones in the arid and semi-arid. Evolutionary implications of trends in leaf size are discussed in Chapter 5.

Seed of as many species as possible was obtained and germinated for morphological examination and basic germination trials (see Chapter 4). Due to difficulties in obtaining seed and to problems in germination and identification uncertainties, seedlings were obtained for only 62% of the species. Apart from Sect. *Plagiopterae*, of which no seedlings have been seen, each section was represented by at least 50% of the species in it.

Seedling morphology usually reflects that of mature plants in indumentum, leaf arrangement and leaf apex and base. However, the shape of the first 2-10 juvenile leaves varies considerably from the adult foliage in those species with simple adult leaves. Lubbock described these juvenile leaves for *Dodonaea viscosa* in 1892. All of the 21 simple-leaved species, for which seedlings were available, have deeply lobed to almost pinnate juvenile leaves. In contrast, in those species with pinnate foliage the first leaves produced after the cotyledons are identical with the adult leaves, apart from size. Thus, seedlings of almost all species of the genus so far examined possess lobed or deeply lobed to pinnate juvenile leaves, whether or not they eventually develop simple or compound leaves. This tends to suggest that simple leaves are primitive within the genus. Discussion of relationships of pinnate and simple leaves within *Dodonaea* is contained in Chapter 5.

3.6 INFLORESCENCE

The inflorescences of *Dodonaea* are described in this treatment following the terminology developed by Briggs & Johnson (1979) for the Myrtaceae with slight modification to adapt their system to this genus.

The basic branching system of the vegetative parts of *Dodonaea* is spiral or scattered (with the exception of *D. ericoides*). The inflorescence exhibits a similar branching pattern. The terminology proposed by Briggs & Johnson was applied by them to opposite or decussate branching and requires some minor modification to apply it to alternate systems. The term 'diad' is here used to describe those inflorescences composed of one terminal and one lateral flower. It appears to be an intermediate stage between the triadic and monadic conditions. Inflorescences are described according to their highest degree of branching. In addition, the anthotelic branches or partial inflorescences forming part of a compound inflorescence (e.g. panicle) are mentioned. This means that a panicle may be described as being composed of (lateral) monads to botryoids.

Dodonaea uniflorescences are anthotelic. The genus includes examples of anthotelic/blastotelic flexibility both in different species and within some species (e.g. *D. platyptera*). While in species such as *D. rupicola* and *D. viscosa* the inflorescence pattern appears to have stabilised to a terminal anthotelic condition; in others (e.g. *D. peduncularis*) it consists of anthotelic lateral flowering branches of a blastotelic seasonal growth unit, and still other species show a stabilised condition with lateral inflorescences of metabotryoids to monads (e.g. *D. inaequifolia*).

In closely related taxa, such as species within a genus, a common basic inflorescence form can be expected, but given the morphological diversity evident on other features of *Dodonaea* the varying degrees of elaboration of the inflorescence in different species are not unexpected. The variation is the result of different degrees of branching, the number of nodes on a branch and the number of flowers in any lateral flowering branch.

In most inflorescence types (particularly the paniculate) there is a gradual acropetal transition from leaves to bracts. Each flower is subtended by a bract or reduced foliar organ. These bracts are very similar in all species and provide no useful distinguishing characters.

The most complex inflorescence in the genus is the frondobracteose panicle as found in *D. viscosa*, *D. polyzyga*, *D. rupicola* and *D. truncatiales* (fig.3.14a). These panicles are composed of lateral flowering branches ranging from metabotryoids to (distal) monads. It is suggested that the other less complex forms have been derived from this condition by a process of reduction. Details of this hypothesis are discussed in Chapter 5, p.61.

The various inflorescences found in *Dodonaea* are illustrated in figure 3.14. Examples of panicles are given above. Sections *Dodonaea*, *Pinnatae* and *Platypterae* each have several species with compound, terminal inflorescences. For example, *D. vestita*, *D. coriacea*, *D. hackettiana* and *D. platyptera* have compound inflorescences composed of monads to botryoids (fig.3.14c). *D. multijuga* has axillary panicles composed of (lateral) monads to metabotryoids, but at each lateral node abortive buds are present (fig.3.14b). Axillary metabotryoids and few-flowered botryoids (fig.3.14d) are present in *D. pachyneura*, *D. stenophylla*,

D. megazyga, *D. rigida*, *D. larreoides*, while monadic and diadic inflorescences (fig.3.14e) are found commonly in species of Sections *Apterae*, *Cornutae* and *Inappendiculatae*, e.g. *D. humifusa*, *D. caespitosa* and *D. humilis*. *D. ericoides* (Sect. *Apterae*) the only species with opposite arrangement of vegetative parts, is also unique in having solitary, terminal flowers (fig.3.14f).

3.7 FLOWERS

The flowers of *Dodonaea* show little variation in size and structure and are of limited value in classification and identification. They are small, lack petals and are inconspicuous. This and the fairly short flowering period has resulted in flowering material being very poorly represented in herbarium specimens of many species.

Most species of *Dodonaea* are dioecious, 14 of which are rarely polygamo-dioecious (e.g. *D. procumbens*); 4 species are solely polygamo-dioecious (e.g. *D. coriacea*) and only 2 are polygamous (e.g. *D. polyzyga*). Given that the majority of species have only unisexual flowers, the descriptions include features of the organs (i.e. stamens and ovaries) in male and female flowers separately. The various breeding system strategies of the genus are discussed in Chapter 4.

3.8 PEDICELS

The flowers are all pedicellate. Pedicels vary slightly in length and indumentum type between species and they provide some diagnostic information at the species level. There is some tendency towards ribbing in a small number of species (e.g. *D. ceratocarpa*). Each pedicel is jointed below the middle; this is easily seen in the longer

pedicelled species, such as those of Section *Platypterae*, but is not obvious in short pedicels. This node is probably indicative of the ancestral position at which a flower would have developed (Chapter 5). In all species the pedicels elongate in fruit; the lengths given in the species descriptions are taken from flowers at anthesis. Unless otherwise indicated the pedicel descriptions also apply to the peduncle.

3.9 SEPALS

The sepals in *Dodonaea* are very rarely fused together and are described as individual units rather than as a calyx. They vary in shape, size, number and indumentum characteristics, all of which are sometimes useful in distinguishing species. Sepal morphology is remarkably constant within species, but it is not of much value in defining higher order groups.

For each species the position of the sepals at anthesis is described for male, female and bisexual flowers. In male flowers the sepals are always free at anthesis, but they occupy differing positions relative to the stamens in different species. Sepals of female flowers at anthesis are usually valvate at least at the base, with the style protruding from between them. In some cases the sepals are free from each other, but in all species they are in a position which surrounds the ovary. Of some diagnostic significance at the species level is the loss or retention of the sepals in fruit; this is given in each species description.

The indumentum of the sepals varies considerably throughout the genus. Very few species have completely glabrous sepals (e.g. *D. amblyophylla*, *D. triquetra*), although several are glabrous on the outer

surface (e.g. *D. bursariifolia*, *D. falcata*). Usually the sepal outer surface has a similar indumentum to that of the foliage and branchlets, but the inner surface is very often covered with sticky, flexible, villous hairs found nowhere else on that plant.

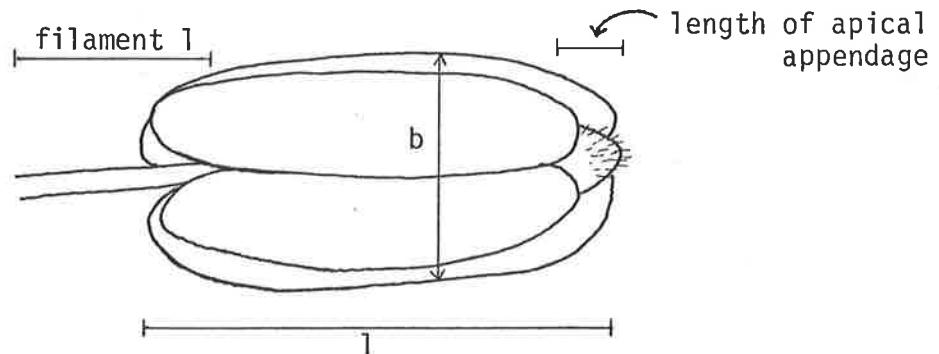
3.10 ANDROECIUM

In *Dodonaea* the stamens are usually twice the number of sepals with large, usually oblong, 2-lobed, basifixed, laterosely dehiscent anthers on relatively short filaments. Anther sacs are adnate to the filament throughout and the connective usually extends beyond the anthers to form a small apical appendage. The shape, size and indumentum of this appendage varies between species.

The stamens provide several diagnostic characters at the species level. Stamens usually number 8-10, but some species characteristically have fewer (e.g. 6 in *D. hexandra*) or more (*D. polyandra* with 12-14). Although filament length is usually 0.2-0.5mm long, some exceptions do occur (e.g. in *D. glandulosa* 1.7-3.5mm long) and in these species it is a useful distinguishing character. Some species have pubescent anther lobes (e.g. *D. rupicola*), but most are glabrous.

The position of the stamens relative to the sepals at anthesis varies considerably. This may be partly associated with the habit of the plant and with anemophily. In prostrate species, such as *D. procumbens*, the stamens exceed the sepals in length and are divergent, while in open, erect shrubs with sparse foliage (e.g. *D. hexandra*) the sepals are the same length as the stamens and surround them (see Chapter 4 for further discussion).

Filament, anther and apical appendage measurements included in the species descriptions are derived as shown below.



Rudimentary stamens or filaments only occasionally occur in female flowers and stamens of bisexual flowers are usually the same as in male flowers for that species.

3.11 POLLEN

Erdtman (1952) and Muller & Leenhouts (1976) described pollen of *D. attenuata* (= *D. angustissima*) and Merville (1965) examined African *D. viscosa* material. In carrying out pollen sterility studies I have examined several species, at least one from each section of the genus as described here, for gross pollen morphology. In addition pollen from the *D. viscosa* complex has been examined with the scanning electron microscope (SEM).

All reports indicate little variation in pollen morphology between species. *Dodonaea* has subtriangular to prolate spheroidal, tricolporate pollen with relatively long colpi and small endoapertures (fig.3.15). Further SEM examination of the sporoderm may reveal sculptural diversity in the genus.

3.12 GYNOECIUM

The ovary of *Dodonaea* species is (2-)3-5(-6)-carpellate and usually angled. *D. polyandra*, *D. viscosa* ssp. *viscosa* and *D. glandulosa* have two carpels, while *D. physocarpa* sometimes has six.

The gynoecium of most species is glabrous, but some possess a distinctive indumentum, such as the villous tufts of *D. vestita* ovaries.

Each locule contains two superposed, anacampylotropous ovules. The upper one is ascending and apotropous, the lower one pendulous and epitropous. Corner (1976, fig.512) illustrates the ovules as attached to the placenta in *D. viscosa*, which is typical for the genus. The funicle is thickened at the base.

The style is composed of usually 3-4 parts which are fused to various lengths, almost always for more than half their length. Some styles are twisted spirally, most are viscous, some are pubescent near the base, while others have a distinctive red colour.

Male flowers of most species have a very small rudimentary ovary. The ovary of bisexual flowers is usually the same as that of the female flowers of that species.

Sepal position relative to the ovary is given for each species. In most species the style protrudes from between the valvate sepals at anthesis, the sepals separating after anthesis.

Radlkofer (1933) described the small disk-like stalk, on which the ovary is slightly raised, as a carpophore. From sections obtained in examination of the floral vasculature it appears that this is actually a gynophore (fig.3.17), and that the small disk is part of the gynophore.

3.13 FLORAL VASCULATURE

Floral vascular anatomy was studied on a small number of species. Fresh male and female flowers and buds of *D. viscosa* ssp. *cuneata* and ssp. *spatulata*, *D. humilis* and *D. baueri* were preserved in F.A.A. for at least 24 hours. The material was dehydrated in a T.B.A. series, embedded in paraffin and longitudinal and transverse sections were cut at 10 μ . The sections were stained in safranin-fast green and mounted in XAM.

The floral vascular anatomy is essentially the same in all species examined. It is described and illustrated here by *D. baueri* female flowers and male flowers of *D. viscosa* ssp. *cuneata*.

The vascular tissue enters the flower as a single solid bundle and divides radially into 8 bundles, 4 of which give rise to the sepal traces. The sepal bundles divide again to 3-6 bundles in each sepal.

In MALE FLOWERS (fig.3.16) the remaining 8 discrete bundles of the central column divide to give rise to the stamen traces (usually 8) with the remaining bundles fusing laterally to form a central circular trace, which continues to the top of the rudimentary ovary without further division. Each stamen has a single bundle running through the filament to the centre of the anther.

In FEMALE FLOWERS (fig.3.17) the bundles of the central column are less discrete. Simultaneous with the sepal trace divisions some bundles are formed in an irregular pattern between the sepal bundles. These intersepal traces soon disappear and do not enter any specific part of the flower. A small lobe of tissue is visible in the corresponding position in longitudinal section, and may indicate the position of either a rudimentary stamen or the remains of a petal trace (fig. 3.17g). The remaining bundles fuse laterally to form a central vascular cylinder in the

gynophore. At the base of the ovary this large bundle gives rise to traces which enter each of the carpels (in this case 4), and continue for the length of the ovary on the dorsal face of each carpel. The central vascular cylinder later divides into 8, one of which enters each carpel at the placental attachment of the ovules and the remaining 4 continue into the style without further division.

Three-dimensional reconstruction of the floral vasculature of both male and female flowers is shown diagrammatically in fig.3.18. Although the floral vascular anatomy is of no taxonomic use within *Dodonaea* it does provide information on the development and spatial relationships of various organs. Through examination of both transverse and longitudinal sections the stipe of the gynoecium is interpreted as a gynophore rather than a carpophore as described by Radlkofer (1933). The disk-like gynophore bears the entire gynoecium, and there is no evidence of the carpophore prolongation of the receptacle between the carpels or of the later separation of the carpels as in *Geranium* or members of the Umbelliferae.

3.14 FRUIT

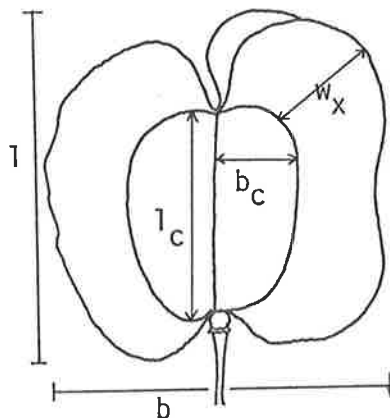
The diagnostic importance of the fruits of *Dodonaea* has long been recognised. Both Bentham (1863) and Radlkofer (1933) based their classifications in part on fruit morphology. The diversity of capsules is a feature of the genus and the system proposed in this treatment relies on capsule characteristics at the section and species levels.

Dodonaea has a dry, dehiscent capsule of 2-6 valves. The most obvious and variable feature of the fruit is the appendage on the dorsal face of each carpel. This ranges from a broad, membranous,

rounded wing of equal width throughout in Sect. *Dodonaea* and Sect. *Pinnatae*, to an oblique, longer than broad, membranous wing of Sect. *Platypterae* and Sect. *Plagiopterae*, in Sect. *Cornutae* the appendage is horn-like and at the capsule apex only, and a very small lobe-like appendage or no appendage at all is found in Sect. *Apterae* and Sect. *Inappendiculatae*.

The winged, membranous fruits usually change from green to brilliant red or shades of pink and purple just before maturity. They are spectacular and very conspicuous at this stage and I believe this to be the main reason that the great majority of *Dodonaea* specimens in herbaria are fruiting, while very few are in flower.

Because of the variability in capsule morphology each species description includes description and measurements of the capsule as a whole and of the carpels and appendage. The component parts of the fruits were measured as shown in the diagram below. The capsule of each species is illustrated in Chapter 7.



b_c = breadth of carpel excluding appendage

l_c = length of carpel excluding appendage

w_x = maximum width of appendage

The appendage dimension (w_x) has been measured in the same manner for each species, but it is described in some sections as length and in others as breadth. Theoretically w_x is the appendage *length*, as the carpel from which it extends is attached to the central axis of the fruit. However, it is described as length only in those sections in

which w_x is obviously the longest dimension of the appendage (e.g. Sections *Platypterae*, *Plagiopterae* and *Cornutae*). In those sections with rounded wings of equal width throughout or with lobe-like appendages (Sections *Dodonaea*, *Pinnatae* and *Apterae*) w_x is given as appendage breadth.

Carpel shape is described on the basis of its central attachment to the central axis of the capsule, while the capsule as a whole is described from its attachment to the pedicel.

At the specific and infraspecific levels the carpel and appendage texture can be useful in distinguishing taxa. Many species have viscous fruits, especially those with wings, and some bear trichomes. For instance, *D. hirsuta*, *D. rupicola* and *D. vestita* have hirsute capsules, *D. ericoides* has pubescent or tomentose fruit, while capsules of others, such as *D. triangularis*, *D. adenophora*, *D. camfieldii*, are often sparsely pubescent mainly on the carpels. Two species, *D. humilis* and *D. glandulosa*, have multicellular, glandular hairs on the capsules.

Capsules of most *Dodonaea* species dehisce septifragally, but a small number are septicidal, e.g. *D. bursariifolia*, *D. platyptera* and *D. adenophora*. *D. physocarpa* and *D. petiolaris* have greatly inflated membranous capsules which dehisce irregularly. They are not readily dehiscent and seed appears to be released after mechanical breakdown and shredding of the carpel walls.

3.15 SEED

Seed characters are useful in the taxonomy of *Dodonaea* (mainly at species level), but are often of limited value in identification since many herbarium specimens are collected when the fruits are most spectacular, that being prior to reaching maturity.

Although there are two ovules in each locule usually only one develops. The number of seeds maturing in each fruit varies greatly both intra- and interspecifically.

Dodonaea seed is usually black and lenticular (fig.3.19), although some species have globose seeds, e.g. *D. platyptera*, *D. petiolaris* (fig.3.20) and some are lenticular with a flattened or compressed margin, e.g. *D. camfieldii* (fig.3.21). The seed is covered with a hyaline membrane which lifts only at the margin in such species as *D. triquetra* and *D. humilis* (fig.3.22) or over the whole seed surface, e.g. *D. physocarpa* and *D. glandulosa* (fig.3.23). In most species it remains close to the testa. This membrane is shiny in some species and dull in others and provides some distinctive characteristics.

An ARIL is present on the seed of species of Sect. *Cornutae* and most of those of Sect. *Apterae* (fig.3.24). Van der Pijl (1957) and Corner (1976) disagreed on the arillate nature of the Sapindaceous seed and the origin of the aril or arillode structure. Van der Pijl (1957) argued that the sarcotesta (fleshy testa) is primitive and has given rise to various arilloid structures by reduction. He regarded an aril as a secondary post-floral outgrowth of the funicle, which was therefore free from the seed. He employed the terms 'arillode' for an outgrowth of the integument near the micropyle and 'arilloid' for any outgrowth on or near the seed that resembles an apparently independent aril. Corner (1976), on the other hand, maintained that the aril is a primitive structure and that the sarcotesta is a specialisation of the chalaza. He examined seed of several species including *Dodonaea viscosa*, which was described as having an aril derived from the head of the short funicle and persisting as a minute cushion near the hilum.

In view of this controversy between van der Pijl and Corner, I decided to examine the developmental stages of the seed of some *Dodonaea* species in order to determine the origin of the aril. The method of Blackburn and Christophel (1976) was used in an attempt to clear various stages from young ovules to almost mature seeds of *D. viscosa*, *D. baueri* and *D. ceratocarpa*. However, even lactic acid pretreatment did not result in cleared ovules. Since time did not allow me to microtome longitudinal sections, ovules of various species at various stages of seed development were dissected, sectioned and examined with a high power dissecting microscope.

Without cellular level examination it is impossible to determine whether the majority of *Dodonaea* species which appear to lack any aril do possess a small funicular aril as described by Corner (1976) for *D. viscosa*. Since there is no obvious arrillate structure in these taxa they are described here as having no aril.

The white, infundibular outgrowth associated with the mature seed of species of Section *Cornutae* and most of Section *Apterae* is definitely of funicular origin and does not develop until long after anthesis. It is described as a true aril.

Two species of Section *Apterae*, *D. baueri* and *D. tepperi*, appear to be intermediate between the forms described above in having a slightly enlarged funicle, but no true aril.

Thus, the well developed aril in *Dodonaea* is a post-floral outgrowth from the funicle. Possession of an aril is regarded as an advanced character relative to those species lacking an aril (see Chapter 5 for further evolutionary discussion), and it is a useful taxonomic feature.

3.16 CHROMOSOME NUMBER

Prior to this study all chromosome numbers reported in the literature referred to extra-Australian taxa and mainly to the *Dodonaea viscosa* complex. (These determinations are included in table 3.1). Guervin (1961b) reported a chromosome count for *Dodonaea triquetra* ($2n=30$), an endemic Australian species. *D. viscosa* is often misidentified as *D. triquetra*, but it is not possible to confirm Guervin's taxonomic identification since he did not cite any voucher specimens.

Given the high degree of morphological variability in *Dodonaea* in Australia and especially in the *D. viscosa* complex, attempts were made during this study to determine chromosome numbers of as many taxa as possible. It was hoped that the results would supplement morphological data and help in evolutionary interpretations of the genus.

The determinations were made from bud material fixed in 3 parts 70% alcohol and 1 part glacial acetic acid (whenever possible before 11a.m.) from plants in the field and from glasshouse-grown plants. After 24 hours the fixed material was washed with 70% alcohol and stored in ice (if in the field) until transfer to 4°C. Pollen mother cell squashes were prepared by the iron aceto-carmine method of Radford et al. (1974, p. 254).

Chromosome numbers of 18 Australian taxa (including infra-specific taxa here proposed for *D. viscosa*) from 52 populations are presented in table 3.1. Determinations were obtained for species from each section of the genus, although, due to lack of material and availability of time, only one chromosome count was obtained for species of Sections *Platypterae*, *Cornutae*, *Plagiopterae* and *Inappendiculatae*. It may be possible to obtain mitotic determinations of some of these taxa through root tip preparations in the future.

Table 3.1 Chromosome numbers in *Dodonaea*

Taxon	Chromosome number	Source of reference or voucher specimen in AD
Sect. <i>Dodonaea</i>		
<i>D. bursariifolia</i>	n = 14	West 1124, 1963, 1983, 2070
<i>D. eriocarpa</i>	n = 14	Carr (1978)
<i>D. hackettiana</i>	n = 14	West 3253
<i>D. lobulata</i>	n = 14	West 936, 3416, 3445
<i>D. triquetra</i>	n = 14	West 822
	*2n = 30	Guervin (1961b)
<i>D. viscosa</i>	n = 13	Sutaria (1930)
	n = 14	Mehra et al. (1972)
	n = 14	Sarkah et al. (1975)
	n = 14	Sarkah et al. (1976)
	2n = 28,32	Brizicky (1963)
	2n = 30	Guervin (1961a)
ssp. <i>angustissima</i>	n = 14	West 1081, 1149, 1189, 1254 1644, 1714, 1899, 1902 1923, 1927, 2111, 2176
ssp. <i>cuneata</i>	n = 14	West 1355, 1661, 2540
ssp. <i>spatulata</i>	n = 14	West 1023, 1186, 1219, 1679 1764, 2001, 2039, 2463 2472
intermediate		
ssp. <i>angustissima</i> -		
ssp. <i>spatulata</i>	n = 14	West 483, 1183
Sect. <i>Platypterae</i>		
<i>D. truncatiales</i>	n = 14	West 2568
Sect. <i>Apterae</i>		
<i>D. baueri</i>	n = 14	West 1738
<i>D. hexandra</i>	n = 14	Short 229 West 1350
<i>D. tepperi</i>	n = 14	West 1342
Sect. <i>Cornutae</i>		
<i>D. pinifolia</i>	n = 14	West 3193, 3372
Sect. <i>Pinnatae</i>		
<i>D. concinna</i>	n = 14	West 2954
<i>D. larreoides</i>	n = 14	West 3274
<i>D. rupicola</i>	n = 14	CBG 7708609 (cult.)
<i>D. stenozyga</i>	n = 14	West 1967, 2681
Sect. <i>Plagiopterae</i>		
<i>D. inaequifolia</i>	n = 14	West 3282
Sect. <i>Inappendiculatae</i>		
<i>D. humilis</i>	n = 14	West 1291, 1320, 1346, 2016

* taxonomic identification doubtful

All determinations made during this study yielded counts of $n=14$. Figure 3.25 illustrates one pollen mother cell with 14 chromosomes resulting from a preparation of *D. viscosa* ssp. *angustissima*. This consistency in chromosome numbers of morphologically variable species in Australia is not very useful taxonomically or in any evolutionary appraisal of the genus.

However, reports from extra-Australian material (table 3.1) suggest an aneuploid series ranging from $n=13$ to $n=16$ within *D. viscosa*. Attempts are being made to obtain seed of this species from a wide range of morphological forms and geographical areas beyond Australia in order to obtain a greater range of determinations for this extremely widespread polymorphic complex.

If Guervin's (1961a) suggestion that $x=15$ is the base number of the subfamily Dyssapindaceae is correct, then the determinations of $n=14$ obtained for all Australian *Dodonaea* material examined implies that this is part of an aneuploid series in the subfamily. Brizicky (1963) referred to an aneuploid series from $2n=20$ to $2n=32$ for Sapindaceae. Further comparisons of chromosome numbers, distribution patterns and morphological features need to be assessed before any final decisions can be reached.

CHAPTER 4
REPRODUCTIVE BIOLOGY IN *DODONAEA*

4.1 INTRODUCTION

Intraspecific floral polymorphism is of widespread occurrence in the angiosperms and it is well known in the family Sapindaceae (Radlkofer, 1933; Tomlinson, 1974). Perfect, staminate and pistillate flowers can be found on the same or different individuals in various combinations described as monoecy, dioecy, androdioecy, gynodioecy, polygamy and polygamo-dioecy.

Species of the genus *Dodonaea* exhibit a range from dioecy through polygamo-dioecy to polygamy (see Chapter 3). Floral morphology examined in natural populations of several *Dodonaea* species previously described as dioecious, indicated evidence of polygamo-dioecy. It is important from an evolutionary viewpoint to relate any such deviations from dioecy with other morphological evolutionary patterns in the genus.

In order to better understand the breeding system(s) of *Dodonaea* attempts were made to gain more information on the general floral biology which characterises the reproductive strategies employed by a particular species. With the recent discussions in the literature relating to the evolution and adaptive significance of dioecy, it is of interest to examine factors that may have influenced the postulated trend towards dioecy in *Dodonaea*.

This chapter presents results of population studies in the field as well as field and glasshouse observations and tests involving floral morphology, self compatibility, relative frequencies of staminate and pistillate flowers at the individual and population levels, floral rewards, pollination and apomixis. Although field population studies were

carried out on four species - *Dodonaea viscosa*, *D. baueri*, *D. hexandra* and *D. bursariifolia* - the results given here are for *D. viscosa* only. Since the populations of the other three species were less accessible, it was not possible to revisit those sites as frequently as the three *D. viscosa* populations and so the field data gathered for *D. baueri*, *D. hexandra* and *D. bursariifolia* is less complete. Nevertheless, observations and tests carried out on plants of several species grown in the glasshouse served to confirm results obtained for *D. viscosa*.

The three natural *D. viscosa* populations used for these studies occurred within 30km of Adelaide, South Australia; one at Coromandel Valley, another at Eden Hills and the third in Torrens Gorge. These populations were chosen on such criteria as the size of the population, the distance from the laboratory for continual monitoring, the lack of human disturbance to the area as a whole and relative inaccessibility at the site, so that experiments with labels and pollination bags would not be vandalised. The breeding system studies continued for a period of five years (1975-1979) encompassing five flowering and four fruiting seasons.

Since *Dodonaea* species are perennials many problems arose in attempting to do breeding system studies. As a result of these problems and the limited time available for the study, some of the data presented here remain inconclusive. However, they do suggest trends and possible reproductive strategies in *D. viscosa* and are included for that reason.

4.2 FLORAL MORPHOLOGY AND POLLINATION BIOLOGY

Floral morphology

Most species of *Dodonaea* are dioecious, some 14 of which are rarely polygamo-dioecious, another 4 are solely polygamo-dioecious and 2 are

polygamous. Plants of the two polygamous species, *D. polyzyga* and *D. lanceolata*, possess both perfect and imperfect flowers, while the polygamo-dioecious species consist of pistillate plants and staminate plants bearing some perfect flowers among the dominant staminate flowers. For the purposes of this discussion these predominantly male plants will be referred to as staminate plants. (Terminology follows that of Radford et al. (1974)).

In several *Dodonaea* species the perfect flowers on these staminate plants form fruits. Bawa (1974) reported the same phenomenon in *Simaruba glauca* (Simarubaceae).

In Australia *D. viscosa* is dioecious or polygamo-dioecious. The pistillate and perfect (or bisexual) flowers have usually 3-4-carpellate ovaries with two ovules per locule. The staminate flowers usually possess an aborted or rudimentary gynoecium, while pistillate flowers may possess an aborted androecium or lack any sign of stamens at all. Occasionally some of the anthers of perfect flowers are abortive.

In a study in New Zealand of mostly cultivated plants, Rivers (1971) reported polygamy in *D. viscosa*. Of the results presented by her 7% of the plants were polygamous, 39% were polygamo-dioecious, 52% dioecious and 2% possessed perfect flowers only. Examination of herbarium material and field observations have not revealed any polygamous or purely perfect-flowered individuals of *D. viscosa* in Australia. Rivers also recorded a small proportion of the polygamo-dioecious plants (27%) as having some perfect flowers on predominantly pistillate plants. In Australia I have not observed, either in the field or on herbarium specimens, any polygamo-dioecious predominantly pistillate plants.

Observations made on cultivated populations of *D. viscosa* near Christchurch, New Zealand in January, 1979 indicated polygamy may have been present in purple-leaved plants. Sex ratio measurements are required for naturally occurring New Zealand populations to confirm the presence of polygamy.

Flower size and colour

D. viscosa shows considerable constancy in flower size. The flowers of all *Dodonaea* species are small (usually <5mm in length or breadth) and inconspicuous. They lack petals and, apart from the yellow anthers and reddish style at anthesis, the flowers are green.

From field observations and herbarium material it is clear that most of the dioecious and polygamo-dioecious species do not exhibit sexual dimorphism in flower size as determined by sepal dimensions. However, at anthesis the different forms appear sexually dimorphic. In general the sepals in pistillate flowers remain erect, surrounding the ovary with the style protruding between them at the apex. The sepals of staminate and perfect flowers are widespread at anthesis exposing the androecium and gynoecium (either abortive or functional). This is probably because *Dodonaea* is anemophilous (see below) and the sepals of staminate flowers fold back in order to allow unhindered dispersal of the pollen grains from the anthers. As the style, with its distal receptive stigmatic surfaces, extends well beyond the sepals there is no reason for them to open out away from the ovary. In fact it is possible that in continually surrounding the ovary the sepals protect it and the enclosed ovules from desiccation or predation.

In bud the flowers also show sexual dimorphism. The pistillate flowers are \pm ovoid and narrower and longer than the rounded, \pm globose

staminate and perfect flowers. The large stamens surrounding the gynoecium cause the flowers to be wider and shorter, and so the males are easily recognised in bud stage.

The equivalent size of pistillate and staminate flowers in *Dodonaea* is in contrast to that found by Baker (1948) in temperate dioecious taxa, in which pistillate flowers were smaller than staminate, and by Bawa & Opler (1975) who reported larger pistillate flowers in 14 out of 20 species of tropical dioecious trees.

Staminate/pistillate flower ratios

In any population of dioecious plants three factors contribute to the staminate/pistillate flower ratio - the number of flowers per inflorescence; number of inflorescences per plant; and what is usually regarded as the sex ratio, the relative number of staminate and pistillate plants.

i) Number of flowers per inflorescence

In the three natural *D. viscosa* populations studied in detail the number of flowers was counted for 10 inflorescences (randomly chosen) on each of 5 staminate and 5 pistillate plants. Table 4.1 and the associated analysis of variance shows that there were significantly more flowers per inflorescence in staminate inflorescences than in pistillate.

These results are further complicated since *D. viscosa* plants may be polygamo-dioecious and then predominantly staminate plants contain a small proportion of perfect flowers. In determining the ratio of staminate/pistillate flowers per inflorescence (table 4.1) the populations were assumed to be dioecious and any staminate inflorescences containing perfect flowers were avoided.

Table 4.1 Number of flowers per inflorescence counted for 50 staminate and 50 pistillate inflorescences in each of 3 *Dodonaea viscosa* populations.

<u>Population</u>	<u>Mean number of flowers/inflorescence</u>		<u>Staminate/pistillate flower ratio</u>
	<u>Staminate</u>	<u>Pistillate</u>	
1. Coromandel Valley	15.6±0.49	6.5±0.34	2.4
2. Eden Hills	19.1±0.49	10.6±0.51	1.8
3. Torrens Gorge	17.4±1.05	10.0±0.78	1.7
	17.4	9.0	

Analysis of variance

<u>Source of variation</u>	<u>Sum of squares</u>	<u>Degrees of freedom</u>	<u>Mean square</u>	<u>F</u>	<u>Significance of F</u>
Population	753.95	2	376.97	17.67	.000
Sex	5191.68	1	5191.68	243.29	.000
Population x sex	39.68	2	19.84	0.93	.40
Residual	6273.87	294	21.34		
Total	12259.18	299			

Table 4.2 Number of staminate and perfect flowers in each inflorescence containing perfect flowers. Counted for at least 6 inflorescences on 10 individuals in each of 3 *Dodonaea viscosa* populations.

<u>Population</u>	<u>Mean number of flowers/inflorescence</u>		<u>Perfect flowers %</u>	<u>Staminate/perfect flower ratio</u>
	<u>Staminate</u>	<u>Perfect</u>		
1. Coromandel Valley	13.2	1.5	10.2	8.8
2. Eden Hills	20.0	2.0	9.1	10.0
3. Torrens Gorge	15.0	2.2	12.8	6.8
	16.1	1.9	10.7	

The actual proportion of perfect flowers per staminate plant was also determined by searching for inflorescences containing staminate and perfect flowers and recording the relative number of each flower type. Perfect flowers constitute a very small proportion of the larger number of flowers produced on staminate plants in *D. viscosa*, and so inflorescences containing perfect flowers had to be sought out rather than randomly chosen as in the case of dioecy. In each population at least 6 inflorescences containing perfect flowers were counted for each of 10 staminate plants. The proportion of perfect flowers in those inflorescences possessing them was very similar in the three populations and ranged from 9.1 - 12.8% with an average of 10.7% (table 4.2).

To extrapolate the staminate/pistillate flower ratio per inflorescence and to counteract some of the bias resulting from non-random sampling of perfect-flowered inflorescences, counts were made of the numbers of inflorescences per branch or section of individual and this subsample was used to estimate the total number of inflorescences per plant. Although these estimates are rough, they yielded very similar results in all three populations. The average percentage of inflorescences containing perfect flowers on staminate plants for the three populations is 4.7%.

Given that 10.7% of flowers in a staminate and perfect-flowered inflorescence are perfect (table 4.2) and approx. 4.7% of the inflorescences on the staminate plants contain perfect flowers, then approx. 0.4% flowers on staminate plants are perfect. This is a very small proportion of the total number of flowers, and since the perfect flowers are difficult to see among the many male flowers it is not surprising that perfect flowers had not previously been recorded for several polygamo-dioecious *Dodonaea* species.

ii) Number of inflorescences per plant

Accurate counting of all inflorescence numbers on large, perennial shrubs with many flowers proved impossible. Instead, estimates of inflorescence number were made by counting the inflorescences in a certain proportion of the plants (depending on the size and shape of the bush) and extrapolating from this subsample to estimate the total number of inflorescences. These estimates were made for 5 staminate and 5 pistillate plants in each of the three populations. The considerable variation encountered between plants may be due to environmental factors or age of the plants. In each population the number of inflorescences on the staminate plants was slightly greater (average of 5% more) than on the pistillate plants.

iii) Sex ratio

Dodonaea is no exception to the predominance of males reported in samples from populations of various dioecious species (Godley, 1964 & 1976; Lloyd, 1973; Bawa & Opler, 1975; Bawa, 1977).

Staminate/pistillate plant ratios were determined for several naturally occurring, and little disturbed, populations of *Dodonaea* species studied in the field. In dioecious species this is possible even after flowering, since the pistillate plants usually possess capsules and the staminate individuals are either sterile or sometimes old calyces remain. Sex ratios for 11 species determined from flowering populations are given in table 4.3. The staminate bias of sex ratios was further substantiated by those non-flowering populations for which sex ratios were determined.

Thus, all three factors influencing staminate/pistillate flower ratios contribute to an excess of staminate flowers over pistillate flowers in *D. viscosa*. The main excess of staminate flowers is derived from the

Table 4.3 Sex ratio (i.e. staminate/pistillate plant ratio) of naturally occurring populations of *Dodonaea* species.

<u>Species</u>	<u>Populations</u> (& J.G. West voucher specimens at AD)	<u>Sample size</u>	<u>Sex ratio</u>
<i>D. baueri</i>	Cummins, Eyre Pen., S.A. (1971-1978)	29	1.2
† <i>D. bursariifolia</i>	Hatter Hill, W.A. (996-1008)	20	1.2
	90 Mile Desert, S.A. (2280-2283)	125	2.5*
<i>D. ceratocarpa</i>	Cape Naturaliste, W.A. (3234-3245)	58	2.2*
† <i>D. glandulosa</i>	Kulin, W.A. (3144-3153)	60	1.7
<i>D. hexandra</i>	Monarto, S.A. (1348-1350)	109	2.0*
<i>D. humilis</i>	Vivonne Bay, K.I., S.A. (1291-1298)	99	1.7*
<i>D. ptarmicaefolia</i>	Ravensthorpe, W.A. (969-975)	115	3.8*
<i>D. stenozyga</i>	Nullarbor Plain, S.A. (2681-2685)	30	2.0
<i>D. triquetra</i>	Merimbula, N.S.W. (828-835)	23	1.1
† <i>D. truncatiales</i>	Nowra, N.S.W. (2566-2570)	22	2.1
† <i>D. viscosa</i>			
ssp. <i>angustissima</i>	Wilpena Pound, S.A. (386-398)	31	1.2
	American R., K.I., S.A. (1254-1258)	47	1.6
ssp. <i>cuneata</i>	Monarto, S.A. (1351-1356)	44	1.8
ssp. <i>spatulata</i>	Coromandel Valley, S.A. (1217-1227)	39	1.3
	Eden Hills, S.A. (1242-1253)	170	1.3
	Torrens Gorge, S.A. (2663-2672)	125	2.3*
	Keith, S.A. (431-443)	29	1.6

† Species which are usually dioecious, rarely polygamo-dioecious, counted as if dioecious for sex ratio determinations.

* Statistically significant at 5% level by χ^2 test.

extra staminate flowers per inflorescence and the larger number of staminate plants. Although there are slightly more inflorescences on staminate plants the overall difference is not significant. The possible significance of this excess of staminate flowers in *D. viscosa* is speculated upon below.

Floral rewards

The only reward offered to any flower visitor to *Dodonaea* is the pollen of staminate and perfect flowers. No nectar has been found in any flowers. This is one of the factors leading to the suggestion that *Dodonaea* is anemophilous.

Visitors

After many hours in the field observing *Dodonaea* populations the only species seen visiting flowers is the introduced honey bee.

The viscous surface of new leaves and young fruit in most *Dodonaea* species may attract some insects. Several species of ant have been observed on *D. viscosa*, *D. baueri*, *D. lobulata* and *D. ptarmicaefolia*. In the case of *D. viscosa* and *D. baueri* the ants are present only after flowering when the plants are producing new foliage and the amount of viscous material is at its greatest.

I also observed Chrysomelid beetles and the bug *Choerocoris paganus* on *D. viscosa*. Gross (1975) mentioned this latter species as a seed predator of *Dodonaea* species.

Pollination

Population studies, morphological observations and certain tests indicate *Dodonaea* to be anemophilous. This was suggested by Delpino (1890), but Muller & Leenhouts (1976) stated "Although detailed observations are lacking, no genus of Sapindaceae appears obviously adapted to wind

pollination. All flower types are probably insect pollinated ...". In their study of pollen and macromorphology Muller & Leenhouts examined only one *Dodonaea* species (*D. attenuata* = *D. viscosa* ssp. *angustissima*). The characteristics of the genus and other factors contributing to my belief that *Dodonaea* is pollinated by wind are discussed below.

i) The flowers lack petals or any brightly coloured tissues that might attract animal pollen vectors. The absence of petals allows unhindered dispersal of pollen grains by air currents.

ii) Since no nectar is produced, the female flowers lack any floral reward to attract pollinators.

iii) The anthers and stigmatic surfaces are fully exposed at anthesis. The sepals fold back away from the anthers in staminate and perfect flowers and in pistillate flowers the style protrudes well beyond the sepals enclosed around the ovary.

The two prostrate species, *D. procumbens* and *D. humifusa* usually have long pedicels in the staminate flowers and long styles in the pistillate and rare perfect flowers. This may help to raise the reproductive structures above the foliage for wind pollination.

iv) The stigmatic surface area varies in size, but the stigma is branched or tri-partite, so increasing the pollen receptive surface area.

v) The inflorescences are almost always produced at the ends of the branches, and so the flowers are projected beyond the foliage, which otherwise may be an obstruction to free pollen movement in the air.

vi) Pollen

a) *Dodonaea* flowers have large anthers producing copious amounts of pollen, which can easily be seen as yellow pollen 'rain' at anthesis. It is well known that in temperate areas anemophilous dioecious trees

produce enormous quantities of pollen relative to the number of ovules available for pollination (Faegri & van der Pijl, 1971).

The average number of pollen grains per staminate flower was measured for 5 flowers in each of three *D. viscosa* populations by the haemocytometer slide method described by Lloyd (1965, p. 58). Each flower was found to contain more than 96,000 pollen grains and the average over the three populations was 131,000. Measurements of the amount of pollen in perfect flowers with all stamens functional gave similar results.

The pollen/ovule ration (p/o) (Cruden, 1977) for *D. viscosa* therefore, is a minimum of 16,000 and on average 22,000 (assuming 6 ovules per pistillate flower). According to Cruden's correlation of p/o's and breeding systems, this high p/o indicates *D. viscosa* is a xenogamous species.

b) The pollen of *D. viscosa* is capable of travelling considerable distances. Licitis (1953) recorded air-borne *D. viscosa* in atmospheric pollen surveys in New Zealand.

Using a crude adaptation of the pollen trap method, namely exposure of slides covered in glycerine jelly and stained with fuchsin, I collected *Dodonaea* pollen 2.1km from the nearest known population. Although this technique is open to contamination, the pollen of *Dodonaea* was readily distinguishable from that of the small number of other species flowering in the area at the same time and the density of *Dodonaea* pollen on each slide decreased with increasing distance from the source population (fig. 4.1).

c) Although not directly related to anemophily, pollen viability is another factor to be considered. There is no advantage in a species producing large amounts of pollen which is released to the air if the gamete is not capable of fertilisation.

Pollen sterility tests were carried out by the double staining technique as described by Owczarzak (1952). Both fresh pollen and pollen from dried herbarium material was tested for *D. viscosa* ssp. *spatulata*, ssp. *cuneata* and ssp. *angustissima*, *D. baueri*, *D. bursariifolia*, *D. tepperi* and *D. humilis*. Anthers from both staminate and perfect flowers were used. This method does not measure pollen fertility directly, but the proportion of "functional", expanded and double stained pollen does give an approximation to it, even though some grains may be incapable of fertilisation.

All the *Dodonaea* species for which pollen sterility tests were done have more than 83% functional pollen and the great majority more than 90%. So it appears that of the species tested only a very small proportion of *Dodonaea* pollen grains are sterile.

d) *Dodonaea* pollen grains are relatively small - approx. $30 \times 20\mu$ (see also Erdtman, 1952; Merville, 1965; Muller & Leenhouts, 1976). Whitehead (1969) suggested that the majority of wind pollinated species possess small pollen grains (i.e. $20-40\mu$), as they have low collection efficiencies and are less likely to be intercepted by leaves and branches. Obviously, if the grains are too small it becomes increasingly difficult for the stigmas to intercept the pollen.

vii) Species of *Dodonaea* appear to be gregarious. Similar to several other dioecious, anemophilous species (Bawa & Opler, 1975) *Dodonaea* individuals are usually closely spaced and there are many examples of it being the only shrub species in a community.

viii) *Dodonaea* species are absent from dense heath communities and true rainforests. They are usually found in habitats of relatively open vegetation such as open sclerophyll forests, woodlands, mallee communities or arid shrublands.

ix) In those populations studied on a long term basis it appeared that pollen was released under a favourable climatic regime for wind pollination to be successful. Flowering occurred in early summer or late spring (see phenology below) at a time when mean rainfall and humidity drop to summer minimums, mean temperature and the number of clear days increase and the average wind speed reaches its maximum for the year (S.A. Year Book, 1979).

The latrose dehiscence of the anthers appears to be effected by dessication. Anthers were observed releasing pollen only on dry, warm and/or windy days.

x) The flowering times of bushes in any one population appears to be closely coordinated. The flowering sequences of the different flower forms are discussed below.

Thus, the above factors suggest *Dodonaea* is wind pollinated. Each of the characteristics discussed contributes to high pollination efficiency in the genus.

Phenology

During the five years (1975-1979) in which the three *D. viscosa* populations were studied in detail the plants came into flower and the capsules and seeds matured at the same time each year. Flowering occurred in early summer usually for a duration of $2\frac{1}{2}$ - 3 months from early October to late December.

In these populations the capsules took almost one year to ripen. Mature seeds were present in December each year. This long fruit maturation period is in contrast to many other species of the genus and also to *D. viscosa* in populations of western New South Wales (K. Hodgkinson, pers. comm. 1979). Transplant experiments would give some indication of whether this difference might be due to environmental or genotypic influences.

Flowering sequence

The different flower forms show a consistent sequence of flowering in *D. viscosa*. The styles of the perfect flowers on predominantly staminate plants protrude first. The sepals of these perfect flowers continue to surround the immature anthers below the ripe stigmatic surface. The staminate plants of the population which lack perfect flowers usually reach anthesis before the staminate flowers of the staminate plants containing perfect flowers. This flowering sequence and the protogynous perfect flowers enhance outcrossing for those few perfect flowers of the population. The pistillate flowers open last in the flowering sequence. By this time the staminate plants in the population are releasing large amounts of pollen and pollination of most pistillate flowers is relatively assured.

This same flowering sequence was observed in plants propagated vegetatively from the three studied populations and grown under uniform conditions in the glasshouse.

Self compatibility

By tagging perfect flowers in the natural populations it was clear that the mature fruits and viable seed found on the staminate plants resulted from successful fertilisation of these bisexual flowers. Thus, some perfect flowers in the natural populations and in the glasshouse grown plants were used to test for self compatibility in *D. viscosa*. This was carried out by bagging at least 10 perfect flowers in each population with pollination bags of glassine paper in the bud stage to prevent pollination by pollen grains from any other staminate plant. During these tests the plants of two populations were checked daily and the third population was visited every alternate day.

As soon as the style protruded from between the sepals of these perfect flowers, pollinations were performed by hand on five consecutive days using pollen from flowers on the same individual. The bags were retained on the flowers until after the stamens of those flowers had released their pollen grains. Hand pollination was thought necessary since the perfect flowers appeared to be protogynous, as described above, and I suspected that the stigma may have been past its receptive period before the anthers of the same flower dehisced.

Inflorescences on pistillate plants were also bagged so that comparisons of percent fruit set, seed production, ovule/seed ratios and percent effective pollination could be made between perfect and pistillate flowers. In each test some inflorescences or individual flowers were used as controls. These were not bagged, but were tagged so that their development could be monitored.

In these experiments successful pollinations were measured by seed production and the comparison between seed production resulting from self and cross pollination was used as a test for self compatibility in the species.

The ovule /seed ratio and the percent effective pollination were calculated from the potential number of ovules in the actual fruit set. The potential fruit set was also calculated from the original number of flowers tagged or bagged.

Only seeds which appeared viable were counted in these tests. Any showing signs of insect damage, but which appeared to be normal were included, as they were the result of successful pollinations even though attacked later. Samples of the seeds were tested for viability by germination. The oldest of these seedlings are only three years old and

are not likely to flower for at least another two years, and therefore the fertility of the next generation cannot be assessed until that time.

Since there are very few perfect flowers on each staminate plant the sample size in these tests is very small. For this reason the results of these tests are inconclusive and should be used to indicate possible trends only.

The results of some of these tagging and bagging experiments in field populations are shown in table 4.4. Tests carried out in each population and in the glasshouse produced very similar results.

Table 4.4 gives percent fruit set, seed production, ovule/seed ratios and percent effective pollination for bagged and non-bagged perfect flowers on staminate plants, and for comparison the same data for bagged and non-bagged pistillate flowers.

The hand pollination was probably not necessary since in most cases the anthers of the bagged flowers dehisced sooner than the anthers in non-bagged perfect flowers of the same plant. This also occurred in the bagged flowers on the plants in the glasshouse and was probably due to warmer conditions inside the bag (although more humid) increasing the rate of maturation of the pollen grains. In addition, effective pollination took place in those perfect flowers which were bagged but not hand pollinated.

Tagged inflorescences on several pistillate plants, including those in table 4.4, showed a loss of 1-5 flowers per inflorescence between the time of anthesis and maturation of the capsules. Since seedless capsules do form normally (reported also by Joshi (1938) in India) the reductions in flower numbers are probably not because the flowers were not pollinated. Some appear to develop normally initially, and then at a later stage simply dry off and drop from the inflorescence. In some species insect attack is

Table 4.4 Percent fruit set, seed production, ovule/seed ratios and percent effective pollination for bagged and non-bagged pistillate flowers and perfect flowers on staminate plants.

<u>Individual</u>	<u>No. of flowers</u>	<u>No. fruit formed</u>	<u>Percent fruit set</u> %	<u>No. Seeds</u>	<u>Seed/fruit</u>	<u>Percent effective pollin⁰*</u> %	<u>Ovule/seed ratio*</u>
A. Pistillate flowers							
1. Eden Hills 1242		509		800	1.6	26.2	3.8
bulk sample tagged (untreated)	36	35	97	48	1.4	22.9 (22.2)	4.4 (4.5)
bagged	32	6	18.8	9	1.5	25 (4.7)	4 (21.3)
2. Coromandel Valley 1224		68		199	2.9	48.8	2.1
bulk sample tagged (untreated)	25	22	88	50	2.3	37.9 (33.3)	2.6 (3)
bagged	20	0	-	-	-	-	-
3. Coromandel Valley 2659		56		76	1.4	22.6	4.4
bulk sample tagged (untreated)	18	17	94.4	26	1.5	25.5 (24.1)	3.9 (4.2)
bagged	25	0	-	-	-	-	-
B. Perfect flowers							
1. Coromandel Valley 1220							
tagged (untreated)	4	4	100	5	1.3	20.8	4.8
bagged	5	5	100	7	1.4	23.3	4.3
emasculated & bagged	3	0	-	-	-	-	-
2. Coromandel Valley 1227							
tagged (untreated)	5	4	80	7	1.8	29.2 (23.3)	3.4 (4.3)
bagged	6	4	66.7	6	1.5	25 (16.7)	4 (12)
emasculated & bagged	4	2	50	3	1.5	25 (12.5)	4 (12)
3. Coromandel Valley 2658							
tagged (untreated)	7	5	71.4	6	1.2	20 (14.3)	5 (7)
bagged	3	2	66.7	3	1.5	25 (16.7)	4 (6)
emasculated & bagged	3	0	-	-	-	-	-

* Calculated for actual fruit set and potential fruit set (given in brackets below) from the original number of flowers tagged or bagged.

high, but in *D. viscosa* these predators appear to have greater effect after fruit maturation by destroying ripe seeds.

Seed produced from pistillate plants must be the result of cross pollination. Providing the technique used to exclude "foreign" pollen was successful, then seed produced from bagged perfect flowers was the result of self pollination, while that from non-bagged perfect flowers could be from either self or cross pollination.

Table 4.4 shows the seed production from the bagged perfect flowers (selfed) to be very similar to that from the non-bagged pistillate flowers (out-crossed). These results indicate *D. viscosa* to be self-compatible.

Because of my concern that the bagging technique was not successfully excluding all pollen, I isolated two glasshouse grown plants vegetatively propagated from the same parent plant. One of these two plants possessed only pure staminate inflorescences and the other contained inflorescences with some perfect flowers. This was repeated for three separate individuals. In each case the perfect flowers produced some viable seed. This too indicates *D. viscosa* is self-compatible.

While the above tests and the lack of seed from bagged pistillate flowers and bagged emasculated perfect flowers, suggest the bagging technique was capable of excluding foreign pollen, occasionally bagged flowers (and not hand pollinated) produced viable seed. For example, the effective pollination for bagged pistillate flowers (West 1242) was 4.7% and 12.5% in bagged, emasculated perfect flowers (West 1227) (table 4.4). Viable seed was also produced from bagged pistillate flowers in the glasshouse and in pistillate plants grown in isolation of all other *Dodonaea* material.

These results suggest *Dodonaea viscosa* may be apomictic. Similar bagging tests carried out on other *Dodonaea* species in the glasshouse resulted in no seed production. However, there are reports of viable seed being produced from isolated pistillate plants of other *Dodonaea* species. For instance, Mueller (1862) reported production of viable seed from the dioecious *D. hexandra* pistillate plants in the absence of staminate plants in the Melbourne Botanic Gardens and an isolated pistillate plant of *D. microzyga*, another dioecious species, has formed viable seed in Kings Park Perth (G. Keighery, pers. comm. 1979).

Given the selective pressures for outbreeding in dioecious species (Bawa, 1974), apomixis would seem unlikely in *Dodonaea*. However, apomixis has been reported from other dioecious genera. Small (1978) reported a claim of apomixis in the dioecious, anemophilous *Humulus lupulus* (Cannabidaceae). A table of agamospermous flowering plants listed by Grant (1971) included ten partly agamospermous genera whose sexual species are dioecious and/or monoecious. Further, Grant stated "Dioecism and monoecism, which are relatively uncommon in the angiosperms as a whole, have a disproportionately high frequency of occurrence in partly agamospermous genera."

Venkateswarlu & Rao (1975) discussed apomixis in *Coix aquatica* (Gramineae) using a number of characteristics frequently associated with apomictic species. These include the occurrence of polyploid series, disturbed meiotic behaviour, polymorphic species, the perennial growth habit and the ability to form intra- and interspecific hybrids. Although no polyploidy has been observed in *Dodonaea viscosa* and its meiotic behaviour appears to be regular, the species is highly polymorphic, it is a perennial shrub or small tree and, as discussed in Chapter 7, *D. viscosa*

forms interspecific hybrids and many intermediate forms are present in the species. Thus, *D. viscosa* does fulfill some of these criteria for apomixis.

Further tests for apomixis, especially on dioecious species, need to be completed before it can be established for certain that along with sexual reproduction, facultative apomixis occurs in *Dodonaea*.

4.3 EVOLUTION AND SIGNIFICANCE OF DIOECY

Recently there has been much discussion about the evolution and significance of dioecy in the flowering plants (e.g. Kaplan, 1972; Bawa & Opler, 1975; Charnov, 1979; Willson, 1979; Webb & Lloyd, 1980). The position of *Dodonaea* with respect to some of these hypotheses is briefly discussed below.

Stebbins (1951) proposed that dioecious plants evolved in temperate species in response to selective pressures favouring wind pollination. However, the high incidence of dioecism reported in tropical insect pollinated species (Whitehead, 1969; Bawa & Opler, 1975) suggests that this is not the case.

Dioecy could evolve via a number of different pathways, including from gynodioecy, monoecy, hermaphroditism and heterostyly. Bawa & Opler (1975) suggested that in most species studied by them " ... dioecism has probably evolved from a self-compatible breeding system in response to selective pressure for outcrossing." They proposed four hypotheses which favour the evolution of dioecy when selective pressures for outcrossing arise. The hypotheses suggested by Bawa & Opler are based on 1) the relatively simple genetic and physiological changes needed for dioecy to arise, 2) the greater pollination efficiency allowed by dioecism under certain conditions, 3) a greater chance of escape from seed predation as a

consequence of increasing seed set and 4) the ability of dioecious species to exploit a wider variety of microhabitats than hermaphroditic species.

Willson (1979) suggested that sexual selection has contributed to the evolution of certain aspects of differential pollen/ovule ratios including dioecy. She maintained that both competition for mates and differential fitness of mates could be responsible for the successful separation of the sexes.

These hypotheses and others are further considered in relation to the significance of and maintenance of sex ratios which depart from unity.

In sexually dimorphic plants male-biased sex ratios similar to those presented here for *Dodonaea*, have been reported in a variety of species (e.g. Godley, 1964; Lloyd, 1973; Lloyd & Webb, 1977; Opler & Bawa, 1978; Webb & Lloyd, 1980). Cases are also given of female-biased sex ratios (e.g. Melampy & Howe, 1977 in *Triplaris americana*), but in general male-biased ratios appear to be more common than female-biased ratios in perennial species (Webb & Lloyd, 1980).

Several models and hypotheses have been proposed to explain sex ratios in natural populations or to predict sex ratios. Explanations for deviations from 50:50 are usually based on the genetics of sex determination (Lloyd, 1974) or on ecological factors (Harris, 1968; Putwain & Harper, 1972; Lloyd & Webb, 1977; Opler & Bawa, 1978). Since many of these hypotheses were discussed in detail by Lloyd (1973, 1974a & 1974b), Lloyd & Webb (1977) and Webb & Lloyd (1980), they will be mentioned only briefly here.

Kaplan (1972) considered sex ratios in terms of optimal strategies for the population and proposed a model relating seed production to sex ratio in uni-ovulate anemophilous plants. His model indicated that at low densities maximum seed production was reached with equal numbers of

male and female plants, while at higher densities the maximum occurs at lower sex ratios. Anemophilous plants with different floral and pollen features will show different degrees of this density-dependent shift depending on the rate of increase of the number of pollen grains per stigma as the number of staminate plants increases. Kaplan's model implies that with more than one ovule per flower as in *Dodonaea*, a larger proportion of male plants would be necessary to reach maximum seed production.

Charnov (1979) examined the problem of sex allocation from the point of view of fitness gain. He proposed a model which is based on the assumption that the equilibrium allocation of resources to male versus female function maximises the product of fitness gain through the male function (m) (e.g. pollen) times the gain through the female function (f). So that changes, such as evolution of dioecy, will only occur if the equilibrium sex allocation maximises the fitness gain of male by female function ($m \times f$). Changes will not occur if this is not so.

Opler & Bawa (1978) suggested gamete selection, differential mortality and differential attainment of reproductive status may be responsible for the biased sex ratios in some tropical tree species.

In the case of *Rumex acetosella* (Polygonaceae), Putwain & Harper (1972) showed that females allocate more biomass to sexual reproduction than males, so leaving females less for vegetative reproduction. Although no experimental evidence is available, I have observed in several *Dodonaea* species, healthy new vegetative growth on male plants, while the female plants of the same population are laden with fruit and show no new foliage. Webb & Lloyd (1980) have proposed that the greater reproductive cost to females than males results in differential longevity of the sexes.

Several of the hypotheses relating to the evolution of dioecy and the maintenance of male-biased sex ratios may apply to *Dodonaea*. It seems clear that dioecy is a derived condition which has evolved within the genus and that the few rarely polygamo-dioecious species are in the process of adopting dioecy. The original bisexual condition of the staminate and pistillate flowers is still shown in the presence of an aborted gynoecium in staminate flowers and an aborted androecium in pistillate flowers.

4.4 FRUIT AND SEED DISPERSAL

The broad wings of the light, membranous capsules in Sections *Dodonaea*, *Pinnatae*, *Platypterae* and *Plagiopterae* are clearly well adapted for wind dispersal. Fruits of several species belonging to these sections have been collected as far as 100 metres from the nearest plant.

Since it is suggested that *Dodonaea* has migrated long distances by long distance dispersal (see Chapter 5), the floating ability of capsules of *D. viscosa* was tested by placing fruits in dishes of sea water for various lengths of time. After 100 days 30% of the capsules were still floating. The viscous nature of the fruits may reduce permeability to water and aid in their ability to float. Although these fruits were sitting in still water at room temperature and not subjected to the turbulence and changing temperatures of the open seas, it is clear that the capsules are able to float for a considerable length of time. Guppy (1906) in discussion of agencies of dispersal of *D. viscosa* in the Pacific concluded that "placed in their order of effectiveness they (the agencies of dispersal) would be first birds, then the currents, and lastly man."

Observations on populations in the field suggest that capsules of those *Dodonaea* species lacking any dorsal wing development (Sections *Apterae*, *Cornutae* and *Inappendiculatae*) are not dispersed by wind. These fruit are mostly crustaceous and thicker and heavier than those blown around in the wind and the fruits are generally found only close to the parent plant. However, capsules of *D. aptera*, *D. baueri*, *D. hexandra*, *D. ceratocarpa* and *D. pinifolia* have been found washed downhill in natural gutters and run off areas.

The glandular hairs on capsules of *D. humilis* and *D. glandulosa* may aid in dispersal by animals. A house mouse (*Mus musculus*) on Kangaroo Island was observed to have a capsule containing 4 seeds attached securely to its underbelly fur.

It is significant that in general those species with wings on the fruits and which are probably wind dispersed are widespread, while the species lacking or with very reduced appendages exhibit restricted distribution patterns.

The figures in table 4.4 indicate *D. viscosa* produces between one and three seeds per capsule. An individual pistillate plant of most *Dodonaea* species produces a large amount of fruit and viable seed. The results obtained from counting seeds produced (in bulk samples) indicated that in some *D. viscosa* populations up to 25% of the viable seed crop is harvested by insects.

Germination tests of as many species of which seed was obtained indicated the arillate seeds have a resistant testa which prevents germination for a period of at least 6 months after ripening. Seed of many exarillate species germinated within 7 weeks of harvesting. Seed of both types is capable of germination for a period up to 18 months after sowing.

In order to test its viability after possible long distance dispersal in sea water, *D. viscosa* seed from the same plant was soaked in sea water for periods up to 6 months. After 3 months 88% of the seed germinated and 79% after 6 months. These results suggest it is feasible for *D. viscosa* to germinate and establish itself in an area following a considerable period of time in sea water.

Species of *Dodonaea* germinate readily after fire. *D. viscosa* s. lat. is regarded as a fire weed in some areas of New South Wales and Floyd (1976) reported on *D. triquetra* germination following prescribed burns (see *D. triquetra*, p. 287).

4.5 CONCLUSION

Studies of the floral morphology and pollination biology in *Dodonaea* indicate that the genus is wind pollinated. It appears from self-compatibility tests that *D. viscosa* is self-compatible and that apomixis may occur. Dioecy is well established in most sections of *Dodonaea* and the few polygamo-dioecious species probably represent a stage in the evolution of this breeding system.

The breeding system of any species or group of species reflects the gene flow patterns in the group, and so, to successfully apply taxonomic delimitations, an understanding of the reproductive strategies of the group is very important. The breeding system studies have contributed significantly to an understanding of relationships between and within the species of *Dodonaea*. For instance, given the variability and flexibility in the breeding system of a species such as *D. viscosa* it is not surprising to meet with difficulty in delimiting taxa in the *D. viscosa* complex (discussed in Chapters 6 and 7).

CHAPTER 5

RELATIONSHIPS, EVOLUTION AND BIOGEOGRAPHY

In this chapter morphological evolutionary trends of certain features such as the inflorescence, fruit and seed are examined. Relationships between sections (as proposed in this treatment) and between species within these sections are discussed largely on the basis of these evolutionary trends in morphology. Present-day distributions, macromorphology, dispersal characteristics and fossil evidence are used to speculate on ~~the origin of and~~ radiation and adaptation within *Dodonaea*.

5.1 MORPHOLOGICAL TRENDS

Fruit

The capsules of *Dodonaea* provide some of the most obvious diagnostic characters on which to base the taxonomy of the genus. The variation in capsule texture and appendage shape and size show morphological trends through the genus. In Section *Dodonaea* and Sect. *Pinnatae* the capsule appendage is a broad, membranous or rarely chartaceous, rounded wing of equal width throughout. This relatively large wing is slightly reduced to a smaller, oblique, longer than broad, membranous or rarely coriaceous wing, sometimes not extending right from capsule apex to base in Sect. *Platypterae* and Sect. *Plagiopterae*. In Sect. *Cornutae* the appendage is crustaceous, horn-like and at the capsule apex only, while fruits of Sect. *Apterae* have a very small lobe-like appendage at the capsule apex, or the appendage is absent. Since the large, rounded wing appears to be the least specialised, is more common in the genus and correlates with other characters regarded as being unspecialised, it is

considered to be the most primitive with a gradual reduction of the appendage to the species of Sect. *Apterae* and Sect. *Inappendiculatae* which generally lack capsule appendages. In addition, specialisations such as enlarged glandular hairs are present on the carpels in Sect. *Inappendiculatae*.

The texture of the capsules parallels this trend with variation from transparent, membranous fruits in Sections *Dodonaea* and *Pinnatae*, through coriaceous capsules of Sections *Platypterae* and *Plagiopterae*, to the small crustaceous, often thickened and hardened fruits of Sections *Cornutae*, *Apterae* and *Inappendiculatae*.

Seed

The nature of the aril in those species of Sect. *Cornutae* and most of Sect. *Apterae* is described in Chapter 3. The aril in *Dodonaea* is a post-floral funicular outgrowth which is free from the seed. Following van der Pijl's (1957) argument relating to the origin of the aril, its presence is here regarded as an advanced character.

As discussed in Chapter 4 the arillate seeds are also those which appear to possess dormancy factors inhibiting germination, whereas those without arils usually germinate readily.

Inflorescence

The form and variation of *Dodonaea* inflorescences are described in Chapter 3. The more complex, many-flowered frondobracteose panicles of *Dodonaea viscosa* and *D. polyzyga* are considered to be the most primitive state. Other less complex forms may have been derived from this condition via an evolutionary reduction series.

Briggs & Johnson (1979) pointed out that the features of an inflorescence which may show flexibility and result in reduction of the paniculate condition are:

1. number of nodes on the axes
2. degree of branching
3. number of flowers.

In most situations it is probably combinations of these factors which manifest the reduction process.

Dodonaea shows a series from panicles through metabotryoids, triads and diads to monads whether of an anthotelic or blastotelic seasonal growth unit (fig. 5.1). The highest degree of branching of a panicle (fig. 5.1a) or a metabotryoid (fig. 5.1b) can be reduced to a botryoid by a change in the number of nodes and the degree of branching (fig. 5.1c&d). One species, *D. multijuga*, appears to exhibit an intermediate stage in this reduction phase. The axillary inflorescences of male and female plants of *D. multijuga* examined on herbarium specimens, in field populations and on plants in the glasshouse all show abortive buds at the lateral nodes (fig. 5.1e). Further reduction in the number of nodes results firstly in triads (fig. 5.1f&g), then diads (fig. 5.1h&i) and finally, with a change in the degree of branching as well, monads (fig. 5.1j&k).

The node in the lower half of the pedicel, as described in Chapter 3, also suggests reduction in the degree of branching and/or the number of flowers in the inflorescence.

This reduction series could be derived by a variety of pathways and it is through examination of closely related species that suggests the origins are among the complex many-flowered inflorescences of Sect.

Dodonaea and Sect. *Pinnatae*. Examples of the reduced botryoidal inflorescences are common in Sect. *Platypterae* and Sect. *Plagiopterae* and less so in the former two sections. The species of Sections *Apterae*, *Cornutae* and *Inappendiculatae* have predominantly monadic or diadic inflorescences.

Breeding system

Variation in the breeding system of *Dodonaea* was discussed in Chapter 4. While most species are truly dioecious, a significant proportion (14 species or 23%) are also polygamo-dioecious in having plants with female flowers only and male plants bearing some bisexual flowers among the predominant male flowers. Four species are solely polygamo-dioecious and two are polygamous. The polygamous and polygamo-dioecious forms are considered to be primitive with the more derived breeding system involving dioecism having evolved within the genus. The presence of an aborted gynoecium in male flowers and an aborted androecium in female flowers provides evidence of the original bisexual condition of these unisexual flowers.

The two polygamous and four polygamo-dioecious species all belong to Sect. *Dodonaea* or Sect. *Pinnatae*. Those species which are basically dioecious and rarely polygamo-dioecious occur in each section except Sect. *Plagiopterae* - five in Sect. *Dodonaea*; three in Sect. *Pinnatae*; three in Sect. *Apterae*; and one in each of Sections *Platypterae*, *Cornutae* and *Inappendiculatae*. Dioecy therefore, is the predominant form in each section of the genus. Since almost all sections contain polygamo-dioecious taxa, it appears that the trend towards dioecy has taken place within several groups of closely related species.

Leaves

All the species in Sections *Pinnatae*, *Plagiopterae* and *Inappendiculatae* have compound mature leaves, while the species in the remaining sections, (Sections *Dodonaea*, *Platypterae*, *Apterae* and *Cornutae*) have simple mature leaves.

Since the morphological trends in other features, e.g. capsules, seeds and inflorescences, appear to occur in parallel through the simple- and compound-leaved groups it is difficult to determine the more primitive leaf form.

Although there are exceptions, there are several examples, such as *Acacia*, in which it is believed that compound leaves preceded simple leaves, or phyllodes in the case of *Acacia*.

Takhtajan (1969,1976) put a strong case for the role of neoteny in the evolution of the angiosperms. Other workers, such as Melville (1976) in regard to leaf shapes in *Parsonsia* populations in New Zealand, believe neoteny has played a significant part in enabling juvenile characters to be passed on into the adults. While it is believed that the earliest angiosperms had pinnately-veined simple leaves (and therefore that the simple, entire leaf with pinnate venation is primitive as far as extant angiosperms are concerned), it is quite feasible that compound "mature" leaves have evolved in certain groups via the neotenic process.

Seedlings of almost all of the 62% of *Dodonaea* species so far examined possess lobed or deeply lobed to pinnate juvenile leaves whether or not the mature foliage is simple or compound. It is possible that neoteny has been responsible for the retention in adult plants of certain characters, in particular pinnate or lobed leaves, which were originally only juvenile characters. It is significant from an evolutionary genetic

point of view, that neoteny allows for maximum phenotypic effect with minimal genotypic change.

Davis and Heywood (1963) explained the opposite trend, i.e. the early arrest of the progression from simple to dissected leaves in *Ranunculus*, as a neotenic relationship. Presumably the direction of such morphological trends would greatly depend on selection pressure and the characteristics of the group concerned.

It would seem then that the compound leaves on adult plants of *Dodonaea* Sections *Pinnatae*, *Plagiopterae* and *Inappendiculatae* could have evolved via neoteny compared with Sections *Dodonaea*, *Platypterae*, *Apterae* and *Cornutae*, which have simple adult leaves and lobed to compound juvenile leaves.

5.2 RELATIONSHIPS BETWEEN SECTIONS WITHIN *DODONAEA*

Given that the above examination of several features of *Dodonaea* reveals morphological evolutionary trends enabling assessment of the probable primitive and advanced state of certain important characters, it should be possible to establish the basic characteristics of the most primitive group(s) of species within the genus.

The discussion above indicates the primitive species in *Dodonaea* would possess relatively large, membranous capsules with rounded wings, complex, many-flowered paniculate or metabotryoidal inflorescences, exarillate seeds and probably simple adult leaves. These characteristics are true of Sect. *Dodonaea* and except for the compound leaves, also of Sect. *Pinnatae*. Using this method Sections *Apterae*, *Cornutae* and *Inappendiculatae* possess the advanced states of the studied characters. The species of these groups have small, crustaceous capsules which may be

inappendiculate or possess small, lobe-like or horn-like appendages at the apex only, flowers are arranged in mostly reduced monadic or diadic inflorescences and the seeds are arillate. Between the derived and primitive extremes lie Sections *Platypterae* and *Plagiopterae*, which exhibit intermediate morphology in these evolutionary trends.

It is obvious that there are both simple- and compound-leaved groups at each stage in the morphological trends discussed. If this interpretation is correct then features of the capsules, inflorescences and seeds have evolved in parallel in the simple- and compound-leaved sections of *Dodonaea*.

Alternatively, specialisations seen in the capsules, inflorescences and seeds of *Dodonaea* may have developed along one evolutionary line. The pinnate foliage then must have arisen more than once, and probably at least three times, in the genus.

A critical argument against this latter hypothesis is the fact that the inflorescence, capsule and seed characters shared by any groups are at the primitive end of the lineage. The more specialised or derived capsule and seed characters are unique to each group in which they occur. For instance, glandular hairs on the inappendiculate capsules in the pinnate-leaved Sect. *Inappendiculatae* and the arillate seeds and horn-like appendages on the capsules of the simple-leaved Sect. *Cornutae*.

Although there is not enough evidence to distinguish between these two hypotheses, I have chosen the evolutionary scheme involving parallel development of capsules, seeds and inflorescences in the pinnate- and simple-leaved groups. The weight of available evidence is in favour of this hypothesis and it corresponds more closely with the more natural classification of *Dodonaea* as proposed in this treatment.

Another method of estimating phylogeny is that of computing Wagner Trees. The method as devised by Farris (1970) involves assumptions similar to those made above on the primitive or advanced state of each character and requires considerable computation and computer time. Whiffin & Bierner (1972) described a simplified method for computing Wagner Trees. Their method does not require prior assessment of primitive and advanced states of all characters employed, although it does necessitate the choice of one taxon to represent the most primitive taxon. This method of determining phylogenetic schemes naturally involves a level of subjectivity in the character selection, but as discussed in Chapter 6, the computation of such models treats each character as equal and is therefore less subjective.

Table 5.1 lists the characters which are used to distinguish the infrageneric groups. The total number of characters for which pairs of taxa exhibit different states is calculated from this table and presented in table 5.2.

For reasons given above Sect. *Dodonaea* is selected as the most primitive or ancestral taxon and the infrageneric taxa are listed in order of absolute difference from this ancestral stock (table 5.3). Following Whiffin & Bierner (1972) a Wagner Tree was constructed (fig. 5.2). The main characters on which the evolutionary scheme is based are given for each section.

The resulting evolutionary scheme gives an hierarchical expression of interrelationships of the sections based on observable morphological attributes. As such it must be remembered that it is not proposed as a true phylogeny, but as a working hypothesis revealing preliminary branching patterns of the group.

Table 5.1 The character states for each section of *Dodonaea*
 (+ = possession of a character state
 - = absence of a character state)

Character states	Sect. <i>Dodonaea</i>	Sect. <i>Platypterae</i>	Sect. <i>Apterae</i>	Sect. <i>Cornutae</i>	Sect. <i>Pinnatae</i>	Sect. <i>Plagiopterae</i>	Sect. <i>Inappendiculatae</i>
1. LEAVES							
a. simple	+	+	+	+	-	-	-
b. compound	-	-	-	-	+	+	+
2. <u>Margin of leaf/leaflet</u>							
a. entire	+	+	+	+	+	+	+
b. not always entire	+	+	+	+	-	-	-
3. <u>Apex</u>							
a. toothed/lobed	+	-	+	-	+	-	+
b. entire	+	+	+	+	+	+	-
4. <u>Petiole</u>							
a. present	+	+	+	-	+	+	+
b. absent	+	+	+	+	-	-	-
5. FLOWERS							
a. polygamous	+	-	-	-	+	-	-
b. polygamo-dioecious	+	+	+	+	+	-	+
c. dioecious	+	+	+	+	+	+	+
6. INFLORESCENCES							
a. simple - monadic, diadic or botryoids	+	+	+	+	+	-	+
b. complex - metabotryoids, panicles	+	+	-	-	+	+	-
CAPSULES							
7. <u>Carpel texture</u>							
a. membranous	+	-	-	-	+	-	-
b. coriaceous	+	+	-	-	+	-	-
c. crustaceous	-	+	+	+	-	+	+

Table 5.1 (cont.)

	Sect. <i>Dodonaea</i>	Sect. <i>Platypterae</i>	Sect. <i>Apterae</i>	Sect. <i>Cornutae</i>	Sect. <i>Pinnatae</i>	Sect. <i>Plagiopterae</i>	Sect. <i>Inappendiculatae</i>
8. <u>Indumentum</u>							
a. ± glabrous	+	+	+	+	+	+	-
b. rarely pubescent	+	-	+	-	+	-	+
c. glandular hairs present	-	-	-	-	-	-	+
9. <u>Appendage</u>							
a. wing	+	+	-	-	+	+	-
b. horn-like, lobe-like	-	-	+	+	-	-	-
c. absent	-	-	+	-	-	-	+
10. <u>Position of appendage</u>							
a. extending from apex to base	+	+	-	-	+	+	-
b. at apex only	-	-	+	+	-	-	-
SEEDS							
11. <u>Aril</u>							
a. present	-	-	+	+	-	-	-
b. absent	+	+	+	-	+	+	+
12. <u>Hyaline membrane</u>							
a. not obvious	+	+	+	+	+	+	-
b. lifting at margin only	+	-	+	-	-	-	+
c. lifting over entire seed	-	-	-	-	+	+	+

Table 5.2 Total number of absolute character state differences between each pair of sections of *Dodonaea*

	Sect. <i>Dodonaea</i>	Sect. <i>Platypterae</i>	Sect. <i>Apterae</i>	Sect. <i>Cornutae</i>	Sect. <i>Pinnatae</i>	Sect. <i>Plagiopterae</i>	Sect. <i>Inappendiculatae</i>
Sect. <i>Dodonaea</i>	-	5	6	10	4	9	11
Sect. <i>Platypterae</i>		-	8	6	8	7	10
Sect. <i>Apterae</i>			-	6	10	11	8
Sect. <i>Cornutae</i>				-	12	9	9
Sect. <i>Pinnatae</i>					-	5	8
Sect. <i>Plagiopterae</i>						-	7
Sect. <i>Inappendiculatae</i>							-

Table 5.3 Sections listed in order of absolute different from Sect. *Dodonaea*

Sect. <i>Pinnatae</i>	4
Sect. <i>Platypterae</i>	5
Sect. <i>Apterae</i>	6
Sect. <i>Plagiopterae</i>	9
Sect. <i>Cornutae</i>	10
Sect. <i>Inappendiculatae</i>	11

The evolutionary scheme reveals two main evolutionary lines within the genus. From the ancestral stock near Sect. *Dodonaea* one line clearly has evolved via Sect. *Pinnatae*, through Sect. *Plagiopterae* and finally to Sect. *Inappendiculatae*. Also from the ancestral stock has evolved a lineage involving Sections *Platypterae*, *Apterae* and *Cornutae*. Sect. *Platypterae* appears to be the most primitive of this lineage. Due to inadequacies of the Whiffin & Bierner method it is difficult to determine the positions of Sections *Apterae* and *Cornutae* with respect to Sect. *Dodonaea* and Sect. *Platypterae*. There is no provision in their method for those cases in which the next taxon entering the tree is equally similar to (i.e. has the same absolute difference from) more than one taxon already in the tree. Step nine of the method covers this case only for the situation in which two taxa have the same absolute difference from the ancestral taxon. Table 5.2 indicates Sect. *Cornutae* to have the same absolute difference from Sections *Apterae* and *Platypterae*. For the purposes of this scheme it has been positioned in order to imply independent development from the Sect. *Platypterae* line as well as via Sect. *Apterae*, the section showing most resemblance to it.

The obvious difference between these two evolutionary lines is that one group has pinnate leaves and the other compound foliage. However, with the removal of character one (i.e. simple versus compound leaves), or even with the removal of all those characters relating to leaves (characters 1-4, table 5.1), a similar evolutionary scheme results.

Nevertheless, the major differences between Sect. *Dodonaea* and Sect. *Pinnatae* lie in the leaves. From the most primitive member of the pinnate-leaved line, Sect. *Pinnatae*, has evolved Sect. *Plagiopterae* with reduced capsule appendages, crustaceous capsule carpels and strictly

dioecious plants. Several species of the former section show widespread distribution patterns in Australia, while the three species of Sect. *Plagiopterae* are more restricted in their distribution. At the end of this line of evolution is Sect. *Inappendiculatae* with very reduced leaves, capsules lacking appendages but possessing specialised features such as glandular hairs, reduced inflorescences and very restricted distributions.

It appears that similar changes have occurred along the simple-leaved line of evolution from the ancestral stock close to Sect. *Dodoniaea*. In its reduced capsule appendages, non-membranous carpels and dioecious or rarely polygamo-dioecious breeding system Sect. *Platypterae* shows similar divergence from Sect. *Dodoniaea* as Sect. *Plagiopterae* does from Sect. *Pinnatae*.

Sect. *Apterae* probably arose through divergence from Sect. *Platypterae* rather than independently from the ancestral stock. It exhibits several derived characters such as crustaceous capsules with very reduced appendages or lacking appendages altogether, mostly arillate seeds, reduced inflorescences and mainly small leaves. In temperate and semi-arid areas of southern Australia some species of this section are widespread, while others exhibit restricted distributions.

Sect. *Cornutae* shows the greatest divergence from the ancestral stock in this line of evolution in its crustaceous capsules with horn-like appendages, arillate seeds, reduced inflorescences, mostly dioecious plants and usually reduced leaves. This section may have evolved from the Sect. *Apterae* line with a change in capsule appendage, further specialisation of other features and restriction in distribution to south-west Western Australia. It is also possible that Sect. *Cornutae*

diverged from the Sect. *Platypterae* line and that the morphological similarities with Sect. *Apterae* are probably a result of evolutionary parallelism. However, I think it is more likely that Sect. *Cornutae* is derived from the Sect. *Apterae* line.

Thus, given the assumption that Sect. *Dodonaea* does represent the primitive stock within the genus, the evolutionary scheme as determined here indicates two main lines of evolution based on morphological attributes. Although tentative, this model adequately accounts for the origins of and shows the interrelationships of present-day infrageneric sections as proposed in this treatment. In particular it confirms the parallel nature of evolution in the simple- and compound-leaved groups as postulated from an examination of primitive and derived characters.

5.3 RELATIONSHIPS WITHIN SECTIONS OF *DODONAEA* IN AUSTRALIA

The following discussion on the relationships of species and infraspecific taxa within the sections of *Dodonaea* is based on morphology and to some extent distribution patterns. Evolutionary schemes are postulated in light of the infrageneric evolutionary hypothesis presented in the previous section. The distribution of all species in each section is shown in figures 5.3 to 5.8 and postulated evolutionary schemes are given diagrammatically at the end of discussion on each section.

Sect. *Dodonaea* (Fig. 5.3)

The polymorphic *D. viscosa* appears to be the most primitive member of Sect. *Dodonaea*. The species (as here circumscribed) is widespread in Australia. There are close similarities between several other species in this section and the infraspecific subspecies of *D. viscosa* as proposed in this treatment.

The morphological diversity of species comprising Sect. *Dodonaea* implies several lines of variation which may have begun near to *D. viscosa*. These evolutionary lines include cases of closely related species pairs.

Dodonaea viscosa is discussed at length in Chapter 6 with respect to numerical analysis of leaf morphology and later in this chapter with reference to generic evolution. Its large winged, membranous capsules, compound inflorescences, polymorphic leaves, polygamo-dioecy and exarillate seeds all contribute to a primitive interpretation. Within the species there are some morphological trends. For instance, the wings vary from the broad membranous capsule appendages of *D. viscosa* ssp. *viscosa* to the narrower, coriaceous wings of ssp. *cuneata*; the large leaves of ssp. *viscosa* and ssp. *burmanniana* are reduced to the very narrow ssp. *angustissima* or the short, cuneate leaves of ssp. *cuneata*.

D. polyandra is closely related to *D. viscosa* ssp. *viscosa* and also shares some characters with *D. triquetra* and *D. lanceolata*. The latter two may have been derived from the ancestral stock independently of *D. polyandra*, but from the number of similar characters it seems just as likely that these species arose along the same evolutionary line. *D. triquetra* and *D. lanceolata* share similar capsules, which are slightly reduced from those of *D. polyandra*, similar seeds and leaves (lacking sessile glands) smaller than those of *D. polyandra*. *D. polyandra* now occupies a similar geographical area to *D. viscosa* ssp. *viscosa*, while *D. lanceolata* var. *subsessilifolia* and *D. triquetra* extend down the east coast of Australia. *D. lanceolata* var. *lanceolata* appears to be an inland form of the species extending across northern Australia.

The geographically restricted *D. serratifolia* appears to have arisen along this line of evolution also. This species is very similar to *D. triquetra* except that it shows some more derived features such as smaller leaves with serrate margins and botryoidal inflorescences.

A second evolutionary line in Sect. *Dodonaea* involves a number of southern Australian species showing certain variations and morphological specialisations. Despite their variability these species do appear to be a natural group with several characters linking them more closely to each other than to any of the other possible evolutionary lines.

D. hackettiana is probably the most primitive of this group of species. It shows several similarities with *D. viscosa* and varies only in its villous indumentum on the branches, the pubescent leaf margins and the compressed seed.

Diverging from the *D. hackettiana* line of evolution are *D. amblyophylla* and *D. bursariifolia*, two species forming a closely related species pair. These two taxa show similarities to *D. triquetra* and *D. lanceolata* in lacking sessile glands and having seeds with the hyaline membrane lifting at the margin. They have smaller leaves, smaller, coriaceous or crustaceous capsules and reduced inflorescences compared with *D. hackettiana* or their probable ancestral stock. *D. amblyophylla* occurs in south-west Western Australia, while *D. bursariifolia* extends across the Nullarbor Plain to South Australia and north-west Victoria. The very narrow capsule wing and septicidal nature of the fruit are slightly more advanced characters than those of *D. amblyophylla*.

D. procumbens and *D. camfieldii* appear to have diverged from this evolutionary line with some morphological variations and restricted geographical distributions. *D. procumbens* is a prostrate species with

crustaceous capsules, small leaves and reduced monadic or diadic inflorescences. *D. camfieldii* is often prostrate and also possesses crustaceous or coriaceous capsules, flowers in monads or diads and leaves with decurrent bases and slightly winged branches.

D. ptarmicaefolia and the variable *D. lobulata* form another closely related species pair in this line of development. The two species have very narrow leaves, relatively small fruits and reduced inflorescences. *D. lobulata* exhibits considerable leaf morphological variability and has a more extensive geographical distribution than *D. ptarmicaefolia* with its regular leaf serrations and restricted distribution to south-west Western Australia.

A third evolutionary line derived from ancestral stock similar to *D. viscosa* is that involving *D. coriacea*, *D. peduncularis* and *D. hirsuta*. The three species show several morphological trends from the most primitive *D. coriacea* to the most derived *D. hirsuta*. Polygamodioecious *D. coriacea* has larger leaves, large capsules with broad membranous wings and a more complex inflorescence than the other two species. It is widespread across eremean northern Australia, while *D. peduncularis* occurs in inland Queensland and New South Wales and *D. hirsuta* occupies a restricted geographical area in north-east New South Wales.

D. peduncularis and *D. hirsuta* are both dioecious species. The latter shows certain specialisations suggesting it to be more advanced than the former. *D. hirsuta* consistently has small obtriangular leaves compared with the more variable and larger, usually angular-obovate to oblanceolate leaves of *D. peduncularis*. The flowers of *D. hirsuta* are monadic (in *D. peduncularis* they vary from monads to botryoids) and, as the name implies, all organs of this species are hirsute.

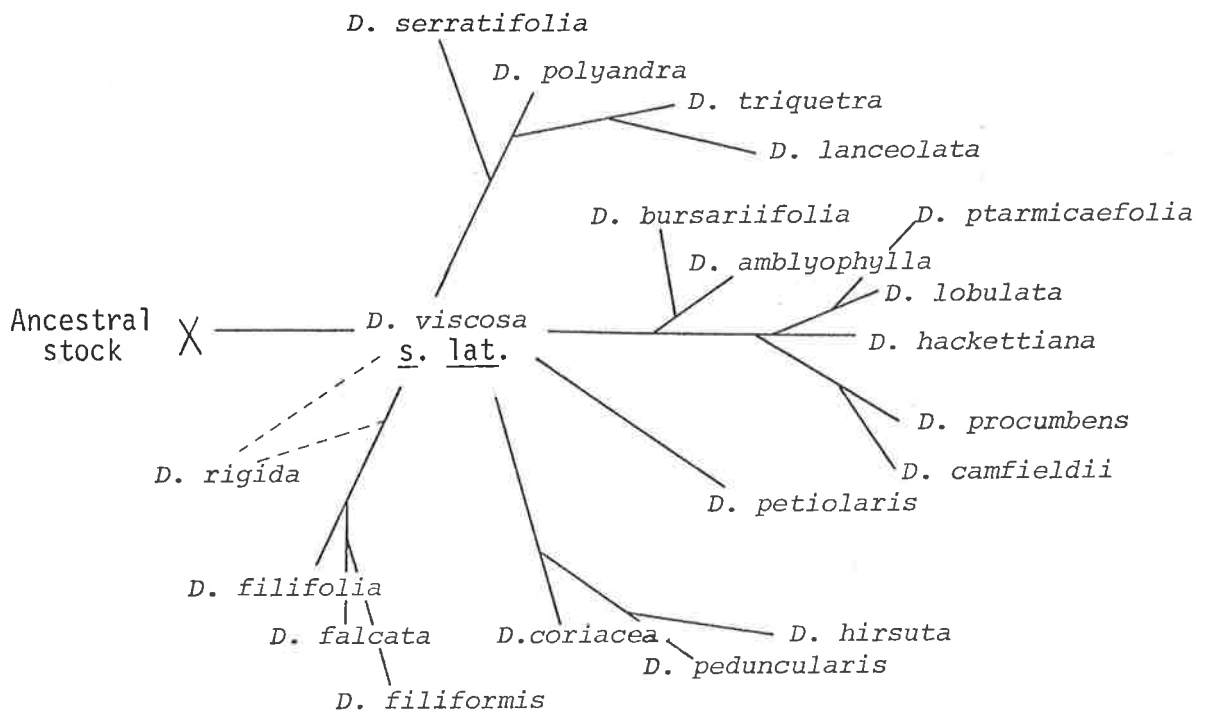
The placement of *D. petiolaris* in an evolutionary scheme is difficult as this species shows a number of morphological variations not shared with any other species in this group. *D. petiolaris* is sympatric with and shows most resemblance to *D. viscosa* ssp. *mucronata*, but its characteristic undulate leaves, globose seeds and inflated capsules distinguish it. For these reasons it is postulated that *D. petiolaris* arose from the ancestral stock independently of all other species in the section.

A fourth line of evolution in Sect. *Dodonaea* involves the filiform-leaved species *D. filifolia*, *D. falcata*, *D. filiformis* of eastern Australia and the Western Australian *D. rigida*. *D. filifolia* with its larger leaves, larger capsules and more complex inflorescence, appears to be the most unspecialised of the three closely related eastern species. It is relatively widespread in eastern Queensland, while *D. falcata* occurs in a more restricted area of eastern New South Wales and *D. filiformis* is confined to Tasmania. There is a gradual reduction in leaf and fruit size from *D. filifolia* to the more derived *D. filiformis*. Pedicel length also decreases - the flowers of *D. filiformis* are almost sessile - and *D. filiformis* has only five stamens (compared with eight in the other two species).

Although showing many resemblances to these three species, *D. rigida* from Western Australia differs from them in several respects. Its leaves are rigid, pungent-pointed, usually 4-ribbed and covered with brown verruculose glands, it has axillary inflorescences (terminal in the eastern species) and simple juvenile foliage (pinnate or pinnatifid in *D. filifolia* and *D. filiformis*). *D. rigida* occupies more arid habitats than the eastern species. It is feasible that *D. rigida* diverged from the same

ancestral stock as *D. filifolia*, *D. falcata* and *D. filiformis* and that the two main stocks became isolated and restricted to the eastern and western parts of the continent by certain geographical barriers. The onset of aridity in southern and central Australia during the Quaternary (Bowler, 1976) is one possible way in which the two lines of variation may have become isolated.

The similarity between *D. rigida* and the narrow leaved form of *D. viscosa* ssp. *angustissima* in Western Australia suggests an alternative origin of *D. rigida*. The dioecious *D. rigida* with its rigid, erect, shorter leaves and less complex inflorescence structure than *D. viscosa* ssp. *angustissima* possesses some advanced features which may indicate an independent origin from the ancestral stock close to *D. viscosa*. At this stage the evidence supports either of these hypotheses and it is not possible to decide with any certainty on one or the other.



Postulated evolution in Sect. *Dodonaea*

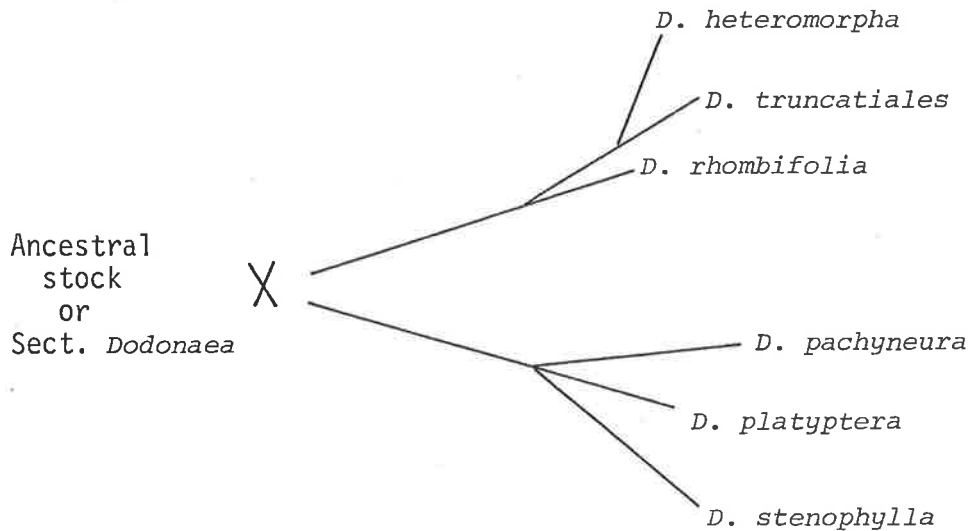
Sect. *Platypterae* (Fig. 5.4)

The species of Sect. *Platypterae* show morphological features intermediate between Sect. *Dodonaea*, from which they may have evolved, and Sect. *Apterae*. There appears to be two lines of evolution in the group, one involving *D. platyptera*, *D. pachyneura* and *D. stenophylla* all of northern Australia and the other, the south-eastern Australian species, *D. truncatiales*, *D. heteromorpha* and *D. rhombifolia*.

D. rhombifolia with its septifragal capsules with broad membranous wings and large viscous leaves seems to be most closely related to Sect. *Dodonaea*. The ecological preferences of this species for granite and basalt outcrops and its apparent associated disjunct distribution pattern may be partly understood given that *D. truncatiales* and *D. heteromorpha* probably evolved from *D. rhombifolia*. Figure 5.4 shows that *D. truncatiales* and *D. heteromorpha* occur between the disjunct areas, in which *D. rhombifolia* is found. *D. truncatiales* is a coast and tablelands species with narrower capsule wings and narrower leaves than *D. rhombifolia*. *D. heteromorpha* is very closely related to *D. truncatiales* and appears to have evolved from it in response to colonisation of the semi-arid western slopes and plains. The retention of some compound leaves, even though irregular, in this species may indicate a link between the pinnate- and compound-leaved groups.

The second evolutionary line evident in Sect. *Platypterae* is one with septicidal fruits and with *D. platyptera* being the most primitive taxon. This species has large leaves, paniculate inflorescences and relatively large, septicidal fruits with broad, sometimes coriaceous wings. *D. pachyneura* and *D. stenophylla* appear to have evolved from *D. platyptera* the former occurring in the Western Australian Hamersley Ranges and the

latter through central Queensland to north-east New South Wales. Those two species possess smaller fruits with reduced wings, narrow leaves and usually botryoidal inflorescences.



Postulated evolution in Sect. *Platypterae*

Sect. *Apterae* (Fig. 5.5)

This section appears to be linked to its ancestral stock through the morphologically more variable *D. triangularis* with its botryoidal inflorescences, lobe-like or sometimes wing-like (although reduced) capsule appendages, exarillate seeds and larger, flat leaves. This relatively widespread eastern Australian species is most clearly related to *D. trifida*, a Western Australian species with a very restricted south coast distribution. These two species are both pubescent, have similar ovary and fruit morphology and both possess exarillate seeds with the hyaline membrane lifting at the margin, a character shared with species of Sect. *Dodonaea*.

The South Australian species, *D. baueri* may have evolved via the *D. triangularis* - *D. trifida* pathway, but I think it more likely to be

independently derived from the ancestral stock. *D. baueri* is a very distinct species and is linked to other species of this section mainly via its capsule characteristics. *D. baueri* shows affinities to members of Sect. *Dodonaea*, for example in leaf characters, which resemble those of *D. intricata*. *D. baueri* seed lacks a true aril, but appears to have an enlarged funicle, and in this way may form a link between the exarillate and arillate seeds.

D. tepperi shows most resemblance to *D. baueri* and may have arisen through hybridisation of *D. baueri* and *D. viscosa* (Sect. *Dodonaea*). Several factors, including comparative morphology, distribution of the possible parent species, habitat types and spasmodic distribution of *D. tepperi* appear to indicate a hybrid origin for *D. tepperi*, but this has not been confirmed and requires further investigation.

D. hexandra is a species of the semi-arid areas of South Australia. It resembles *D. pinifolia* of Sect. *Cornutae* and only diverges from that group in lacking the horn-like appendage on the capsule. If it is considered that Sect. *Cornutae* evolved from Sect. *Apterae*, one alternative discussed above, then *D. hexandra* must be considered as the linking taxon.

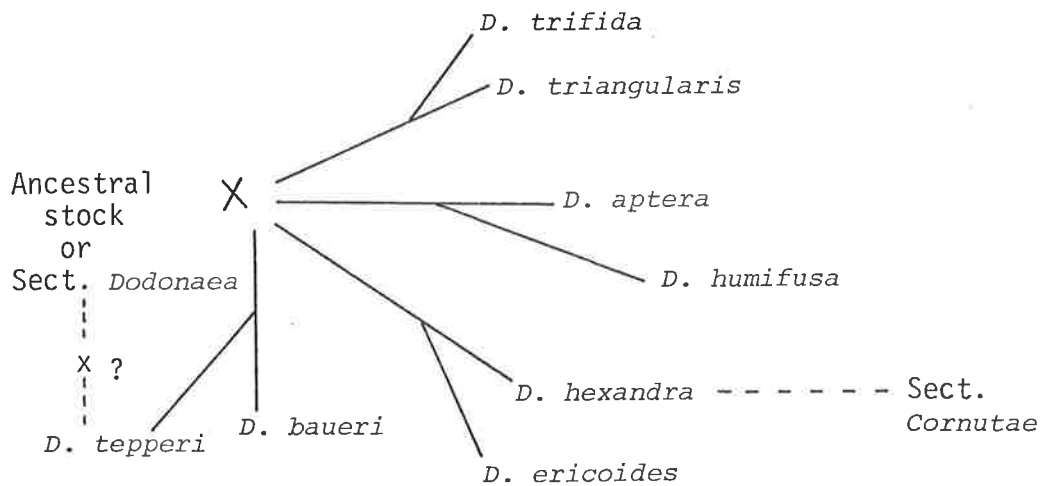
D. ericoides appears to be the end point of this Sect. *Apterae* line of evolution. This species differs from all *Dodonaea* species in having opposite leaves, solitary terminal flowers and tomentose capsules. *D. ericoides* is morphologically consistent and shows narrow ecological preferences.

D. aptera and *D. humifusa* of Sect. *Apterae* have evolved in a slightly different trend from the above species. *D. aptera* possesses some more primitive characters linking it to Sect. *Dodonaea*. For example,

this species exhibits flexibility in inflorescence structure (from botryoids to panicles), it has larger, flat leaves and relatively long peduncles, especially in fruit.

Characteristics of leaves, fruits and inflorescences indicate that the more derived *D. humifusa* evolved from *D. aptera*. The former species is always a prostrate plant of a specific habitat type - *Eucalyptus wandoo* woodlands. In its habit and narrow ecological preferences *D. humifusa* is similar to the only other truly prostrate species, *D. procumbens* (Sect. *Dodonaea*) of south-eastern Australia.

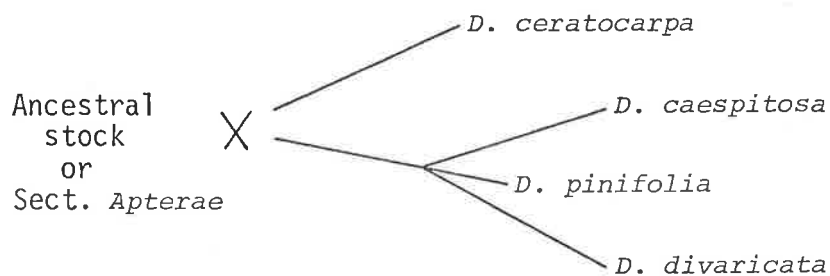
Members of Sect. *Apterae* seem to have diverged along three and possibly four lines of evolution from the ancestral stock. Species of this group show affinities to species of Sections *Dodonaea* and *Cornutae*. There are trends in distribution and habitat preferences associated with increasing morphological specialisation, from the more widespread and morphologically variable, eastern *D. triangularis*, through the more geographically restricted and morphologically consistent South Australian *D. hexandra* and *D. baueri* to the four Western Australian species occupying specific habitats and occurring in restricted distributions.



Postulated evolution in Sect. *Apterae*

Sect. *Cornutae* (Fig. 5.6)

The four species belonging to this more advanced section are restricted to south-west Western Australia. *D. ceratocarpa* with its larger, flat leaves similar to members of Sect. *Dodonaea* appears to be the most primitive of the section. This species is confined to coastal limestone and near-coastal granite outcrops. *D. pinifolia* shows the greatest amount of morphological variability in leaf and fruit characters, is rarely polygamo-dioecious and is also the most ecologically and geographically widespread. Two independent evolutionary lines may have given rise to *D. ceratocarpa* and *D. pinifolia* from the Sect. *Cornutae* ancestral stock. *D. caespitosa* and *D. divaricata* are both closely related to *D. pinifolia*, but possess several more advanced features. These two species not only occupy restricted geographical areas, but they also occur in specific habitat types and each exhibits a characteristic habit. They show high morphological consistency with usually 3-partite, almost sessile fruits, narrow leaves, solitary flowers and they are always dioecious. *D. caespitosa* and *D. divaricata* have probably both evolved via the more variable *D. pinifolia*.

Postulated evolution in Sect. *Cornutae*

Sect. *Pinnatae* (Fig. 5.7)

Sect. *pinnatae* is regarded as the most primitive of the pinnate-leaved groups. It is widespread in Australia and the development of the section appears to have followed four main evolutionary lines. One group of species from northern Australia shows morphological trends from the most primitive, *D. polyzyga* with paniculate inflorescences, polygamy, large fruits with broad wings and a relatively large number of leaflets (29-47) to, on the one hand *D. physocarpa* with less complex inflorescences, irregularly dehiscent, inflated capsules and a smaller number of leaflets (6-10(-12)) and on the other, *D. oxyptera* with monadic or diadic inflorescences, smaller, pubescent capsules and 4-8(-12) leaflets. Both *D. physocarpa* and *D. oxyptera* are dioecious or rarely polygamo-dioecious.

A second line of evolution in this section involves *D. pinnata* as the most primitive member. From this east coast species has diverged two species of south-east Queensland, *D. rupicola* and *D. vestita*. They are very similar taxa morphologically and it is possible that they have evolved along parallel lines. Each species contains both primitive and derived states of various characters and without weighting particular attributes it is difficult to determine one as being the most primitive. *D. rupicola* is now restricted to the Glasshouse Mountains areas and may represent relict populations of a much more widely distributed ancestor.

D. multijuga appears to be the species from which several other taxa have diverged in this evolutionary line. Close to *D. multijuga* and sharing such features as sunken glands on the leaflet margins is the more widespread and morphologically variable *D. boroniaefolia*. *D. uncinata*, with its very restricted distribution north of Townsville, is an extension of *D. boroniaefolia* and shows further specialisation of features of this

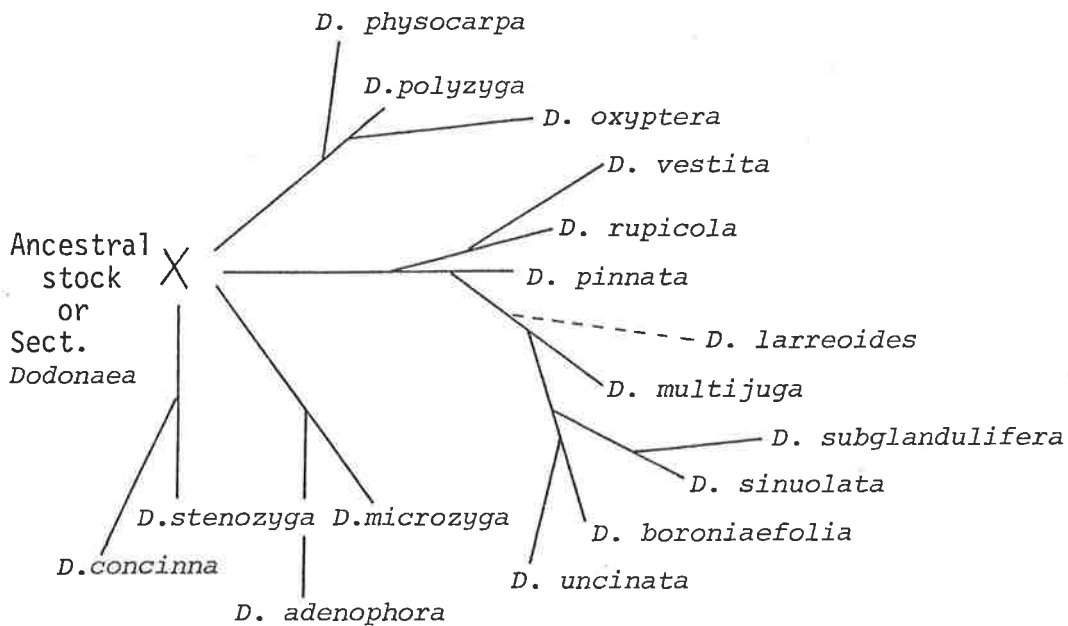
species. *D. sinuolata* ssp. *sinuolata* and its more arid form ssp. *acrodentata*, show greater divergence from *D. multijuga*. The phylogenetic position of the rarer *D. subglandulifera* is difficult to assess, but from leaflet and capsule characters it appears to be close to *D. sinuolata*. The present restricted distribution of *D. subglandulifera* on the western extension of this group of species may indicate the waning population of a once more extensive form.

In contrast to the northern and eastern Australian distributions of the species in the evolutionary lines described above, the remaining two trends involve taxa with present distributions extending across southern Australia to Western Australia. *D. stenozyga* and the more derived *D. concinna* show features of a closely related species pair. While *D. stenozyga* occupies a broad geographical and ecological range and has larger leaves and capsules, *D. concinna* occurs in a restricted area of south-west Western Australia and possesses smaller leaves and capsules.

The last evolutionary line of Sect. *Pinnatae* to be discussed is the only one containing species which have been successful in arid Australia. *D. microzyga* is found in South and central Australia, and in Western Australia it occurs as a form with smaller (septifragal) fruits and a slightly different leaflet shape (i.e. var. *acrolobata*). This form shows close relationships with *D. adenophora*, a species of semi-arid south-west Western Australia with very small, septicidal fruits and reduced leaves.

Several species of Sect. *Pinnatae* show affinities to species of Sect. *Dodoneae* and some, e.g. *D. boroniaefolia*, form putative hybrids with members of that section. In this manner *D. larreoides* shares many characters with *D. inaequifolia* (Sect. *Plagiopterae*), which occupies a similar geographical

range. *D. larreoides* appears to have evolved as a western equivalent of the *D. boroniaefolia* group of species of eastern Australia and it is here tentatively placed in that position in the postulated evolutionary scheme shown below.



Postulated evolution in Sect. *Pinnatae*

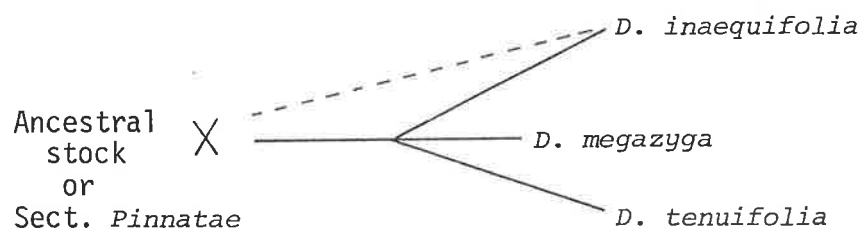
Sect. *Plagiopterae* (Fig. 5.8)

D. megazyga of eastern Australia seems to be the most primitive member of Sect. *Plagiopterae*. The evolutionary trends in this section closely parallel those of Sect. *Platypterae*. *D. megazyga* has broad, membranous capsule appendages, paniculate inflorescences and larger leaflets than either *D. tenuifolia* or *D. inaequifolia*. These two species have capsules with reduced appendages, botryoidal inflorescences and narrower leaflets.

The large geographical disjunction of the three species of Sect. *Plagiopterae* may be speculated upon relative to the distribution of those

species of the probable ancestral stock, Sect. *Pinnatae*. Figure 5.7 shows a greater number of species of Sect. *Pinnatae* in eastern and western Australia than in the south or north. Given these present distribution patterns of the likely ancestors of Sect. *Plagiopterae* and given that Sect. *Pinnatae* extends right across the continent in the south, it is likely that the ancestral stock from which members of Sect. *Plagiopterae* evolved extended across southern Australia. The evolutionary lines of the ancestral stock giving rise to *D. inaequifolia* of Western Australia may have been isolated from those leading to the eastern *D. megazyga* and *D. tenuifolia* by such events as the onset of aridity in central, southern Australia.

This speculation may be more compatible with the idea of independent evolution of *D. inaequifolia* from the ancestral stock rather than via *D. megazyga* as suggested above.

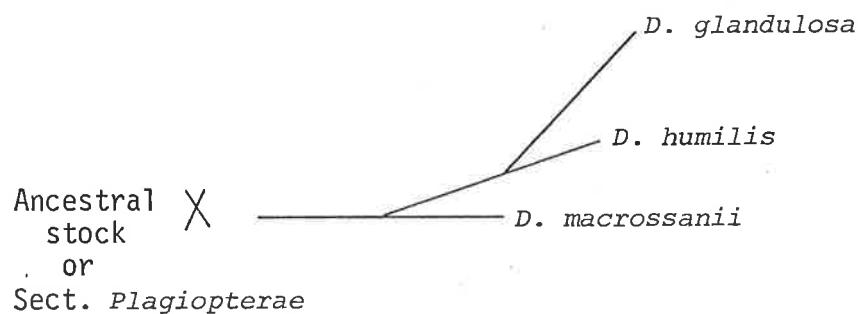


Postulated evolution in Sect. *Plagiopterae*

Sect. *Inappendiculatae* (Fig. 5.8)

The three species of this section show certain specialisations, such as the presence of glandular hairs, unique to Sect. *Inappendiculatae*. The geographical disjunctions and the different morphological features of each

species might suggest that each has independently evolved from the ancestral stock. Alternatively, since *D. macrossanii* shows least capsule specialisation, *D. humilis* and *D. glandulosa* may have diverged from that line. *D. glandulosa* appears to be the most advanced in this evolutionary line with glandular hairs on vegetative parts as well as the fruit (as in *D. humilis*), bi-carpellate capsules and very small leaflets. Each species has narrow ecological preferences and may have become restricted to a particular geographical area following divergence from a more widespread ancestral stock.



Postulated evolution in Sect. *Inappendiculatae*

5.4 SPECULATION ON THE ORIGIN AND DIVERSIFICATION OF *DODONAEA*

Having discussed the relationships and possible evolutionary schemes of the species of *Dodonaea* in Australia, it is appropriate in speculating on the origin and diversification of the genus to examine it on the world scale. The position of *Dodonaea* in the family Sapindaceae and the available fossil evidence may also reveal information which will contribute to an hypothesis on the origin of the genus.

5.4.1 Extra-Australian *Dodonaea*

The world distribution of *Dodonaea* is shown in figure 5.9. It is clear that the genus exhibits a pan-tropical distribution with some extension into the temperate regions of the Americas and Africa.

Although the extra-Australian *Dodonaea* taxa have not been included in this study it appears from the limited amount of material examined that it is all very closely related to or is part of the *Dodonaea viscosa* complex. The supposedly distinguishing characters used in treatments such as that of Degener (1960) for the species of Hawaii and Lippold (1978) for the American species illustrate the close relationships of these taxa.

If the most recent treatments of *Dodonaea* (excluding Australia) are to be followed, then besides the polymorphic *D. viscosa* with its infra-specific taxa, eight species of *Dodonaea* would be recognised outside Australia. These taxa are all closely related to *D. viscosa* and show no evidence of the considerable morphological diversification that has taken place in the genus in Australia.

5.42 *Dodonaea* as part of the family Sapindaceae

The most recent comprehensive treatments of Sapindaceae, those of Radlkofer (1933) and Muller & Leenhouts (1976), place *Dodonaea* in the tribe Dodonaeae of subfamily Dyssapindaceae (= Dodonaeoideae). Apart from the extra-Australian *Dodonaea* taxa, the Dodonaeae are restricted to Australia and New Caledonia. The tribe includes three genera: *Diplopeltis*, which is restricted to Western Australia and the Northern Territory, *Distichostemon*, a northern Australian genus and *Loxodiscus* from New Caledonia.

Distichostemon is most closely related to *Dodonaea*. The two genera are differentiated on stamen number, but there appears to be some evidence that they may be considered congeneric. These two genera lack petals and have symmetrical flowers, while *Diplopeltis* and *Loxodiscus* have asymmetrical, petaloid flowers.

The contrasting phylogenetic schemes for the family as proposed by Radlkofer (1933) and Muller & Leenhouts (1976) were discussed in Chapter 2. Muller & Leenhouts regard morphological specialisations and reductions as derived features which are likely to occur in few taxa. They proposed a group of morphologic-typological series which they believed to be phylogenetic. In combining their macromorphological system with their phylogenetic series derived from pollen morphology the tribe Dodonaeae appears to be the most primitive of the family. Muller & Leenhouts suggested that all four genera are well defined although it is difficult to define their interrelationships. They believed the Dodonaeae may have been separated from the rest of the family for a long time.

According to Muller & Leenhouts' macromorphologic-typologic series the only derived character possessed by *Dodonaea* is the lack of petals. While this is true for the one species of the genus (*D. attenuata* = *D. viscosa* ssp. *angustissima*) examined by them, it is not so for all members of the genus. Some species possess derived states of certain characters which parallel the advanced forms in the rest of the family. For instance, the stamen number in *Dodonaea* is usually 8, but *D. filiformis* consistently has 5 stamens, *D. coriacea* 4-5 and *D. polyandra* has more than 10 stamens. The pistil number is reduced from the usual 3-4 to 2 in *D. glandulosa* and species of Sect. *Cornutae* and most of those in Sect. *Apterae* possess arillate seeds. So that, even though the tribe Dodonaeae is probably the most primitive in the family and *Dodonaea* the most primitive genus, it is significant when considering the origin and diversification of the genus that some species of *Dodonaea* possess advanced characters relative to other members of the family.

In Australia *Dodonaea* is by far the most morphologically variable and geographically extensive genus of Sapindaceae.

5.43 Fossil material of *Dodonaea*

About 15 fossil species attributed to *Dodonaea*, represented by leaves and/or fruits, have been described from the Tertiary deposits (Oligocene and Miocene) of western Europe (Berry, 1914). Berry described species from the Lower Eocene (*D. wilcoxiana* and *D. knowltoni*) (Berry, 1914) and the Middle and Upper Eocene (*D. viscosoides*) (Berry, 1914 & 1924) of southeastern United States. MacGinitie (1953) based *D. umbrina* from the Pliocene of Colorado on leaf material and Axelrod (1939) described *D. californica* from the Miocene of southern California from fossil leaves. Berry (1924) mentioned species from the Pliocene of Bolivia and the late Tertiary of Brazil.

Since the time of the original descriptions of these *Dodonaea* fossils doubt has been cast on the identification of several of them. Berry (1916) expressed reservations on the "rather doubtful material" on which a number of the European taxa were based. Axelrod (1939 & 1950b) discussed the difference in venation of *D. viscosoides* Berry (of eastern and central United States Tertiary floras) from the extant species *D. viscosa*, to which the fossil species was referred. On the other hand, Axelrod (1939) stated that material of *D. californica* "cannot be separated from the living *Dodonaea viscosa*".

D. californica is represented in three southern Californian fossil floras - the Miocene Tehachapi (Axelrod, 1939), and the Anaverde (Axelrod, 1950a) and Mount Eden (Axelrod, 1950b) of the Pliocene. The Florissant beds of Colorado (MacGinitie, 1953) have recently been dated at 35 million years (D.I. Axelrod, pers. comm. 1979).

Although specimens referred to Sapindaceae have been found in the Australian Tertiary floras, such as the southern Australian Anglesea or Maslin Bay Floras, no fossil material similar to modern *Dodonaea* has so far been located (D.C. Christophel, pers. comm. 1979).

Martin (1973) described fossil pollen (*D. sphaerica*) similar to the modern *D. pinnata* and *D. camfieldii* from southern New South Wales, tentatively dated Pliocene. This apparently resembles the Lower Pleistocene pollen of New Zealand described as *Dodonaea* aff. *viscosa* by Couper (1960).

Thus, providing the identifications are correct (and that may not be a valid assumption), and the stratigraphic dates are reasonably accurate, members of the ancestral stock of modern *Dodonaea* occurred in south-west United States during the Miocene and Pliocene and in south-east Australia and New Zealand at least in the late Pliocene and Pleistocene.

5.44 Hypotheses relating to the origin and diversification of *Dodonaea*

The previous sections have outlined some of the available information which may be useful in speculating on the origin and diversification of *Dodonaea*. These points and others relevant to this discussion are summarised below.

- * The present distribution of *Dodonaea* in Australia (figs. 5.3 to 5.8) and on the world scale (fig. 5.9).
- * The leaf fossil material of south-western United States (Miocene), which is probably close to the progenitors of extant *Dodonaea*.
- * The present, mainly tropical distribution of Sapindaceae.
- * Eocene sub-tropical forest leaf fossils of Sapindaceae in southern Australia.
- * Morphological (and geographical) diversification of *Dodonaea* in Australia.
- * *Dodonaea* appears to be adapted for long distance dispersal (refer Chapter 4 - tests of germination after soaking in sea water).

- * The continental drift and plate tectonics theory involving movement of continents, formation of land bridges, climatic changes and vegetation history.

Given these facts, there appear to be three main possibilities which might explain the origin of *Dodonaea* - i.e. i) origin from tropical north, ii) Gondwanaland origin and iii) Australian origin. These three hypotheses, which are not necessarily completely mutually exclusive, are discussed below.

i) Origin from the tropical north

The greatest concentration of extant members of the family Sapindaceae is found in the tropical regions of the world (Radlkofer, 1933; Muller & Leenhouts, 1976). Sapindaceae is well represented in subtropical floras of the Eocene in North America (Takhtajan, 1969) and Australia (Christophel, pers. comm. 1979) and it is generally believed to be of tropical origin.

While it is recognised that high species diversity now is not necessarily indicative of the centre of origin of any particular group of organisms, it is quite possible that the progenitors of *Dodonaea* were part of the tropical flora during the Tertiary.

Following the formation of the land bridge between Australia and south-east Asia in mid Miocene (15-20 million years ago) (Kemp, 1978) the ancestral stock of *Dodonaea* might well have entered Australia from the north. The diversification in the genus in Australia today must therefore have taken place during the last 15-20 million years.

This hypothesis is consistent with the presence of fossils from the Eocene subtropical flora in southern North America. A northern tropical

origin of Australian *Dodonaea* is also compatible with the present distribution of those genera closest to *Dodonaea* - i.e. other members of the tribe Dodonaeae in north Australia and New Caledonia. The progenitors of these genera may have also been in the tropics.

However, an hypothesis based on a tropical origin of the ancestral stock of *Dodonaea* requires extreme conservatism in the extra-Australian lines of evolution. Given that the *Dodonaea viscosa* group is regarded as the most primitive of the genus now, that the extra-Australian material is similar to *D. viscosa* and that the Eocene fossil leaf material shows resemblance to extant *D. viscosa* (Axelrod, 1939), then the extra-Australian *Dodonaea* stock has undergone very little change (e.g. in the Americas and Africa) in the last 35 million years. In contrast there has been extreme radiation and diversification in Australia in 20 million years.

Another point against this hypothesis is that most Malesian elements of the Australian flora do not show bimodal concentrations of species in the south-west and south-east of Australia, particularly of the advanced taxa as in *Dodonaea* (Raven & Axelrod, 1972).

Speculation that Australian *Dodonaea* originated in the tropical regions must cease if fossils (preferably fruit) greater than 20 million years old are found in Australia. This would indicate the presence of *Dodonaea* progenitors in Australia before the formation of Wallace's line and the connection of Australia with the northern island arc system in the mid Miocene.

ii) Gondwanaland origin

The second possible origin of *Dodonaea* relies on the ancestral stock growing in Gondwanaland before the separation of Australia, Africa and

South America from Antarctica (i.e. approx. 100 million years ago). As each of the continents broke away and moved northwards it carried with it *Dodonaea* progenitors.

The extensive radiation in Australia would then have taken place after Australia's separation from Gondwanaland, i.e. in the last 50 million years. It is possible too that the ancestral stock invaded Australia from the north after the Australian-Asian connection was made (20 million years ago).

In terms of this hypothesis the presence of the south-west United States Eocene fossils can be explained either by the progenitors migrating through South America or (possibly more likely) via Africa and Laurasia. Although land connections were absent in Central America, Africa had drifted northwards and North America and Europe were still juxtapositioned 65 million years ago (Raven & Axelrod, 1972). Figure 5.9 shows the absence of extant *Dodonaea* from the southern-most part of South America. This region appears to be climatically unsuitable to maintenance of *Dodonaea* populations now, but it is quite possible that progenitors of the genus were present in South America when that country and most of Gondwanaland supported sub-tropical forests under warmer conditions (Harris, 1965; Kemp, 1978).

As Australia moved northwards during Eocene, Oligocene and early Miocene (between 50 and 20 million years ago) climatic fluctuations took place which probably promoted major changes in the plant community structure and composition (Kemp, 1978). The period from late Eocene to early Miocene was a time of world-wide decrease in temperature. Simultaneously however Australia was moving towards lower latitudes and warmer climates and was experiencing an associated gradual onset of

aridity. Elements of the flora became restricted to particular areas of distribution. These changing conditions in Australia after the Gondwanaland separation may have contributed to the radiation of *Dodonaea* in Australia.

The Gondwanaland origin hypothesis suffers from the same problem as a tropical northern origin: i.e. requiring extreme conservatism in the evolution of extra-Australian *Dodonaea*.

iii) Australian origin

A third hypothesis which may be applied to the speculation of the origin and diversification of *Dodonaea* is that the ancestral stock originated in Australia and the extreme morphological diversification has taken place since Australia separated from Gondwanaland (approx. 50 million years ago). During its northward drift the great climatic fluctuations may have been a stimulus contributing to the radiation of *Dodonaea*.

It is suggested that the ancestral stock reached Africa and the Americas by long distance dispersal from Australia. The Asian elements of the genus may be the result of material reaching that area prior to the formation of the Australian-Asian land bridge. Following this union 20 million years ago ancestors of the present inhabitants may have migrated northwards through New Guinea and to the south-east Asian islands. The present distribution of the primitive *D. viscosa* ssp. *viscosa* and *D. polyandra* in north-east Queensland and extending into New Guinea would tend to support this idea.

This hypothesis is attractive primarily because of its simplicity and it does not require the same degree of conservatism in the evolution of the extra-Australian populations as the previous two possibilities.

However, an Australian origin and relatively recent invasion of Africa, the Americas and Asia casts doubt on the validity of the North American fossils. While the Eocene *D. californica* leaves show similarities to extant *D. viscosa*, the venation patterns and leaf characters also closely resemble other Sapindaceae genera, e.g. *Sapindus*. The identification of these fossils as *Dodonaea* cannot be disputed without a thorough examination of the material. It is quite possible that they represent an earlier line of progenitors of a genus close to *Dodonaea* (in leaf morphology at least), which either became extinct or has developed along different evolutionary paths.

Positive identification of fossils (preferably the distinctive capsules) outside Australia would not, for the reasons given above, necessarily discount an Australian origin. On the other hand, location of *Dodonaea*-like capsules in Australia in deposits exceeding 35 millions years in age would confirm a southern origin and disprove the hypothesis of a northern tropical origin.

Australian diversification

None of the above possible explanations relating to the origin of *Dodonaea* is able to adequately account for the extreme diversification in Australia and conservatism in the rest of the world. With a country such as Africa exhibiting a very similar range of habitat variability as Australia, it is difficult to explain the greater diversity in one country relative to the other on the basis of availability of suitable environmental conditions.

Nevertheless, the recent onset of arid conditions in Australia as postulated by Bowler (1976, 1980) may have influenced the radiation and adaptation of *Dodonaea*. If this was the case then one would expect to

find greater numbers of *Dodonaea* species in temperate and tropical areas and less in the semi-arid and arid. In fact, of the 61 Australian species only five are confined to arid regions, while another seven extend into the arid from the surrounding areas; six from the semi-arid and one from the tropical north. Fifteen of the remaining 49 species occur in semi-arid regions and 32 are confined to temperate or tropical areas beyond the semi-arid.

All species occurring in the arid zone, whether restricted to it or extending into it from the semi-arid, belong to the primitive groups; ten from Sect. *Dodonaea*, one from Sect. *Pinnatae* and one from Sect. *Platypterae*. Certain evidence, such as the temperate distribution of the species most closely related to the arid taxa, suggests that those species now occupying the arid entered that region from temperate and tropical surrounding areas (West, in press). The interspecific morphological diversity decreases from the tropical and temperate areas of Australia to the arid zone.

Dodonaea viscosa s. lat. provides some evidence for recent radiation of the genus from more temperate or sub-tropical vegetation types into the arid region. The continuous morphological variation in this species in southern temperate Australia is discussed in Chapter 7. In arid areas, however, several infraspecific taxa are morphologically distinct and appear to show genetic segregation under these environmental conditions. It is possible that the morphologically distinct forms of *D. viscosa* which occur in the arid regions of Australia diverged from some geographically and ecologically marginal populations of the southern ancestral form as the species adapted to the more arid conditions. It is only at the geographical and ecological extremes that the distinct

morphological differences between *D. viscosa* ssp. *angustissima*, ssp. *cuneata* and ssp. *mucronata* are maintained. Elsewhere intermediates occur with gradual intergradation into the polymorphic complex of southern Australia.

In order to speculate on the origin of *Dodonaea* with more certainty a complete study of the genus on the world scale must be undertaken. Comparative studies of Australian and extra-Australian material are necessary. Presumably many of the morphological leaf variations occurring throughout extra-Australian *Dodonaea* are the result of island isolation for long periods of time. Relationships between populations on nearby islands or continents may reveal useful biogeographic data. For instance, the similarity of *D. viscosa* of New Zealand and Norfolk Island on the one hand and the form of east coast Australia and Lord Howe Island on the other is compatible with postulated palaeogeographic origin of those areas (Gill, 1975; Raven & Axelrod, 1972; Kemp, 1978). Studies must be made on the aggressive nature of the genus to assess its ability as a coloniser and its establishment abilities. In Australia, there are several reported examples of *Dodonaea viscosa* s. lat. and *D. lobulata* showing opportunistic invading properties (see Chapter 7).

CHAPTER 6

THE *DODONAEA VISCOSA* COMPLEX - A NUMERICAL APPROACH

6.1 INTRODUCTION

The species *Dodonaea viscosa* Jacq. is probably the best known in the genus not only because of its world wide distribution, but also because it represents an extremely diverse and difficult taxonomic group. This species is pantropical with some extension into the southern temperate regions of Australia, South America and Africa (fig.6.1).

D. viscosa has long been recognised as comprising a variable morphological complex both outside and within Australia. Radlkofer (1933) presented a somewhat complicated system of dividing this widespread species into infra-specific taxa (varieties, forms and subforms), based largely on extra-Australian material. Brizicky (1963) when dealing with the species in the Southeastern United States commented on the weak boundaries between taxa and the presence of many intermediate specimens.

Morphological studies carried out during this project have shown *D. viscosa* to be a taxon of considerable polymorphism. My observations indicate that in Australia this species exhibits almost continuous variation in leaf morphology with two other species, namely *D. angustissima* DC. (formerly *D. attenuata* A. Cunn.) and *D. cuneata* Sm. No significant morphological variation in other organs, such as fruits and flowers was observed for the three taxa. In some instances fruit size may vary, but not consistently enough to be regarded as a diagnostic character on which to base a classification.

In the past distinctions between *Dodonaea viscosa*, *D. angustissima* and *D. cuneata* have been based almost solely on features relating to leaf shape and size. Bentham (1863) used leaf shape to separate the three species, while Radlkofer (1933) combined leaf shape with some apical and margin characters as the diagnostic features. Since Radlkofer's monograph consider-

ably more material has become available and this, together with extensive field work, indicates that intermediate specimens and populations exist which break down the disjunctions delimited between these three species. This was recognised by Willis (1972), who distinguished the species on leaf morphology and then stated: "*D. viscosa*, *D. cuneata* and *D. angustissima* are co-extensive in many parts of Victoria and appear to intergrade, so that the distinction between any pair of them may often be hazy. Floral and fruiting characters are very similar in all three, and leaf-form is the principal criterion for delimitation".

Table 6.1 sets out the main leaf characters used by previous workers to distinguish the species. The features listed are combinations of at least three sets of previous data. It is evident that existing classifications include considerable overlap in some characters, and especially leaf shape, between the three taxa.

	<u><i>D. cuneata</i></u>	<u><i>D. angustissima</i></u>	<u><i>D. viscosa</i></u>
Length (cm)	1 - 3	1.5 - 8	3 - 12
Breadth (cm)	0.5 - 1	0.2 - 0.4	0.5 - 4
Shape	narrow- to broad- cuneate	linear linear-cuneate narrow-linear to cuneate linear to narrow- oblancheolate	oblong-lanceolate to oblanceolate elliptic-oblong lanceolate to oblong linear to spatulate linear to cuneate
Apex	+ truncate or rounded or apicu- late or toothed	mucronate obtuse shallowly notched	
Margin		sinuate obscurely toothed revolute slightly repand- denticulate	entire obscurely toothed + repand revolute

Table 6.1. Summary of leaf characters used by previous workers to distinguish the species of the *D. viscosa* complex.

The three species comprising this polymorphic group - henceforth referred to as the *Dodonaea viscosa* complex - have themselves each been divided into infraspecific taxa in the past. This, together with the characters on which the divisions were based, is shown for Australian material in table 6.2. The extra-Australian *D. viscosa* complex has been further subdivided infraspecifically (e.g. Sherff, 1945 & 1947). This sometimes resulted in unwieldy classifications which include pentanomial combinations. Synonymy relating to *D. viscosa* within Australia is given in Chapter 7, but the solution to the immense nomenclatural problem in *D. viscosa* outside of Australia has not been treated in this thesis.

The predominant use of leaf morphology (mainly size and shape) in distinguishing the Australian infraspecific taxa within the complex is indicated in table 6.2. Most other features mentioned relate to fruit (and wing) size. At the subspecific level use of such environmentally influenced criteria is generally acceptable as in many cases one is dealing with ecotypic variants of the one biological entity.

Initial macromorphological observations of the *D. viscosa* complex indicated that the three species comprising the complex exist as well defined taxa in some populations. However, extensive field work in southern Australia and further observations of herbarium collections revealed many morphologically intermediate individuals and populations. As mentioned above, floral and fruiting characters are fairly consistent within the complex, but leaf morphology appears to be continuously variable.

In view of this apparent variation in leaf morphology I searched for disjunctions or breaks within the *D. viscosa* complex by employing multivariate numerical analyses on as many foliar characters as possible. Selection of vegetative characters does not reflect a belief that these are more important than floral features. Rather, the choice has been made primarily

Table 6.2. Intraspecific taxa of the *Dodonaea viscosa* complex in Australia and the characters on which the taxa were distinguished.

<u>Taxon</u>	<u>Leaf characters</u>	<u>Non-leaf characters</u>
<i>D. cuneata</i> Sm.		
var. <i>coriacea</i> Benth.	Leaves small, obovate, apiculate, coriaceous	Capsule small, wings broad
var. <i>rigida</i> Benth.	Leaves small, mostly obovate, truncate, apiculate, repand-denticulate, coriaceous, rigid	Capsule rather large, wings narrow
<i>D. angustissima</i> DC.		
var. <i>linearis</i> Benth.	Leaves long, narrow-linear, 1-2mm wide, mostly acute, margins often recurved & obscurely denticulate, rigid	Capsule rather small, terminal sinus narrow
var. <i>denticulata</i> (F.Muell.)Radlk.	Leaves elongate to 10cm, linear-lanceolate, repand-denticulate, ±coriaceous	Inflorescence paniculate, multiflowered, to 5cm long
var. <i>subintegra</i> (Benth.)Radlk.	Leaves long to 12cm (4-10mm wide), ±entire, or slightly toothed, membranous, pale green	" " " "
<i>D. viscosa</i> Jacq.		
var. <i>angustifolia</i> (L.f.)Benth.	Leaves narrow, linear-lanceolate or ±linear, mostly long, acute-acuminate, narrowed at base, veins usually conspicuous	Capsule small with broad wings, terminal sinus open, sometimes narrowed at base, each carpel with wing orbicular, rather broader than long
var. <i>spatulata</i> (Sm.)Benth.	Leaves short, obovate-oblong, oblong-cuneate, spatulate, oblanceolate or broad linear-cuneate, usually obtuse or sometimes truncate, lateral veins usually conspicuous	Capsule very variable, usually between the other two varieties
var. <i>asplenifolia</i> (Rudge)Hook.f.	Leaves linear-obovate, apex acute or obliquely 2-3-toothed	Capsule 2-4-winged, wings 5-12mm broad, variable in length and breadth
var. <i>linearis</i> (Harv. & Sond.)Sherff	Leaves linear, short (±5cm) or long (±7-11cm)	Inflorescence glabrous to sparsely setulose

Table 6.2 (cont.)

<u>Taxon</u>	<u>Leaf characters</u>	<u>Non-leaf characters</u>
<i>D. viscosa</i>		
var. <i>linearis</i>		
f. <i>angustifolia</i> (L.f.) Sherff	Leaves linear-lanceolate to linear-oblongate, mostly of moderate size	Inflorescence glabrous to sparsely setulose
var. <i>arborescens</i> (Hook.) Sherff	Leaves ±sinuate-dentate	Capsule mostly glabrous
f. <i>spatulata</i> (Sm.) Sherff	Leaves mostly spatulate, entire or slightly sinuate-dentate & of small size (3-6cm x 0.7-1.5cm)	" " " "
var. <i>vulgaris</i> Benth.	Leaves large, obovate-oblong, broadly lanceolate or lanceolate, or oblong-lanceolate, acuminate or rarely obtuse, pinnate veins usually numerous & prominent	Capsule suborbicular or obcordate, moderately large
f. <i>repanda</i> (Schumm. & Thonn.) Radlk.	Leaves large, from broad-oblong to lanceolate to ovate, shortly acuminate, sometimes obtuse, base attenuate, ±repand	Capsule often large, ±orbicular, 2-3-winged
f. <i>schiedeana</i> (Schldl.) Radlk.	Leaves long, lanceolate, acuminate, base attenuate & narrowed into petiole	Capsule moderately large, orbicular or ±obcordate, barely emarginate, apical sinus often large
f. <i>burmanniana</i> (DC.) Radlk.	Leaves from narrow-oblong to lanceolate-cuneate, apex acute or obtuse, attenuate with short petiole	Capsule medium, ±orbicular, apex & base open
subf. <i>laurina</i> (Soland.) Radlk.	Leaves thick, obscurely veined	

on the basis of variability, and consideration of criteria such as usefulness (in an identificatory sense), availability and convenience. This choice also reflects the original definitions of the taxa, which were based on leaf morphology.

The very nature of their variability has meant that leaves have been largely omitted from classifications by many taxonomists. However, the use of numerical analyses in taxonomy has shown that it is possible to retrieve information from even highly variable attributes, e.g. Farrell and Ashton (1978), Dancik and Barnes (1974).

Problems associated with handling variability in leaves have been discussed by various authors. Dancik and Barnes (1974) used macromorphological characters to analyse leaf variation within yellow birch individuals. Dolph (1976a & b) emphasised the inadequacy of existing character sets in accommodating variability and stressed the large number of resultant misidentifications. He suggested that some problems arise through a lack of understanding of the interrelationships of characters.

The observed continuous variation in the *D. viscosa* complex indicated a high degree of polymorphism which was difficult to describe or delimit by classical morphological taxonomic techniques. It appeared initially that several characters were varying considerably. For example, leaf shape components such as apex and base angles and the ratio of leaf length to leaf width exhibited large variances. A multivariate numerical analysis was the most suitable method to detect any structure that might exist in the complex.

6.2 DATA COLLECTION

In a multivariate analysis such as this, sample size is an important factor to consider. The number of characters and the number of entities or individuals on which to measure them are the two components contributing to the sample size. The choice of characters (or attributes) and of the operational taxonomic units (OTU's) is governed by several constraints. The most restrictive of these, when working with extant leaves, is usually the time taken in the collection and analysis of data, while in macrofossil work the availability of material (especially complete specimens) is probably the strongest limiting factor. The size of the group and amount of variability in the group being examined should also be considered.

The number of characters and OTU's must be large enough to include the range of variability, but not so large that the data matrix becomes unwieldy even for computer analyses. Large data matrices can be limited by appropriate available analytical techniques, and interpretation and representation of results may be difficult.

It was suggested by I.R. Noble (Research School of Biological Sciences, Australian National University, pers. comm.) that an electronic digitiser might be a helpful device to use when collecting the data for an analysis of this kind. Following consideration of the present availability, flexibility and reliability of digitisers, and of the characters likely to be used in this analysis, I decided to employ the digitiser as an aid in the data collection phase.

Crovello (1976) reported the use of a digitiser in the production of a morphological data bank of herbarium specimens. He showed that leaf length can be easily determined by recording and storing in digital format in the computer the positions of the apex and base of the leaf.

With the exception of the computer description of *Chondrilla juncea* leaf shape using a drum scanner and leaf boundary string description (with Freeman coding) reported by Dale et al. (1971), it appears that this technique has not been used previously to derive the basic data set for a multivariate analysis.

The initial purpose of this numerical analysis was to derive a natural, useful and meaningful biological classification of the *D. viscosa* complex in Australia using essentially leaf morphological data. This was now augmented by the secondary objective of testing the capability, usefulness and potential of an electronic digitiser as a tool in the data collection phase of a multivariate analysis.

6.21 The Digitiser

Use of a digitiser in this analysis enabled me to include a larger number of individuals and to cover more of the morphological variability of the complex than would have been possible if the data had been collected manually. Not only were my analyses carried out by computer, but the original data was collected using high speed electronic methods.

A Tektronix digitiser (graphics tablet 4954) in association with a Tektronix 4015 graphics terminal was used to record the basic leaf data, on which the numerical analysis was based. A digitiser is an electronically sensitive plate (or tablet) which detects the position of an associated tracing pen and transmits in digital format the x, y coordinates of that position to a microprocessor or computer.

In this analysis photocopies of leaves selected for the study (see section 6.3) were placed on the tablet surface and the left and right margins and the midrib of each leaf were traced. The x,y coordinates of the outline and midrib of each traced leaf were then automatically transmitted

through the graphics terminal to be stored on disc in a DEC-10 computer. In this way a digitised "image" of the leaf is stored on file. It is this data (i.e. the digitised leaf outline and midrib) which was later used in the second phase of the data collection process - i.e. to calculate the various leaf parameters that were analysed by the multivariate techniques.

While some digitisers can record up to 400 points per second and at 0.1mm resolution, the one used in this analysis records at a rate of 10 (coordinate) points per second and has a resolution of 0.25mm. Care must be taken when tracing not to move the pen too fast, as a considerable gap will occur between digitised points representing the leaf data. Precautions are included in the computer programs to enable the user to check for any gap error greater than a specified amount. In this analysis a gap error of 10 points ($\approx 2.5\text{mm}$) was considered to be acceptable.

A range of tracing instruments are now available with digitising equipment. These vary from fine point pens and cross-hair cursors to coarse ballpoints, and are suitable for different job requirements.

A tracing pen similar to a "blunt" ballpoint was unfortunately the only instrument available with the Tektronix digitiser at the time this analysis was carried out.

It appeared initially that some inaccuracies may have arisen due to this imprecision, especially in relation to fine point areas such as acute leaf apices. However, examination of those characters most likely to be affected by this insensitivity reveals little distortion in the final data matrix (see section 6.4). Despite this apparent lack of distortion extra characters were included in order to assess and/or counteract any inaccuracies of the digitising system.

Photocopies of the leaves instead of real dried leaves were used in order to avoid leaf damage while tracing, and to eliminate any textural unevenness in the leaf surface, which may have led to slightly inaccurate leaf "images".

6.22 The Digitiser Program

The digitiser used in this study required computer software to run it interactively with its associated graphics terminal. These programs deal with the input of the actual data from the leaves, and not only enable the user to check the leaf "image" on the terminal screen, but also to ensure that the start of a new individual or population is recorded accurately.

Computer programs associated with the digitiser and the calculation of leaf parameters (as discussed in section 6.23) were designed and written by I.R. Noble (Research School of Biological Sciences, Australian National University).

The main digitising program includes a subroutine allowing the interaction of digitiser, user, terminal and computer, through the use of an instruction function or "menu". The menu is relevant to the particular job in hand, and in this analysis it consisted of eight sections. To enable the user to communicate with the terminal while digitising, a small part of the electronic tablet is set aside digitally for response to menu requests. The exact position of these menu instructions on the table is recorded by securing a piece of paper displaying the menu instructions over that section of the digitiser corresponding to the coordinates of the menu boxes. When the digitiser senses the position of the pen in one of the menu boxes, the terminal responds with an appropriate request or command.

A brief explanation of each of the eight menu instructions is given here. Two relate to the input of a new population (POP) or individual (IND), and when called require the user to type the relevant names or header cards into the terminal. Once the individual name is recorded then any of three menu boxes corresponding to the input of the left (LEFT) or right (RITE) margin or the midrib (MID) can be touched and the terminal requests the input of the appropriate "line" or coordinates. By placing the pen in the appropriate box again, any of these lines can be redrawn. Following input of all

three lines (i.e. the two margins and midrib) menu instruction FIN is called indicating the end of a leaf, and initiating display of the summary data for that leaf. The user may select the summary data to be in the form of the number of points recorded for each line or as a plot of the leaf or as a complete listing of all x,y coordinates. If this summary data fulfills certain requirements, e.g. not exceeding specified maximum gap errors between points, then the image of that leaf can be sent off for storage in the computer using another menu instruction (OK).

It is in the FIN stage that the user can reject a whole leaf or any one of the three "sides" simply by retracing any of the lines prior to storing the leaf. The last menu instruction is STOP and must be called in order to exit from digitising mode and to return to normal computer command mode.

This system is capable of handling large amounts of data and when in full digitising mode it is possible to digitise one leaf per minute.

The graphics terminal and software, including the menu instructions associated with this Tektronix digitiser, enabled rapid and simple data input. However, most digitisers now available include their own microprocessors. Although these units have no video screen they can be used as a terminal through which data is transferred to the computer. The nature of communication system between the user, digitiser and computer is not vitally important and the requirements will greatly depend on the form of data being recorded. An important point is that the digitiser be connected to a computer, as the large data sets generated are probably beyond the capabilities of a microprocessor.

6.23 Leaf Parameter Program

The second part of the data collection phase is the calculation of all leaf parameters using the digitised leaf "images" stored in the computer. This analytical program involves a number of subroutines and functions, the most important of which are discussed here.

The first subroutine called after input of the data from the digitiser (CLEAN) acts as a post input check during the analytical phase and is particularly useful in eliminating random extraneous pulses generated by the tablet. CLEAN scans each margin and midrib of the leaf for gaps between successive coordinate points which exceed a prescribed amount. When such a gap is found it rejects the point and continues scanning the margin rejecting points until a point is found which falls within the prescribed limit from the last acceptable point. Failure to locate a coordinate point within this specified limit results in a warning being printed and rejection of that leaf.

ORIENT is the subroutine which reorients the digitised leaf outline so that the apex is perpendicular to and above the lowermost (basal) midrib point (fig.6.2a). Coarseness of the tracing pen and the resolution of the system made it very difficult to begin the tracings of the two margins and midrib at exactly the same point at the apex. Subroutine ORIENT corrects for any distortion which may occur in this way by forcing the apical starting position of the left and right margins and the midrib to coincide by setting them to the median of the triangle formed by the original three starting positions.

Subroutine SECTOR superimposes a series of regularly spaced sectors on the leaf outline. A sector interval distance of 0.5mm was chosen here, but the sectors can be spaced at variable intervals. The first sector passes through the apex. Each sector is parallel to the x-axis, and is perpendicular to a line joining the apex and the basal midrib (fig.6.2b). SECTOR scans the margins and calculates the position of intersection with each sector line. Tracing errors, digitiser insensitivity and distortions introduced on reorientation of the leaf may result in the two margins and the midrib having slightly different basal end points. The sectoring truncates at the end of the shortest of the three "lines".

The SECTOR data is stored as the representation of the leaf shape for all subsequent analyses. This has advantages in that the detailed leaf shape is held in a regular format, and storage is compact since the y coordinates change by a fixed amount from sector to sector and need not be stored. In this analysis a leaf of length L_{mm} requires $3 \times L/\sigma$ words of storage, where σ is the distance between the sectors (here 0.5mm).

The calculation of many leaf characters requires measurements to be made perpendicular to the midrib, e.g. maximum leaf width. In some leaves sector lines produced by SECTOR as described above, may vary considerably from being perpendicular to the midrib. This is particularly true of falcate or geniculate leaves. Subroutine PERPM derives a second sector perpendicular to the midrib at each point along the midrib intersected by the original sectors.

Minor irregularities in the midrib due to tracing or digitiser resolution are smoothed out by fitting a linear regression through several points along the midrib either side of the point under consideration. PERPM is coded so that any number of points can be used in the regression, and it appears from this analysis that four or five points on either side (i.e. 4-5mm total length) are sufficient for satisfactory smoothing. Figure 6.2c,d & e indicate considerable differences in the position of the points of intersection of the perpendicular sectors with the leaf margins when comparing the use of two points in the regression with that of four or five. However, the greater smoothing factors caused minimal difference to the calculation of those leaf parameters dependent on perpendicular sectors. Even so, leaf parameters are calculated in the analysis by fitting the regression over five points each side of the point in question (i.e. a total of 11 points).

Other subroutines in the analytical program are involved with calculation of the leaf characters used in the multivariate analysis. Printing in various formats and plot options are also available.

The program includes a routine - OUTLYR - which calculates means and standard deviations of the leaf characters for each individual using all the leaves representing that plant. Although variation does occur within a single plant the data was averaged for each individual for several reasons including:-

- (1) each leaf is of the same genotype,
- (2) the data set of 834 leaves is far too large to handle and to interpret the results, and
- (3) the purpose of the analysis is to classify individuals within a polymorphic complex and not leaves within an individual.

In calculating the means and standard deviations OUTLYR rejects any outlying values in the data for that individual by the method of Grubb (1950). This is an extra precaution introduced to locate any discrepancies that may have been caused through tracing errors or the digitiser resolution, or aberrant leaves.

6.3 SELECTION OF OTU'S

Herbarium material was the most readily available and appropriate source of leaves for this study. Major Australian herbaria contain a very large number of *Dodonaea cuneata*, *D. angustissima* and especially *D. viscosa* specimens. It was therefore necessary to select the specimens for this analysis from this vast assortment of dried material.

Initially all available material, including that on loan from NSW, BRI, PERTH and MEL, was sorted and mapped. An attempt was made to group specimens as closely as possible into the three species of the complex. This proved very difficult in some cases where intermediate specimens were involved. The high degree of variation within a population became evident, and indicated the necessity to use only those populations represented by collections from two or more individuals.

Since these taxa are believed to be anemophilous (see Chapter 4) any attempt to define a population on the grounds of reproductive isolation presents practical difficulties. Rushton (1978) considered *Quercus* populations to be isolated if two groups of trees were separated by at least one kilometre. In open conditions, in which most *Dodonaea* species are found, pollen may disperse over longer distances. For the purposes of this analysis a population consists of a group of individuals, which are regarded as having the potential to freely interbreed, as long as any one of which is located no more than two kilometres distance from any other. The population structure as here defined is dependent to some extent on local climatic conditions, especially with respect to direction of prevailing winds and long distance pollen transport.

Those populations represented by multiple collections, whether sampled during this study or collected previously by others, were selected and remapped. It is from this reduced amount of material that the OTU populations were chosen. OTU's were selected to cover as much of the morphological

and geographical range of the complex as was possible within the constraints of the sample size.

The difficulty encountered in trying to assign individual specimens to the correct taxon, and the degree of leaf morphological variation throughout this complex indicated that individuals must be treated as the OTU's.

In selecting the OTU's it was necessary to ensure inclusion of populations representing the clearly defined taxa (i.e. *sensu stricto*) as well as some intermediate populations. It was considered desirable to have sample sizes for each of the three taxa and the intermediates which approximated their frequency of occurrence in the field.

Using definitions set up by previous workers I attempted to classify each population into one of the three species: *Dodonaea cuneata*, *D. angustissima* or *D. viscosa*. Even with the addition of extra characters, such as those relating to margins, petioles and venation patterns, there were several populations which could not be readily grouped into any one species. These populations contained individuals with leaf morphology intermediate between any two of the three taxa.

A fourth category or grouping of populations was formed in order to accommodate these intermediates. Any population with two or more individuals exhibiting intermediate morphology, or any population containing individuals that could readily be classified into more than one of the three species was automatically placed in this intermediate category. It was recognised and found acceptable that including intermediates of several types in one category added some artificiality.

Thirty-seven populations were finally chosen for the analysis. Of these, 23 (62%) were populations sampled during this study, and 11 (30%) were represented by previous collections each considered to form an intrabreeding population. Another 3 (8%) groups of individuals were included as examples of infraspecific taxa of *Dodonaea viscosa* defined by Radlkofer (1933) and

later recognised by Sherff (1947). All of the specimens included in the analysis to represent these taxa, namely *D. viscosa* var. *vulgaris* Benth. f. *repanda* (Schum. & Thonn.) Radlk., *D. viscosa* var. *vulgaris* Benth. f. *burmanniana* (DC.) Radlk. and *D. viscosa* var. *arborescens* (A. Cunn.) Sherff, had been annotated and determined by Sherff. Figure 6.3 indicates that these three populations (circled) cannot be considered to be intrabreeding units. However, leaves of specimens in each group appear to be fairly morphologically uniform and distinct, and they are included in the analysis to determine their position (if any) in the *D. viscosa* complex.

Most OTU populations were represented in the analysis by five individuals which were chosen to cover the differences and similarities within each population. In some cases a lack of available material limited the number of individuals, and less than 5 were used. If variation within a population was considered to be excessive, more than 5 plants were sampled. Final OTU selection resulted in 173 individuals for the multivariate analysis.

Certain constraints acted upon the selection of leaves to be used from each specimen. In general five leaves were chosen from each individual, but this varied slightly, depending on the variability and availability of material. Leaves were deliberately chosen to cover the variation within the plants, and damaged or folded leaves were avoided. To ensure inclusion of mature leaves only, selection was restricted to those occupying the eighth, or greater than the eighth, position from the shoot apex. The total number of leaves finally digitised was 834.

Selected leaves were placed on labelled cards (one card per specimen) with rubber glue, so that they could be easily removed at a later date if necessary. Photocopies of the leaves were used for digitising, and the dried leaves themselves were only used for reference when fine detail was not clear on the photocopy. In this way the leaves were not damaged and the card can be returned to the specimen from which the leaves were taken for long term storage and future use.

The number of populations, individuals and leaves finally selected to represent each group are given in table 6.3. Each population was allocated an abbreviated code name (in capital letters) mostly relating to the locality, and each individual is labelled with my collection number or an abbreviation of another collector's name and number (in lower case). Appendix A contains full details of all OTU specimens.

<u>Group</u>	<u>Number of populations</u>	<u>Number of individuals</u>	<u>Number of leaves</u>
<i>D. cuneata</i>	6	29	146
<i>D. angustissima</i>	7	34	171
<i>D. viscosa</i>	13	58	263
Intermediate	11	52	254
Total	37	173	834

Table 6.3. The number of populations, individuals (OTU's) and leaves representing each group.

Populations assigned to the three species *Dodonaea cuneata*, *D. angustissima* and *D. viscosa* and to the Intermediate category will be respectively referred to by those names.

6.4 SELECTION OF CHARACTERS

The character set employed in an analysis of this nature is very important and must be selected carefully. Characters dictate all other aspects of the study, including the types of multivariate analyses to which the data can be applied. Some selection factors for character choice are considered below.

6.41 Types of Leaf Characters

A multivariate analysis, just as any taxonomic study, can be based on various character sets, a number of which have been used in the past for leaf description. Characters can generally be grouped into three main categories:

- i. morphological (including anatomical and architectural),
- ii. biochemical and physiological, and
- iii. ecological and geographical.

The first category has attracted most attention probably because it includes a greater range of easily measured features, and in many cases does not require an experimental approach. Leaf architectural terminology was first introduced for the description of vein patterns by von Ettingshausen (1861). Although his system is complex, its general acceptance is reflected in its influence on several recently proposed leaf architectural classification systems, e.g. Hickey (1973), Dilcher (1974) and Dolph (1976a). Blackburn (1978) proposed a relatively small, but carefully selected and meaningful set of leaf architectural characters to generate an independent leaf based classification. He used *Saurauia* (Actinidiaceae) as a test case.

Features of the epidermis, cuticle and leaf indumentum have been defined by various authors. A classification of stomatal types is detailed by van Cotthem (1970). Variation and range in epidermal cells and cuticular characters useful in taxonomy can be found in the system of Stace (1965).

Some recent publications relating to leaf morphological features have proposed new and revised terminologies to increase precision. These appear only to complicate the situation beyond convenience and to be little more than an exercise in semantics. For example, Melville (1976) proposed an unwieldy system for classifying venation patterns by renaming the existing terms and defining some new subdivisions. Payne (1978) presented a revised system of trichome terminology more complex and confusing than previous usage.

Lewis (1972) took a more physiological approach to leaf diversity by examining the physiological and adaptive significance of variation in leaf structure, especially with respect to xericity and light intensity. His study considered the influence of leaf size, shape and thickness as well as stomatal structure and frequency on transfer rates of heat, water vapour and carbon dioxide between the leaf and its environment. Taylor (1975) used leaf form as an example of a biological parameter affecting leaf temperature, water economy and productivity. His study resulted in a predictive model whereby optimal leaf forms can be defined for any climate.

Characters relating to ecological or distributional data have not been used often for numerical taxonomy in the past (Sneath and Sokal, 1973). Environmental parameters have been successfully employed in cases in which the organisms exhibit some geographical or ecological variation or clination. For instance, Farrell and Ashton (1978) found that seasonal distribution of annual rainfall and distance from the coast correlated with phyllode shape and size in *Acacia melanoxydon* R. Br.

6.42 The Set of Characters Used in This Study

The final character set used in this analysis was dictated by several factors, including relative information content, ease of measurement, and applicability to the complex of taxa concerned. In addition, time taken to measure or record particular characters can often restrict the character

choice. This was not a limiting factor in this study, however, as most leaf parameters were calculated by computer using the digitised leaf "images".

Greater restrictions on the selection of characters apply to numerical studies of a small complex or a group of allegedly closely related taxa, (e.g. the *Dodonaea viscosa* complex and *Eucalyptus globulus* Labill. [Kirkpatrick, 1974]) than in studies at higher (e.g. infra-generic or tribal) levels as in Edmonds (1978), Blackburn (1978) and Macfarlane (1979). In a review of phenetic analyses at the species level and above Sneath (1976) briefly discussed the problems of character choice when working at those ranks.

This study has not involved any detailed physiological or anatomical investigations within the *Dodonaea viscosa* complex, and no other data is available on these aspects. Inclusion of leaf architectural characters would seem desirable, but details of the venation patterns are not evident without first clearing the leaves, and it was not feasible to clear all 834 leaves in the time available. Thus, the analysis was based on a leaf morphological character set.

In an analysis of this nature one usually is forced to evaluate and select the characters to be measured or recorded by testing them initially on subsets of the data. The time taken in manually measuring large numbers of characters for all OTU's is generally too great relative to the rejection of possible characters. There are obvious disadvantages in using subsets of the data only. For example, it is quite possible that a particular character is not significant when tested on selected OTU's, but it can be shown to be a useful delimiter when analysing all entities. In this study, in which the digitised images of leaves were already stored on computer, it was possible to compute the whole character set over all OTU's for evaluation and selection. The use of the digitiser therefore enabled characters to be assessed over the complete data set before any necessary rejection.

An initial set of 14 characters was selected and measured manually on a small number of representative populations, in order to test that these characters were measurable in the *D. viscosa* complex. These attributes will not be discussed in detail here as many of them are included in the final character set and are dealt with in relation to it. However, two characters which were rejected following this initial assessment warrant mention.

1. The number of secondary veins - measured as the average number on either side of the midrib - proved impossible to measure on some leaves, especially linear ones.

Leaves with conspicuous venation patterns on the other hand, would lend themselves to data collection with the digitiser. It would be a simple process to trace the secondary and tertiary venation and to have a digitised leaf "image" which included some venation details. This would also be feasible in a situation in which the veins were not clearly visible, but which involved a relatively small number of OTU's so that the leaves could be cleared to reveal venation patterns.

2. The dentition frequency - computed as the average number of teeth on either margin of the leaf, with the results being grouped into class intervals. This character was rejected because it was not possible to define a 'tooth' satisfactorily. Leaf margins in the complex exhibit a range from entire through sinuate and very small tooth-like glands to finely serrate. Teeth are sometimes quite distinct, while in other leaves it is difficult to decide if the slight projection is obvious enough to justify recording it as a tooth.

It was considered undesirable to include characters in the analysis which were so difficult to define. Although, if errors are relatively infrequent and this is one character of a large character set, then the increase in information may outweigh the increase in random background noise.

Using the digitiser it would be possible to compute such characters as dentition frequency. Leaves with distinct teeth or lobes could be analysed by extending the analytical program to deal with more complex margins. However, given the time limits for this project, only the simplest version of SECTOR was written. This is able to handle horizontal indentations and

extensions of the margin as in figure 6.4a, but it does not deal with vertical lobes or folds (fig.6.4b, c). There appear however to be no technical problems in developing the program to include the last two cases, and more complex ones.

The initial "manually derived" character set formed the basis for the analytical program designed to calculate most leaf parameters.

The final set of characters computed over all OTU's consisted of one binary and one continuous quantitative multistate variable recorded by hand, and 19 numeric variables computed on the digitised leaf images. Some attributes were measured by more than one method either to check on the accuracy of the digitising system or to assess the reliability of a character. The computer variable names associated with each character are given and will be used when referring to the characters, as they are self explanatory and will serve better to recall the character than a numeral. The complete character set will now be described. Bracketed letters refer to features illustrated in figure 6.5.

1. Acuminate apex length - a continuous quantitative multistate character.

ALEN - is the length of the apical portion of the leaf bound by concave sides. It is derived by locating the points where the concave margin changes its direction of curvature. The intersection of a line joining these two points with the midrib defines the relevant apex length. It is expressed in five class intervals:-

apex length (l):	0	/	$l \leq 1\text{mm}$	/	$1 < l \leq 2\text{mm}$	/	$2 < l \leq 3\text{mm}$	/	$l > 3\text{mm}$	/
class	1		2		3		4		5	

2. Presence of mucronate apex - a binary character.

ATEM - is the presence (1) or absence (0) of a mucro.

A mucro is defined as a short, sharp point with a length: breadth ratio < 3 : 1.

Numeric characters.

3. Leaf length (AB) - calculated by three different methods (fig.6.5b):

- i) LENA - the length of the midrib computed by summing the distances between each sector intersection. The distances are derived via Pythagoras' theorem.
- ii) LENA - as for LENA except that the distances between sectors are calculated trigonometrically using the angle as calculated for the smoothed midrib in subroutine PERPM.

LENA proved to be the most reliable method. All other characters depending on length are computed using LENA as the leaf length variable, and by computing the lengths along the midribs by the trigonometrical procedure used in calculating LENA.

- iii) LENT - the distance between the apex and base of the midrib.

4. Leaf width (CD).

WIDX - the maximum leaf width, i.e. the widest sector perpendicular to the midrib.

5. Position of maximum width - computed by two different methods:

- i) PMXW - the distance measured along the midrib from the apex to the maximum width sector at which (CD) intersects (AB); expressed as a proportion of total leaf length LENA (AE/AB).
- ii) WIDE - the first perpendicular sectors either side of WIDX with lengths <90% of WIDX are located ((FG) and (HI)). The point midway between these sectors, as measured from the apex and expressed as a proportion of LENA, is calculated as $[(AJ + AK)/2] \div AB$.

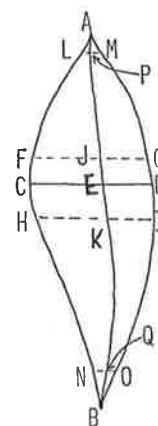
(This method corrects for minor fluctuations in width in an almost parallel-sided leaf).

6. Ratio of leaf length to maximum leaf width (AB/CD).

LTOBR - ratio of LENA to WIDX.

7. Leaf area.

AREA - is based on the ordinary sectors and is calculated using Simpson's rule.



8. Leaf perimeter.

PERM - is calculated using Pythagoras' theorem on the ordinary sectors.

9. Symmetry of the leaf.

PRAT - is the ratio of the lengths of the left and right margins; expressed so that $PRAT \leq 1.0$.

10. Petiole length.

PETIOL - is the length of the petiole which is defined as the basal portion of the leaf which is ≤ 1.0 mm wide; expressed as a portion of LENA.

11. Position of 20% of maximum width from apex.

A2OW - the distance from the apex to the first perpendicular sector whose length $>20\%$ of WIDX (LM); expressed as a proportion of LENA (AP/AB).

12. Position of 20% of maximum width from base.

B2OW - the distance from the base to the first perpendicular sector whose length $<20\%$ of WIDX (NO); expressed as a proportion of LENA (BQ/AB).

13. Apex angle (LAM).

AANG - the angle subtended by lines drawn from the apex to the perpendicular sector of length 20% WIDX.

14. Base angle (NBO).

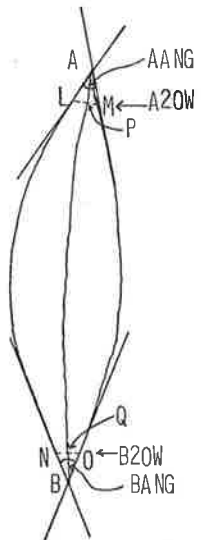
BANG - the angle subtended by lines drawn from the base to the perpendicular sector of length 20% WIDX.

15. Apex quadratic equation.

16.

AQB1 - a quadratic regression equation is fitted to the five sectors nearest the apex on the left and right margins. AQB1 is the average of the linear term (b_1) of the two margins, and AQB2 is the average of the quadratic term (b_2).

(N.B.: the average is calculated as (left- right margin)/2 to allow for the reversal of sign of the fitted coefficients for the left and right sides).



17. Position of maximum width quadratic equation.

18.

WQB1 - as for the apex quadratics (AQB1 and AQB2)
WQB2 - except that the regression is fitted to the two ordinary sectors either side of the sector at the position of maximum width.

19. Form factor.

SIFF - calculated as 4π times the leaf area divided by perimeter squared (PERM, see above).

$$\text{i.e. SIFF} = \frac{4\pi \times \text{AREA}}{\text{PERM}^2}$$

20. Leaf shape index - calculated by two different methods:

i) SIWN - is calculated by summing the lengths of all the perpendicular sectors and dividing by the maximum width and the number of sectors.

i.e.

$$\text{SIWN} = \frac{\sum_{i=1}^n (\text{perpendicular widths})}{n \times \text{WIDX}}$$

where n = total number of sectors.

ii) SIAL - similar to SIWN but calculated as the area of the leaf (AREA, see above) divided by length and maximum width.

i.e.

$$\text{SIAL} = \frac{\text{AREA}}{\text{LENA} \times \text{WIDX}}$$

21. Apex shape index - computed in two different ways:

This is similar to leaf shape index SIWN, but describes the apex only.

i) SIA5 - is the average width of the first five sectors divided by the maximum width to that point.

ii) SIA3 - as for SIA5, but using sectors 3-5 only.

6.43 Assessment of the Value and Contribution of the Characters

- Variability and Correlations of Characters.

The main criteria used for assessing each of the characters listed above are a) the degree of redundancy in comparison with other characters, b)

the amount of variability and reliability in delimiting the taxa, and c) the discriminatory power of the character. These qualities can be tested by various means. In this study correlations between characters determined the redundancy factor (a), variance ratios estimated criterion b, and the principal components and discriminant functions enabled assessment of the discriminatory power (c above).

Correlation analysis is one way of assessing the value of a character in relation to its information content in the data set. Pearson's product moment correlation coefficient was calculated for each pair of characters for all OTU's. The amount of correlation between any two characters gives an estimation of redundancy of information in those characters. If two characters are highly correlated (i.e. have a correlation coefficient approaching one) then inclusion of both of those characters, rather than one only, does not contribute any more information into the system. It is presumed that the one character retained in the analysis includes most of the variation or information, and that the exclusion of one of the highly correlated pair will not decrease the discriminatory power of the character set.

A major problem when dealing with correlations between variables is to define the level at which the correlation coefficient r is acceptable, and above which one of the characters should be rejected. This is dependent on several factors, including the type of analysis employed and on the nature of the OTU's.

In most cases it is not known whether two characters are correlated because of the same causal genetic factor or whether different genetic factors are responsible for the expression of the phenetic characteristics under question. There are often logical reasons for supposing two characters are highly correlated. For instance, the relationship between leaf shape and the length to width ratio or the apex and base angles of leaves can be

explained on a geometric basis. Sometimes functional reasons may explain correlations of characters, e.g. leaf length and the number of secondary veins.

The use of highly correlated characters in classifications based on conventional morphology is of course extremely common. It has been the practise of taxonomists for many years to include as many phenetic characters as possible. Naturally, high correlations will exist between some of these variables because they are dependent on each other. For instance, the presence of a wing on a fruit may be an important discriminator, but it is likely that further analysis of that wing (i.e. further partitioning of the information contained in that organ) will produce secondary characters that are also useful in the classification. Another example is the overlapping data contained in hair density and types of hairs - simple geometric constraints will dictate densities of certain hair types.

Alternatively, the inclusion of two highly correlated characters in a multivariate numerical analysis such as cluster analysis may result in distortion of the results, through the introduction of a weighting factor. Overlapping information contained in the two characters is allocated more significance than if all characters are given unit independence. This may result in exaggeration of distances between OTU's and on a phenogram the distances at which two clusters fuse will be distorted. Rohlf (1971) believed the only effect of including correlated characters is that of elongation of the phenetic clusters, which of course affects the measured distances in the character space.

The real question regarding these correlations is whether the distortion introduced into a classification is biologically significant. Sneath and Sokal (1973) believed that even highly correlated characters should be retained in the data set since they assume at least some independent source of variation in any empirical correlation. This admits the possibility of

selecting correlated characters by design to accentuate a particular structure. In a study of diverse angiosperm leaves Hill (1980) found that the same basic clustering was evident using the complete character set as that obtained when one character of all highly correlated character pairs with $r \geq 0.6$ was removed. Better definition of the OTU's was obtained when all the characters were included. It is feasible that the new information in each character could outweigh any negative effect of high correlations between characters.

Discussion of the 21 variables in relation to the criteria given at the beginning of this section and the interactions between the variables with this particular set of OTU's follows.

Pearson product moment correlation coefficients were computed for all character pairs using the PEARSON CORR subroutine of SPSS. SPSS (Statistical package for the social scientists) (Nie et al., 1975) has been used for several of the statistical analyses in this study. The set of characters described in the previous section included more than one method of deriving four of the variables. Table 6.4 includes the expected high correlations between these different methods.

<u>Variable</u>	<u>Mean</u>	<u>Standard deviation</u>	<u>r</u>
3. LENP	50.86	21.03	
*LENA	49.94	20.58	0.999
LENT	49.63	20.42	
5. *PMXW	0.71	0.07	0.959
WIDE	0.71	0.06	
20. SIWN	0.61	0.05	0.999
*SIAL	0.60	0.05	
21. *SIA3	0.83	0.07	0.969
SIA5	0.57	0.07	

Table 6.4. Means, standard deviations and correlation coefficients (r) for those variables initially calculated by more than one method; computed for all OTU's.

* indicates the final method selected for each variable

Three methods of calculating leaf length produce very similar results (table 6.4). LENT is not as accurate as LENP or LENA as it does not measure the length along the midrib. LENA is slightly more precise than LENP (in its derivation). It is consistently intermediate between LENP and LENT and has slightly lower standard deviation than LENP. The correlation coefficient of 0.999 between each pair of methods further indicates two of them must be eliminated. LENA has been retained in the analysis and is used in the calculation of any other characters dependent on length.

WIDE was included in the analysis to calculate the position of maximum width as a check on the accuracy of PMXW. It was feared that distortions of the midrib due to digitising inaccuracies and the resultant perpendicular sectors (6.23 above) may have resulted in inaccurate computation of PMXW. The two methods produced identical results (table 6.4) and as PMXW is easier to measure than WIDE the former is retained in the analysis and WIDE is rejected.

The leaf shape index is measured using SIWN and SIAL. SIWN is a complex and accurate method applicable only in situations in which leaves are digitised or under some form of sectoring. The method of calculating SIWN - i.e.

$$\text{SIWN} = \frac{\sum_{i=1}^n (\text{perpendicular widths})}{n \times \text{WIDX}} \quad n = \text{no. of sectors.}$$

results in a measure of the average leaf width over the whole leaf. SIAL, while using the same parameters as SIWN, is a simpler and more easily calculated shape index - i.e.

$$\text{SIAL} = \frac{\text{AREA}}{\text{LENA} \times \text{WIDX}}$$

Both indices are independent of size, and as table 6.4 indicates, result in the same value for any particular leaf. This implies that the relatively

simple shape index, SIAL is a reasonably accurate estimate of leaf shape. As SIAL is the simpler to derive it is included in the following analyses and the more complex leaf shape index, SIWN is eliminated.

Leaf shape includes many component variables, some of which would be expected to correlate with an index for estimating leaf shape. Two such variables in this study are PMXW, the position of maximum width and LTOBR, the ratio of leaf length to width, which can be thought of as approximating leaf elongation. Using a combination of leaf shapes as defined by the Systematics Association Committee for descriptive Biological Terminology (1962) and some theoretical shapes, the interrelations of the shape index SIAL and PMXW and LTOBR are shown in two dimensions in figures 6.6a and b. These indicate the independence of the shape index from both PMXW and LTOBR. Figure 6.7 illustrates the relations of these variables in three dimensions, and shows the relationships between the three characters.

Other variables such as apex and base angles may also be expected to contribute to leaf shape. In order to determine the correlation of these features with leaf shape, bivariate scattergrams of SIAL and each of the other variables thought to be important components of shape, (i.e. PMXW, LTOBR, AANG and BANG) were plotted (figs.6.8 to 6.11). Pearson correlation coefficients were computed for each pair of variables and are given with each scattergram. The most significant empirical correlation is that of SIAL with base angle (BANG). This is expected from the geometrical constraints of the OTU's in this analysis, i.e. most leaves possess attenuate bases, and so as the base angle increases the shape index will also increase.

The other character included in this study which relates to shape is that of the form factor (SIFF)-

$$\text{SIFF} = \frac{4\pi \text{ AREA}}{\text{PERM}^2}$$

This variable ranges from 1.0 for a circle to smaller values (towards zero) as the shape elongates. Linear leaves (e.g. as in some of the populations

of the *D. angustissima* group) will have a low SIFF, while small cuneate leaves (*D. cuneata* populations) will tend to be higher (towards one).

Comparison of SIFF with the shape components PMXW, LTOBR, AANG and BANG revealed reasonably high correlations with LTOBR ($r = -0.802$) and AANG ($r = 0.701$). Bivariate scattergrams are given in figures 6.12 and 6.13. The positive correlation of form factor and apex angle is logical geometrically. As the apex angle increases the form factor will increase and tend towards a circle.

Figure 6.12 shows that the negative correlation between SIFF and LTOBR is non-linear. This means that the Pearson correlation coefficient of $r = -0.8$ is not a true indication of the correlation in the character pair, as this correlation coefficient can only be applied to linear relationships. The scattergram (fig.6.12) suggests that the curved relationship between the two variables would result in a higher correlation coefficient if one variable was transformed into logarithmic form. The correlation coefficient between LTOBR and SIFF was therefore re-calculated using logarithmic values of LTOBR for all OTU's and the r value was found to be -0.944 . This high negative correlation can be explained in terms of the simple geometry of the leaf - as LTOBR increases, i.e. as the leaf elongates, there will be a corresponding decrease in SIFF, i.e. it will deviate further from a circle and tend towards zero. Clearly, one of these two characters can be omitted from the analyses.

In a situation in which both variables of a correlated character-pair are significant the least useful one should be eliminated. Examination of bivariate scattergrams of other character-pairs located two more cases in which LTOBR was involved in a negatively curved relationship, viz. LTOBR with WIDX $r = -0.589$ and LTOBR with AQB1 with $r = -0.668$. Both of these correlation coefficients would probably increase considerably if they too were plotted using log. transformations. Assessing characters on the basis of correlation coefficients alone tends to favour elimination of LTOBR from

the data set. This will be discussed further in relation to the variances within characters.

The other group of variables requiring some explanation is that relating to the apex. The leaf apex is the most likely place to suffer from digitising inaccuracies. Many leaves of the *D. viscosa* complex individuals have small mucronate tips, while others possess acute or acuminate apices of varying lengths. Obtuse or rounded apices are relatively rare in this complex. Coarseness of the digitising pen and resolution of the digitiser itself resulted in inaccuracies around the apex, and so extra characters were included to cover the information omitted by the distorted variables, or to check on the accuracy of a variable.

Two of the leaf apex characters, SIA3 and SIA5, are different methods of deriving the shape index SIWN for the apex only. SIA5 is computed using SIWN over the first five sectors, while SIA3 uses only sector numbers three to five. The first sector passes through the apex and the next two sectors (equivalent to 1mm down the leaf) will probably include any mucronate tip and any discrepancies around the apex. A plot of SIA3 and SIA5 over samples of OTU's from all four groups revealed tighter clustering of similar OTU's with SIA3, and probably implies greater distortion when sectors one and two are included. The correlation coefficient r between the two variables is very high (table 6.4), suggesting that one character should be excluded. I decided to eliminate SIA5 and to include SIA3 in the multivariate analyses.

The quadratic equation around the apex gives information in the direction of curvature of the margins. The linear term (AQB1) is a measure of apex "acuteness". A fine acuminate or aristate leaf will register a low AQB1 value, which will increase as the apex broadens and tends towards broad-acute. The quadratic term (AQB2) approximates the curvature of apical margins, and so acute, or more or less straight-sided apices will have low AQB2 values, while a rounded apex indicates a highly convex curvature. The

positive correlation between AQB1 and AQB2 ($r = 0.6317$) implies a trend towards less acute apices with increasing convex curvature.

AANG and A20W relate to leaf shape, but do not exhibit high correlations with each other or with SIAL. Variables relating to the quadratic equation around the apex, (AQB1 and AQB2) are both relatively highly correlated with the apex angle (AANG). Bivariate scattergrams and the correlation coefficient r are given in figures 6.14 and 6.15. The scatter evident in these diagrams suggests that there is independent information in the two variables, and despite the relatively high correlation coefficient for AQB1 and AANG ($r = 0.828$) both are included in the final character set. The positive relationships between the linear and quadratic terms and apex angle are again explanatory in geometric terms. Since the quadratic equation is a curve fitting function it is reasonable to expect AQB1 and AQB2 to increase, i.e. the margins become more curved (over the first 10 sectors), as AANG, the apex angle also increases.

With inclusion of SIA3 and the resultant exclusion of any details of the first 1-2mm of the leaf, the two characters ATEM and ALEN are included. These two characters were recorded by hand to eliminate any digitiser-related discrepancies. It appeared that there were two pieces of data to be included - that relating to the mucronate apex and another on the length of concave margin at the apex. This information was included by defining a binary character ATEM to detect the presence of a mucronate tip, and the continuous quantitative multistate character ALEN for the length of the acuminate apex. Neither shows high correlations with any other apex characters. Inclusion of the seven variables relating to the apex is therefore acceptable. Each appears to be contributing some new information into the system, and to exhibit a relatively low redundancy factor.

Pearson product moment correlation coefficients indicated one other highly correlated character pair. PERM, the perimeter of the leaf has an

$r = 0.9967$ when compared with LENA, leaf length. This is not unexpected given that all the OTU's are basically elongate leaves. Leaf length is a commonly used character in numerical taxonomic studies. It is easier to measure than leaf perimeter, and it is used in the derivation of several other characters in this study. Therefore, it seems logical to retain LENA and to exclude PERM from further analyses.

<u>Character pair</u>	<u>r</u>
WIDX x AREA	0.865
AANG x AQB1	0.828
AQB1 x SIFF	0.806
AQB2 x SIA3	0.781
AQB2 x AANG	0.777
AANG x SIFF	0.701
B2OW x SIAL	-0.861
LTOBR x SIFF	-0.802
LTOBR x AQB1	-0.668
LENA x AANG	-0.639
LENA x SIFF	-0.620

Table 6.5. Correlation coefficients (r) for variable pairs computed for all OTU's.

Table 6.5 lists the highest correlation coefficients over all OTU's for the particular character pairs involved, and bivariate scattergrams for each are given in figures 6.16 to 6.22. Several of these correlated pairs of characters have already been discussed, and most of those remaining can be explained in terms of the physical and geometric features of the leaf (e.g. WIDX x AREA). AQB1 x SIFF and AQB2 x SIA3 correlations imply an increase in SIFF and SIA3 with increase in curvature of the leaf apex as indicated by AQB1 and AQB2. Negative correlation between LTOBR and AQB1 suggests that as LTOBR decreases, i.e. leaf elongation decreases, AQB1

increases and the apical margin becomes less acute. Examination of the OTU's indicates that this is probably accurate.

The above discussion relates to correlations between characters computed over the complete set of OTU's. Examination of correlation coefficients for the same character pairs on OTU's falling only within the three recognisable species of the *Dodonaea viscosa* complex reveals considerably higher values of r . This means that the particular character pairs are more highly correlated within each species than between them and implies that variance within species is less than that between species. This indicates that the leaf parameters are actually measuring meaningful features.

The amount of variability and reliability of a character in delimiting taxa can be assessed by means of an analysis of variance. There are two components of genetic variance that need to be assessed. These are variance within a species and that between species, and both should be considered when selecting characters. A low ratio of intraspecific variance to interspecific variance, i.e. a ratio approaching one, suggests that character has a low discriminatory power in delimiting the species. The converse is true of a character with a high variance ratio.

The variance ratio, or F ratio has been derived using an F test to examine the significance of variance differences. F ratios, i.e. the ratio of intraspecific variance to interspecific variance, were calculated for each character and assessed for their significance. The F ratios were computed on OTU's belonging to the three species groups. Intermediate group populations were not included as they were variable by definition. F ratios and their significance for the 20 variables remaining in the character set are given in table 6.6. Of the variables listed WQB1 (the linear term of the maximum width quadratic) is the only one that does not have an F value within acceptable statistical limits. Thus, for this variable there is no significant difference in intraspecific and interspecific variance. This is

logical since for geometrical reasons WQB1 would be expected to have a value close to zero for all leaves in this OTU set. Therefore, WQB1 is a character possessing low discriminatory power. This suggests it is not a useful delimiting variable, and so it is rejected from the character set.

	<u>Variable</u>	<u>F Ratio</u>	<u>Significance</u>
ALEN	(Acuminate apex length)	15.186	.0001
ATEM	(+/- mucro)	20.176	.0001
LENA	(Leaf length)	66.155	.0001
WIDX	(Max. leaf width)	61.543	.0001
PMXW	(Posn. WIDX)	8.873	.0001
LTOBR	(LENA/WIDX)	169.577	.0001
AREA	(Leaf area)	29.114	.0001
PRAT	(Left/right margin)	21.409	.0001
PETIOL	(Petiole length)	5.284	.006
A2OW	(Apex 20%WIDX)	38.570	.0001
B2OW	(Base 20%WIDX)	73.648	.0001
AANG	(Apex angle)	32.013	.0001
BANG	(Base angle)	38.125	.0001
AQB1	(Apex quadratic b1)	52.857	.0001
AQB2	(Apex quadratic b2)	37.903	.0001
WQB1	(PMXW quadratic b1)	0.347	.712
WQB2	(PMXW quadratic b2)	29.313	.0001
SIFF	(Form factor)	216.512	.0001
SIAL	(Shape index)	51.421	.0001
SIA3	(Apex shape index)	28.917	.0001

Table 6.6. F ratios and their significance for 20 variables computed for *D. cuneata*, *D. angustissima* and *D. viscosa* groups (121 individuals).

The high F ratios of most variables and their significance levels should be noted from table 6.6. These statistics indicate that the characters LTOBR and SIFF are both very good discriminators between species.

SIFF has a higher F ratio than LTOBR. In view of this and for reasons given above, LTOBR is eliminated from most analyses. It is not desirable to eliminate this character altogether as it is a necessary comparative component of one of the analyses performed on the data set.

F ratios were also computed for these 20 variables using all four groups of OTU's, i.e. *Dodonaea cuneata*, *Dodonaea angustissima*, *Dodonaea viscosa* and the Intermediate group. This resulted in a considerable decrease in most F ratios, although all except WQB1 remained statistically significant. The expected decrease in F ratios on inclusion of the intermediate populations indicates an increase in the variance between species, or groups in this case.

The final character set

The final set of characters selected from the original 21 variables are given in table 6.7. Various statistics given for each variable indicate the large variation that exists over the complete set of OTU's.

The fact that the final character set includes only leaf morphological variables is advantageous when making comparisons with previous classifications of the complex. On the other hand, this set has some disadvantages. Although the character set includes a greater refinement of many previously used variables and several characters which have been checked for accuracy and reliability by different methods, it does not include any features relating to venation patterns or stomate or glandular frequency, or physiological or ecological variables. The reasons for the sole use of leaf macro-morphological characters have been given above.

The selection of characters by various criteria has resulted in a relatively small character set. In view of the analysis to be carried out it is believed to be a useful data set in which the interrelations of the variables are understood. Only those variables possessing high discriminatory abilities are included.

<u>Variable</u>	<u>Range</u>	<u>Mean</u>	<u>Standard deviation</u>	<u>S.D./Mean</u>
*ALEN	1.00-5.00	2.249	1.074	0.478
*ATEM	0-1.00	0.376	0.486	1.293
*LENA	14.08-106.22	49.944	20.586	0.412
*WIDX	1.73-26.02	7.867	4.451	0.566
*PMXW	0.49-0.89	0.707	0.067	0.095
*LTOBR	2.03-36.81	8.828	7.352	0.833
AREA	30.23-1628.82	248.184	233.058	0.939
PRAT	0.94-0.99	0.979	0.012	0.012
*PETIOL	0-0.32	0.110	0.070	0.636
*A2OW	0.003-0.07	0.017	0.011	0.647
*B2OW	-0.09-0.38	0.120	0.082	0.683
*AANG	19.05-157.07	88.958	31.134	0.350
*BANG	6.20-66.16	21.553	12.599	0.585
AQB1	0.20-2.60	0.919	0.472	0.514
AQB2	-0.41-1.99	0.310	0.373	1.203
WQB2	-0.007-0.19	0.077	0.037	0.481
SIFF	0.06-0.67	0.290	0.151	0.521
SIAL	0.46-0.72	0.606	0.052	0.086
SIA3	0.63-0.95	0.826	0.068	0.082

Table 6.7. Statistics for variables computed for all OTU's.

* indicates non-computational variables.

6.44 Character Contribution to the Total Sample Variance

It is useful in assessing the value of a character to know the contribution each character makes to the overall variance of the character set. Those characters contributing less to the overall variance are less efficient in delimiting OTU's. Principal components analysis can be used to determine such contributions.

Principal components analysis (PCA) is a method of transforming a given set of variables, e.g. morphological characters, into a new and smaller set of composite variables, or principal components that are orthogonal (i.e. uncorrelated) to each other. The principal components are expressed in terms of the best linear combinations of the observable variates - i.e. that combination of variables that would account for more of the variance of the data as a whole than any other linear combination of variables. The first principal component is the single best summary of linear relationships in the data. The second principal component being orthogonal to the first must account for that part of the variance not included in the first, i.e. the residual variance. Principal components analysis assumes no *a priori* structure in the data. Thus, PCA is suitable for the analysis of the structure of multivariate observations.

Subroutine FACTOR of SPSS was used to obtain the principal components of this data set. There are many analytical alternatives available in the FACTOR subroutine. Details of these alternatives and the theory relating to PCA can be found in the SPSS documentation (Nie et al., 1975), Sneath and Sokal (1973) and Blackith and Reyment (1971). Procedures chosen for the PCA in this study will be briefly outlined.

The PCA procedure of the SPSS subroutine FACTOR was selected as no *a priori* assumptions were to be made on the underlying structure of the variables. This involves a principal factoring analysis (PA1) to extract the principal components, which are defined as exact mathematical transformations of the original variables. The portion of the total variance accounted for by each factor is represented by the eigenvalues associated with each component. Thus, the principal axis corresponding to the largest eigenvalue is the dimension accounting for the greatest amount of variance in the data. Only those factors with eigenvalues ≥ 1 are extracted. This ensures that only those factors accounting for at least as much of the total variance as a single variable will be treated as significant.

FACTOR also offers alternative procedures in axis rotation, either orthogonal or oblique rotation, to achieve simpler and more meaningful factor patterns. Rotation of axes maximises the contribution of the first principal component, or factor. Orthogonal factor axes should be used in situations in which no *a priori* assumptions are made concerning correlations between factors. Oblique rotation assumes correlation between factors. A method of orthogonal rotation known as VARIMAX in SPSS was used in this study. VARIMAX maximises the variance of the squared loadings in the columns of the factor matrix. That is, it tends to maximise separation of the variables on each factor axis.

Principal components analysis using PA1 factoring and VARIMAX rotation was performed on the complete set of OTU's scored for the 19 characters listed in table 6.7, excluding LTOBR. Four principal components with significant eigenvalues were extracted. The factor scores of each variable for the four factors (components) are given in table 6.8, and the eigenvalues of the components together with their contribution to the total variance are listed in table 6.9. The first three factors account for 68% of the variance, and these are plotted in figure 6.23.

Characters exhibiting high scores on the factors contribute much to the total variance of the OTU's. Table 6.10 summarises the main variables contributing to each of the first three factors (components). Since each of the variables listed for factors one and two, apart from LENA, are components of leaf shape, it appears that the first two principal components relate to a shape factor, and in particular to leaf apex shape. In contrast, variance contained in component three is contributed mainly by variables relating to leaf size, with leaf area, length and maximum width being the important characters.

	<u>Factor 1</u>	<u>Factor 2</u>	<u>Factor 3</u>	<u>Factor 4</u>
ALEN	.03418	.73583	.20459	-.14511
ATEM	.67472	-.13326	-.17398	-.08666
LENA	-.60476	.08124	.71573	-.05485
WIDX	.42274	.47329	.67193	-.26136
PMXW	.20692	-.52107	-.43618	-.29116
AREA	.03460	.39591	.83422	-.11675
PRAT	-.51492	-.29608	-.16207	.03829
PETIOLE	-.09490	-.17396	-.62899	-.48985
A2OW	-.07661	.87710	.20328	-.20394
B2OW	.38598	.35951	.13198	-.78923
AANG	.86676	-.37838	-.08414	.01936
BANG	.33212	-.02245	-.24026	.76852
AQB1	.92185	-.11499	.00836	-.11382
AQB2	.73427	-.44247	-.05124	.23199
WQB2	.19558	-.00954	-.62811	.27443
SIFF	.91169	.29240	-.07759	.04850
SIAL	-.15260	-.33765	.00438	.85906
SIA3	.36994	-.64319	-.07317	.32944

Table 6.8. The factor scores of each variable for the four extracted factors (principal components).

<u>Component</u>	<u>Eigenvalue</u>	<u>% of variance</u>	<u>Cum. % of variance</u>
1	5.60907	31.2	31.2
2	4.34418	24.1	55.3
3	2.28191	12.7	68.0
4	1.28155	7.1	75.1
5	0.96088	5.3	80.4
6	0.72932	4.1	84.5
7	0.55825	3.1	87.6
8	0.53389	3.0	90.6
9	0.45710	2.5	93.1
10	0.38640	2.1	95.2
11	0.26443	1.5	96.7
12	0.21859	1.2	97.9
13	0.13618	0.8	98.7
14	0.08415	0.5	99.1
15	0.05481	0.3	99.4
16	0.05015	0.3	99.7
17	0.03543	0.2	99.9
18	0.01371	0.1	100.00

Table 6.9. The principal components with eigenvalues, percentage of the total variance accounted for by each component (factor) and the cumulative percentage of the variance.

<u>Factor 1</u>		<u>Factor 2</u>		<u>Factor 3</u>	
AQB1	0.922	A2OW	0.877	AREA	0.834
SIFF	0.912	ALEN	0.735	LENA	0.716
AANG	0.867	SIA3	-0.643	WIDX	0.671
AQB2	0.734	PMXW	-0.521	PETIOL	-0.629
ATEM	0.675			WQB2	-0.628
LENA	-0.605				

Table 6.10. Summary of variable contributions (factor scores) to the first three extracted factors (principal components).

Blackith and Reyment (1971) and Sneath and Sokal (1973) included reference to numerous studies in which the first principal component has been found to be a size factor and the second relating to shape. This is the reverse of the results presented here. There is no *a priori* reason for the first principal component to be based on size, and it probably depends on the range of variables included in the analyses. Blackburn (1978) found the first two factors related to a combination of size and shape characters. A similar result was obtained in this study when PCA was applied to all OTU's scoring only the non-computational characters, i.e. those which could have been calculated without digitising the leaves (table 6.7 indicates the computational characters). In this case three factors were extracted and the first two related to a mixture of size and shape components. This could be due to the omission in this analysis of some of the more refined measurements of shape.

In summary, those variables with high F ratios (table 6.6) and with high variance contribution can be presumed to be efficient in delimiting the OTU's. In this category are such characters as form factor (SIFF), the linear term for the apex quadratic (AQB1) and maximum width (WIDX). Further discussion of their significance follows.

6.5 ANALYSES

The major purpose of this work is to determine any taxonomic structure that may exist in the *Dodonaea viscosa* complex in Australia. An initial attempt to classify the OTU's into the three currently recognised taxa of the complex resulted in formation of a fourth group of intermediate leaf morphology. The Intermediate group is composed of those intrabreeding populations containing two or more individuals with leaf morphology intermediate between any two of the *D. viscosa*, *D. cuneata*, or *D. angustissima* groups, or populations containing individuals that could be classified into more than one of the species groups, i.e. appearing to be composed of individuals from different species.

Several features of the data need to be analysed. These are:

- 1) to determine the degree of similarity and dissimilarity that exists within and between the three species groups corresponding to the presently recognised taxa of the complex;
- 2) to determine the amount of variation in the Intermediate group with respect to the three species groups, *D. viscosa*, *D. cuneata* and *D. angustissima*;
- 3) to test reliability of the *a priori* allocation of OTU's to the three species groups. That is the percentage of misidentifications occurring when using a reasonably strict definition (as presently recognised) of each taxon;
- 4) to test the discriminatory power of the various characters used in the analysis.

These problems can be tested using two analytical approaches. Firstly, the *a priori* species groups can be assumed to be valid, and allocation or classification of individuals from the Intermediate group into any one of these three groups could be determined. This is accomplished via multiple discriminant or canonical variate analysis. Secondly, each of the 173

individuals studied can be treated as a single entity and attempts made to cluster the OTU's into closely related groups. Ordination techniques such as principal components analysis and various clustering analyses can be applied to this situation.

The application of these multivariate analytical methods to the data set and the resulting classifications will now be discussed.

6.51 Discriminant Analysis

Discriminant analysis is used in situations in which it is desirable to statistically distinguish between two or more groups of OTU's. The mathematical objective of discriminant analysis is to weight and linearly combine the discriminating variables to produce a discriminant function. This function is determined so that functional values for individuals within groups are similar while the different groups are forced to be as statistically distinct as possible. The mathematical details relating to discriminant analysis will not be discussed here. Theory and examples of applications are adequately dealt with by Blackith and Reyment (1971), Sneath and Sokal (1973) and in the documentation associated with the DISCRIMINANT subroutine of SPSS (Nie et al., 1975).

Discriminant functions are formed to maximise separation of groups. Thus, a linear discriminant function is a combination of characters describing OTU's that weight the characters so that as many as possible of the OTU's in one group, or taxon, have high values for that function and as many as possible of another group have low values. The function then serves as a better discriminator between the groups than does any one character. The discriminant functions maximise the variance between groups compared with the within group variance. Discriminant analysis usually results in the character set being reduced in size.

Discriminant functions can be used to obtain statistical information on the success of discriminating variables to actually discriminate between taxa. Once the discriminating variables providing satisfactory discrimination of OTU's of known group membership are known, a set of function values can be derived to classify new OTU's of unknown group membership.

Many examples exist in the literature of applications of either discriminant analysis or canonical variate analysis, which is recognised by Sneath and Sokal (1973, p.406) as being similar apart from minor particulars. The techniques have been applied to *Betula* to test hybridisation hypotheses between two species (Sharik and Barnes, 1971) and to analyse within plant leaf morphological variation (Dancik and Barnes, 1974). Davey and Clayton (1978) used discriminant analysis to examine the variation within *Oplismenus* (Gramineae) and Abbott (1974) used canonical analysis to assess the inter-relationships among some species of passerine birds in Australia.

Discriminant analysis has been criticised for the assumptions made in defining the *a priori* groups. This is recognised as introducing a bias and a prior subjective assessment of the OTU's being analysed. However, use of discriminant analysis, as with any analytical method, is primarily governed by the data in hand and the hypothesis being tested. Studies examining the discriminating power of a classificatory system derived by some other multivariate analysis, or in situations in which a previous accepted classification is being tested, would seem to be legitimate cases for discriminant analysis. Application of this analytical method is even more valid when it is combined with analyses employing ordination and clustering techniques.

Definitions of the *a priori* groups used in this study were described in detail in section 6.3 above. Difficulties encountered in forming species groups at that initial stage are important and must be considered when using those group definitions as the *a priori* groups in a discriminant analysis. Further properties of these species groups will be discussed in relation to the results of the discriminant analysis.

6.511 Discriminant analysis with 18 selected variables.

The SPSS subroutine DISCRIMINANT was used to determine the order of importance of the characters giving the best separation of the three species groups, and to classify individuals of the Intermediate group using the classification functions computed from the discriminatory variables. The stepwise selection method, in which independent variables are selected for entry into the discriminant analysis on the basis of their discriminating power, was chosen. This method begins by selecting the single variable with the highest value on the selection criterion, (see below for explanation) and pairing this initial variable with each other variable until the combination of the new and the initial variable produces the best criterion value. The second variable then enters the discriminating system. This procedure of locating the next variable that will give the best criterion score, given the variables already selected, continues until all variables are selected or inclusion of more variables produces no significant improvement in discrimination.

Selection of optimal set of variables and extraction of discriminant functions.

The stepwise selection criterion employed was that of Wilks' lambda, which is a measure of group discrimination (small lambda implies greater discriminating power). The variable which maximises the F ratio also minimises Wilks' lambda, in which the overall multivariate F ratio is used to test the differences between group centroids. Wilks' method takes into consideration differences between all the centroids and homogeneity of the groups.

Information was also obtained on another of the stepwise selection criteria, that of Rao's V, a generalised distance measure. The selected variable contributes the largest increase in V when added to the previous variables, amounting to the greatest overall separation of the groups. Change in Rao's V can be used to test for statistical significance.

Use of a stepwise procedure results in selection of an optimal set of variables. This procedure is assumed to be an efficient way of locating the best set of discriminating variables. It is not necessarily true that the order in which the variables are selected reflects their relative importance as discriminators.

Table 6.11 presents details relating to the order in which the variables best discriminate between the groups (the first 10 variables only are given). It is evident from this that form factor (SIFF) is the character with the greatest discriminating power. Partial multivariate F ratios of the first four variables, i.e. SIFF, WIDX, SIAL and AREA, are considerably greater than for the remaining characters. This suggests that the discriminatory power of these four selected variables is greater than that for any other characters of the set. Wilks' lambda is low, indicating high discriminatory power, and change in Rao's V indicates change in distance between group centroids is statistically significant.

Step number	Variable entered	F ratio	Wilks' lambda	Sig.	Rao's V	Change in Rao's V	Sig. of change
1	SIFF	216.51225	.21415	.000	433.02449	433.02449	0
2	WIDX	73.64961	.09480	.000	621.05648	188.03199	0
3	SIAL	29.49194	.06284	.000	782.57411	161.51763	0
4	AREA	19.09722	.04718	.000	991.20242	208.62831	0
5	A2OW	8.45300	.04108	.000	1079.47096	88.26854	.000
6	BANG	6.03627	.03712	.000	1118.42612	38.95516	.000
7	PETIOL	5.08965	.03402	.000	1154.22627	35.80015	.000
8	ATEM	2.38574	.03262	.000	1179.51969	25.29342	.000
9	AQB1	3.13849	.03086	.000	1234.97864	55.45895	.000
10	LENA	1.84523	.02985	.000	1252.59530	17.61666	.000

Table 6.11. The first 10 variables selected by discriminant analysis which best discriminate between the *D. cuneata*, *D. angustissima* and *D. viscosa* groups using 18 variables. Multivariate F ratios test the difference between the group centroids, Wilks' lambda is a measure of group discrimination and Rao's V is a generalised distance measure.

Information relating to the extracted discriminant functions is given in table 6.12. By geometric principles the maximum number of discriminant functions that can be derived is one less than the number of groups. Since there are three groups present only two discriminant functions were derived. The eigenvalues denote relative importance of the discriminant function's ability to discriminate between groups. Changes in Wilks' lambda (and the associated chi-square test of significance) indicate that considerable discriminating power exists in the variables being used.

Discriminant function	Eigenvalue	Relative percent.	Canonical correl ⁿ	Functions derived	Wilks' lambda	Chi-square	D.F.	Sig.
1	8.14280	71.5	0.94373	0	0.02581	402.27880	34	0
2	3.23809	28.5	0.87410	1	0.23596	158.85242	16	.000

Table 6.12. The two discriminant functions derived on the *D. cuneata*, *D. angustissima* and *D. viscosa* groups using 18 variables. Eigenvalues, the relative percentage of the eigenvalue associated with the function and the canonical correlations are given.

The data of table 6.12 suggests that the first discriminant function is very important when considering this complete data set. However, the fact that the number of derived functions is limited to two restricts the conclusions to be drawn from such results.

The relative variable contributions to and interpretation of discriminant functions.

The relative contributions of the variables to the two discriminant functions are given in table 6.13. The main variables contributing to discriminant function one are the maximum leaf width (WIDX), form factor (SIFF),

<u>Variable</u>	Standardized Discriminant Function Coefficients	
	<u>Function 1</u>	<u>Function 2</u>
ALEN	- .06985	- .28412
ATEM	- .36589	.25746
LENA	- .48934	- .95262
WIDX	-3.67635	1.68917
PMXW	- .03563	- .18716
A2OW	.55232	.22530
AANG	- .46582	- .32766
BANG	- .12019	- .69626
AQB1	- .95301	- .04441
AQB2	.25895	.08387
SIAL	- .87159	- .35804
PETIOL	.01553	- .60129
SIFF	3.30523	-1.04507
SIA3	- .12599	- .24910
AREA	2.53098	- .30891
PRAT	- .13875	- .07777
WQB2	- .03316	- .30544

Table 6.13. Relative contributions of the variables to the two discriminant functions.

leaf area (AREA), the linear term of the apex quadratic (AQB1) and the leaf shape index (SIAL). Two of these characters relate to leaf size (WIDX and AREA) and the other three correspond to shape features. Examination of these variable contributions, and accounting for the direction (indicated by the sign), suggests that a leaf with a low score for function one would be narrow (low WIDX, low SIFF i.e. tending towards zero), of small area (low AREA value), with an acute apex or reasonably straight apical margins (AQB1) and possess a relatively high shape index (tending towards one). These features approximate to leaves of *D. angustissima*, i.e. long, narrow, oblong or linear leaves. The converse would be true of leaves with high function one values. These leaves would be broader, with a larger area, with rounded

or curved marginal apices and with SIFF tending towards one and indicating a more rounded leaf. The *D. cuneata* group has features similar to these characteristics.

Discriminant function two is also influenced by WIDX and SIFF, but in opposite directions from that in function one. LENA (leaf length), BANG (base angle) and PETIOL (petiole length) also contribute significantly to function two. Application of the variables of function two to the leaves implies that a leaf with a low function two score would be relatively narrow, of moderate length, have a narrow base angle and no petiole. This applies to leaves of both the *D. cuneata* and *D. angustissima* groups. A leaf with a high value on discriminant function two, on the other hand, should be broad and rounded, longer and with a wider base and a petiole. This corresponds to some *D. viscosa* populations within the data set.

The relationships of OTU's of the three species groups according to these two discriminant functions, and the classification of unknown OTU's of the Intermediate group can be seen in figure 6.24. Clusters of the three species around their respective centroids are evident. However, the overall impression of this plot is of two main clusters, one predominantly comprised of *D. cuneata* individuals, and the other a more dispersed cluster of OTU's belonging to *D. viscosa* and *D. angustissima*. There appears to be a reasonable disjunction between the *D. cuneata* group and the other two.

Examination of the variables contributing most to the two discriminant functions, as discussed above, and the plot of all OTU's as in figure 6.24, shows that function one (with WIDX, SIFF, AREA, AQB1 and SIAL being the main influences) clearly separates *D. cuneata* and *D. angustissima*. *D. viscosa* and the Intermediate OTU's fall between the other two species. Function two (with WIDX, SIFF, LENA, BANG and PETIOL being the main contributing variables) delimits *D. viscosa* from *D. angustissima* and *D. cuneata*, with most intermediate individuals falling within the *D. viscosa* group. These results

indicate that the species groups can be separated, more or less distinctly using a combination of leaf shape and size variables and the presence or absence of a petiole. SIFF, SIAL, AQB1 and BANG correspond to leaf shape, while WIDX, LENA and AREA contribute the size factors.

Re-examination of the *a priori* groups.

The discriminant analysis classification results can be used to check on reliability of formation of the *a priori* groups. In this analysis 96.7% of known cases were correctly classified and four (2.3%) individuals were classified into a different species group from that to which I initially allocated them (table 6.14). In each case the reclassification was to the

Actual Group Name	Group Code	No. of cases	Predicted Group Membership		
			<i>D. cuneata</i>	<i>D. angustissima</i>	<i>D. viscosa</i>
<i>D. cuneata</i>		29	27.0 93.1%	0.0 0.0%	2.0 6.9%
<i>D. angustissima</i>		34	0.0 0.0%	32.0 94.1%	2.0 5.9%
<i>D. viscosa</i>		58	0.0 0.0%	0.0 0.0%	58.0 100.0%
Intermediate (Ungrouped)		52	4.0 7.7%	18.0 34.6%	30.0 57.7%

Percent of 'Grouped' cases correctly classified: 96.7%

Chi-square = 218.595 Significance = 0.

Table 6.14. Discriminant analysis classification results with percentages of correctly classified individuals of the *D. cuneata*, *D. angustissima* and *D. viscosa* groups, and the allocation of the Intermediate group individuals to the three species groups.

D. viscosa group. Two individuals from *D. cuneata* populations (GRAMP 3546 and COLMON 819) and two *D. angustissima* individuals, (SIMDES Dmb16 and SIMDES Rhyko) were misclassified. Reference to the plots of these leaves (fig.6.25) indicates that the leaves of these individuals do appear to be different from the other OTU's of their respective group (Appendix B). Figure 6.24 locates these four individuals with respect to all other OTU's.

Characters responsible for the misclassification of these individuals can be determined by examining the position of the particular OTU on the plot of the two discriminant functions (fig.6.24). For instance, GRAMP 3546 appears to have been classified into the *D. viscosa* group primarily on the basis of discriminant function one. Important variables contributing to this function are WIDX, SIFF, AREA, AQB1 and SIAL. The position of GRAMP 3546 in figure 6.24 correctly indicates its leaves are narrower (i.e. lower WIDX and SIFF) than most other individuals belonging to the *D. cuneata* group, and the lower AQB1 value reflects its narrower or less truncate apex (fig.6.25).

These misclassifications of members of the *a priori* groups can be interpreted in several ways. For example, misclassified individuals can be located and used to reanalyse the valid membership of groups. That is, the amount of misclassification gives some indication of the homogeneity of the *a priori* groups. (The probability of membership of groups is also important.) Alternatively, the percentage of correct classifications may be considered an indication of distinctiveness of the groups.

If this latter view is accepted, then 96.7% correct classification would imply the groups are considerably distinct, given the set of characters used. Logical reasons will now be given to explain the reclassification of the particular individuals in question, but these reasons all relate to the initial definitions of the groups.

Reclassification of all four individuals in the discriminant analysis is explicable in terms of the populations to which they belong. Two

individuals misclassified into *D. viscosa* (GRAMP 3546, COLMON 819) are each single individuals in a population in which the other five or four individuals respectively form a more homogeneous *D. cuneata* population. The Intermediate group by definition included only those populations with two or more intermediate individuals, and therefore it is unlikely that the single, unusual individuals within a population will be reclassified.

The two *D. angustissima* individuals (SIMDES Dmb16 and Rhyko), which were reclassified into *D. viscosa*, belong to a population at the extreme of the morphological range of that species as recognised to this time. The position of members of this population in relation to the placement of other OTU's will be further discussed with the cluster analysis results.

Classification of Intermediate individuals.

Details of classification of individuals belonging to the Intermediate group need to be examined. The wide scatter of these OTU's and the overlap between *D. viscosa* and *D. angustissima*, which is largely produced by the intermediate individuals are evident in figure 6.24. The majority of these OTU's fall within the *D. viscosa* group (57.8%) (table 6.14), while 34.6% are classified into *D. angustissima* and only 7.7% into *D. cuneata*. The plot also gives the location of some Intermediate group individuals. Even from this small sample it can be seen that the Intermediate populations do exhibit a great morphological range. Individuals of two of the 11 Intermediate populations (i.e. BLACKMT and ONGERUP) were classified into all three species groups. The majority of members belonging to each of these populations were placed in *D. viscosa* and one individual from each was placed in *D. cuneata* and *D. angustissima*. In the remaining nine populations individuals were classified into either of two species groups. In each case the placement of the OTU is meaningful with respect to the other OTU's with which it is grouped.

That populations, recognised as being intrabreeding units and sufficiently isolated from other populations, are broken up so that plants belonging to a single population are classified into more than one of the taxa *Dodonaea viscosa*, *D. cuneata* or *D. angustissima*, emphasises the polymorphism of the complex. Leaf morphology, as described by the selected characters, can be used to define the three species in a strict sense. However, a range of plants exhibiting intermediate leaf morphology with respect to a number of features, causes breakdown of the delimiting factors between the species. Using a multiple discriminant analysis, and given the chosen character set, it appears as though it is not possible to reliably classify and identify individuals into one of the three species comprising the *Dodonaea viscosa* complex. This multivariate analysis emphasises the variability of leaf morphology in this complex and indicates that there are no reliable distinguishing features to separate the species.

6.512 Discriminant analysis with non-computational variables.

In order to assess the potential of the digitising system and reliability of the variables generated by the associated leaf parameter program a comparative discriminant analysis was performed using the 11 non-computational variables only. By non-computational variables is meant those variables which can be measured without the aid of a digitiser, i.e. ALEN, ATEM, LENA, WIDX, PMXW, LTOBR, A2OW, B2OW, AANG, BANG and PETIOL (indicated by * in table 6.7). This comparison should give an idea of the usefulness of the more refined characters computed from the leaf images relative to those which could have been measured by hand.

Leaf length to width ratio (LTOBR) is included in this discriminant analysis as it is a character commonly used in numerical taxonomic studies. It was previously eliminated from the character set because of its very high negative correlation with form factor (SIFF), which is a computational variable and therefore not included here.

Selection of optimal set of variables and extraction of discriminant functions.

The order in which the variables best discriminate between the groups can be found in table 6.15. Again, the discriminatory power of the first four variables is much greater than that of the remaining variables, but in this case the variables corresponding to these high F ratios are different. In this analysis LTOBR is the character with the greatest discriminatory power, followed by LENA, BANG and A2OW. Of the four most important discriminators of the previous analysis (i.e. SIFF, WIDX, SIAL and AREA) only WIDX is included here and it does not appear to be a very good discriminator. Other comparative data can be obtained from the table.

<u>Step Number</u>	<u>Variable Entered</u>	<u>F Ratio</u>	<u>Wilks' Lambda</u>	<u>Sig.</u>	<u>Rao's V</u>	<u>Change in Rao's V</u>	<u>Sig. of Change</u>
1	LTOBR	169.57737	.25812	.000	339.15453	339.15453	.000
2	LENA	49.44590	.13988	.000	443.18405	104.02953	.000
3	BANG	21.08989	.10258	.000	521.32098	78.13692	.000
4	A2OW	13.62059	.08294	.000	629.18009	107.85912	.000
5	AANG	5.96980	.07507	.000	666.49222	37.31213	.000
6	WIDX	7.77725	.06599	.000	721.31290	54.82068	.000
7	ALEN	4.49716	.06109	.000	751.55486	30.24197	.000
8	PETIOL	1.45700	.05952	.000	761.59463	10.03976	.007
9	B2OW	2.15398	.05728	.000	776.63786	15.04323	.001
10	PMXW	1.09867	.05615	.000	787.58338	10.94553	.004
11	ATEM	1.00535	.05512	.000	797.12789	9.54451	.008

Table 6.15. The ordered non-computational variables selected by discriminant analysis to best discriminate between the *D. cuneata*, *D. angustissima* and *D. viscosa* groups. The multivariate F ratios, Wilks' lambda and Rao's V are given.

The eigenvalues of the two derived discriminant functions (table 6.16) are considerably lower than when all the characters are used. This suggests a lower relative importance of the discriminant functions.

Discriminant function	Eigenvalue	Relative percent.	Canonical correl ⁿ	Functions derived	Wilks' Lambda	Chi-square	D.F.	Sig.
1	4.39017	64.99	0.902	0	0.0551	327.480	22	.000
2	2.36517	35.01	0.838	1	0.2972	137.123	10	.000

Table 6.16. The two discriminant functions derived on the *D. cuneata*, *D. angustissima* and *D. viscosa* groups using non-computational variables. Eigenvalues, relative percentages and canonical correlations are given.

The relative variable contributions to and interpretation of discriminant functions.

The relative contributions of the variables to the two functions are given in table 6.17. It will be noted that these values are much lower than those for the analysis including all variables (table 6.13). The main variables contributing to discriminant function one are length to width ratio (LTOBR), apex position of 20% of maximum width (A20W), leaf length (LENA) and maximum width (WIDX). Two of these features correspond to leaf size and two to shape. Examination of these values indicates that discriminant function one would separate a long, narrow, linear leaf having a low score from a short, broader leaf with a truncate or obtuse apex and having a high score. These leaf types correspond to *D. angustissima* individuals and a combination of *D. cuneata* and *D. viscosa* respectively.

<u>Variable</u>	Standardized Discriminant Function Coefficients	
	<u>Function 1</u>	<u>Function 2</u>
ALEN	-.06637	-.17602
ATEM	.06782	.08806
LENA	-.27134	.13475
WIDX	.25609	.34325
PMXW	.06962	-.08314
LTOBR	-.59017	-.00150
A2OW	.32596	-.39793
B2OW	.00634	.29470
AANG	-.05609	-.68947
BANG	-.07085	-.45069
PETIOL	.00446	-.28490

Table 6.17. Relative contributions of the non-computational variables to the two discriminant functions.

Discriminant function two has as its main contributors apex angle (AANG), base angle (BANG), apex position of 20% of maximum width (A2OW) and maximum width (WIDX). This combination of characters suggests function two relates mostly to leaf shape. High scoring OTU's would be relatively broad leaves having a long acute apex and attenuate base, whereas low scores correspond to rather narrow leaves with large apex and base angles. This latter case appears to correspond with *D. cuneata* and a high function two score with a mixture of *D. angustissima* and *D. viscosa*.

Figure 6.26 shows the relationships of the OTU's of the three species groups and the relative placement of the unknown OTU's of the Intermediate group. Clusters for each species around its respective centroid are again evident, but these clusters are less coherent than in the analysis including all characters and there is no indication of *D. cuneata* being distinct from the other two species.

The plot of the OTU's (fig.6.26) and analysis of the contributing variables indicate that discriminant function one (with LTOBR, A20W, LENA and WIDX being the main variables) is more or less capable of distinguishing *D. angustissima* from *D. viscosa* and *D. cuneata*, but there is complete overlap of these last two species. Function two (with AANG, BANG, A20W and WIDX) cannot adequately separate any of the three species. This is to be compared with the discrimination achieved with all variables (fig.6.24), in which the three species can be distinguished fairly reliably using the two discriminant functions. This is reflected by the eigenvalues of the derived discriminant functions of the two analyses being higher in the better discriminators.

Classification of Intermediate individuals.

The apparent continuum between species clusters visible in figure 6.26 is caused by the classification of the majority of the individuals belonging to the Intermediate group in positions between the centroids of the species groups. Most of these intermediate OTU's are again classified into the *D. viscosa* group (51.9%) (table 6.18), 26.9% are classified into *D. angustissima* and 21.2% into *D. cuneata*. A larger number of Intermediate individuals are placed in *D. cuneata* than in the analysis including the computational variables (fig.6.26).

Re-examination of the *a priori* groups

The non-computational discriminant analysis also results in the reclassification of four individuals belonging to the known species groups, i.e. 96.4% were correctly classified. However, one (FRGAM Eich636) of the re-allocated OTU's shows a reversal in that it is transferred from the *D. viscosa* group to *D. cuneata*. The plots of the digitised leaves representing this individual and all the leaves of these two species (Appendix B) suggest that this is not a very satisfactory result. Its position can be seen on figure 6.26 to be intermediate between *D. viscosa* and *D. cuneata*.

<u>Actual Group</u>	<u>Symbol</u>	<u>No. of cases</u>	<u>Predicted Group Membership</u>		
			<u><i>D. cuneata</i></u>	<u><i>D. angustissima</i></u>	<u><i>D. viscosa</i></u>
<i>D. cuneata</i>		29	28.0	0.0	1.0
			96.6%	0.0%	3.4%
<i>D. angustissima</i>		34	0.0	32.0	2.0
			0.0%	94.1%	5.9%
<i>D. viscosa</i>		58	1.0	0.0	57.0
			1.7%	0.0%	98.38%
Intermediate (Ungrouped cases)		52	11.0	14.0	27.0
			21.2%	26.9%	51.9%

Percent of 'Grouped' cases correctly classified: 96.69%

Table 6.18. Discriminant analysis classification results (using non-computational variables) with percentages of correctly classified individuals of the *D. cuneata*, *D. angustissima* and *D. viscosa* groups, and the allocation of the Intermediate group individuals to the three species groups.

The plot also shows the relative placement of the other three re-classified individuals into *D. viscosa* from *D. cuneata* (COLMON 819) and *D. angustissima* (SIMDES Dmb16 and Rhyko).

6.513 Conclusion

Multiple discriminant analysis based on *a priori* groups derived from prior and existing classifications of the *Dodonaea viscosa* complex indicates that these classifications are unreliable. While the species groups corresponding to the three main taxa of the complex are reasonably distinct, plants initially recognised as having intermediate leaf morphology are classified as intermediates and break down the species-group delimiting factors.

Discriminant analysis using only non-computational variables produced a less satisfactory result with weaker clustering of the species groups, and less reliable discriminators between the groups. The use of computational variables derived through digitised leaf images refined the discriminant functions to produce more reliable discriminators, *but even with this more powerful character set the species of the D. viscosa complex cannot be satisfactorily distinguished.*

6.52 Principal Components Analysis

Principal components analysis (PCA) is now widely used in numerical taxonomy to assess the interrelationships of OTU's. It was discussed in section 6.44 where PCA was used as an R-technique in analysing structure in the variable set. Here PCA is employed as a Q-technique, in which the OTU's are examined in relation to the principal components.

Numerous applications of this technique are now in the literature. Sneath and Sokal (1973) and Blackith and Reyment (1971) included several cases and recently it has been applied to the *Bulbostylis/Fimbristylis* (Cyperaceae) complex (Hall et al., 1976) and to *Capsicum* (Solanaceae) (Jensen et al., 1979). Principal components analysis has proven particularly useful in revealing hybrids among species complexes, e.g. Schilling and Heiser (1976) used it with some *Solanum* species and Rushton (1978) applied the technique to *Quercus robur* and *Q. petraea* populations.

The SPSS subroutine FACTOR was used in section 6.44 to extract four principal components (or factors), which accounted for 75% of the variance in the data set. Since the first three components are responsible for 68% of the variance (table 6.9), only those three will be discussed here. Table 6.10 summarises the variable contributions to these first three components, and, as was discussed previously, it can be seen that components one and two relate to leaf and apex shape and component three to size variation.

Given that the source of variation included in each of the principal components is known, the OTU's were plotted on the first three principal axes to assess the relationships of the individuals (fig. 6.27a to c). None of these plots shows any major disjunctions in the OTU's. Figures 6.27a and 6.27b suggest some separation of the *D. cuneata* and *D. angustissima* groups on principal axis one, but plotting the OTU's on axes two and three (fig. 6.27c) results in overlap of all groups.

Although there are no distinct clusters of OTU's evident in this analysis, discussion of the interrelations of the OTU's is warranted. Principal component one, which relates to leaf shape, (with AQB1, SIFF, AANG and AQB2 as the main contributors (table 6.10)), distinguishes those individuals with obovate leaves, with cuneate or truncate apices, i.e. with high form factor (tending towards one), broad apex angle and with high convex curvature of the apical margins, from narrow, linear, acute leaves. Figure 6.27a supports this in that principal axis one, which accounts for 31.2% of the variance, separates *D. cuneata* leaves (with high scores) from those of the *D. angustissima* group. OTU's belonging to *D. viscosa* lie intermediate between the other two species groups and Intermediate group members range over the extent of the axis.

Principal component two, accounting for 24.1% of the total variance, does not locate any break in the complex. This axis is dominated by the apex characters A20W and ALEN, and so it has as its extremes those leaves with long acute or alternate apices as against obtuse leaves. The OTU's are distributed in figure 6.27a on the second principal axis with individuals with obtuse leaves of all four groups having low scores and the acute leaf apices of the *D. viscosa* individuals scoring high.

The location of OTU's in figure 6.27b supports the previous suggestions that principal component three is mainly a size factor. In this plot principal axis one again separates *D. cuneata* from *D. angustissima*, but not as distinctly as with component two. Principal axis three (with AREA, LENA

and WIDX being the main contributing variables) distributes the OTU's according to size. Small leaves of various shapes are plotted on one extreme and large, mostly ovate to lanceolate leaves on the other. This results in overlap of individuals from the three species groups and the Intermediate group. Even though principal component three accounts for only 12.7% of the variance it is an important factor when considering the interrelationships of the whole data set.

The location of particular individuals when plotted according to any of the first three principal axes are shown in figure 6.27. Those OTU's reclassified in the discriminant analysis (section 6.51), as well as the extremes of each of the groups are indicated.

PCA is recognised as representing the distances between major groups or clusters faithfully, but it is known to falsify relations between close neighbours (Rohlf, 1968). Given this misrepresentation of distances between closely positioned OTU's, and since this principal components analysis was carried out to assess the overall relative positions of OTU's according to their species groups, no further discussion is included here on the classification of particular OTU's.

Using principal components analysis the three species comprising the *D. viscosa* complex are not satisfactorily distinguished. The extremes of two of the taxa are separable using various components of leaf shape (the first principal component), but apex shape (component two) and leaf size variables, (relating to component three), order the OTU's with complete overlap of all four groups.

There is a significant correlation of the factors accounting for 68% of the variance in the data set as extracted via principal components analysis and the morphological characters of leaf shape and size as used by previous workers.

The fact that individuals belonging to the Intermediate group populations are again dispersed over the range of the three principal axes further emphasises the variation in leaf morphology in this complex.

6.53 Cluster Analysis

Clustering is used to group OTU's in multivariate space into disjoint sets, which are thought to correspond to particular characteristics of the sample. Cluster analysis attempts to locate partitions in a set of OTU's.

There are now numerous methods of clustering available and the user must choose appropriate techniques, which can greatly influence the results even with the same data set. The details of all these clustering methods are adequately covered by Blackith and Reyment (1971) and Sneath and Sokal (1973) and will not be discussed here. However, the justification and explanation of the techniques used in this cluster analysis will be presented.

No suitable clustering programs were available at the University of Adelaide, but I was able to use the CLUSTAN package developed by D. Wishart of the University of St. Andrews, Scotland (Wishart, 1970) on the Univac 1100/40 computer at Australian National University. This package, recognised by many to be the most comprehensive cluster analysis package, includes a large number of clustering techniques and a variety of distance and similarity measures.

The basis for locating taxonomic structure in any data set is the resemblance, or similarity matrix. Similarity between OTU's is usually estimated by means of a similarity coefficient, which quantifies the resemblance between any two OTU's given the selected character set. The resulting similarity matrix is used as the input data for analyses such as cluster analysis.

Similarity coefficients can be classed as distance, association, correlation or probabilistic resemblance measures. The mathematic evaluation of these various coefficients can be found in Williams and Dale (1965).

Sneath and Sokal (1973) discussed their relevance and application to particular data sets. Discussion will be restricted here to that used in this analysis, namely a distance similarity coefficient.

Distance coefficients measure the distance between OTU's in some defined space, the most commonly used being a measure of Euclidean distance in multidimensional character space. A distance coefficient is actually the converse of a similarity coefficient in that it estimates dissimilarity.

The CLUSTAN package provides the user with a wide choice of similarity coefficients and several distance resemblance measures. The taxonomic distance measure of squared Euclidean distance was used in this analysis. This is a distance coefficient based on standardised characters in which the Euclidean distance Δ_{jk} between two OTU's j and k in n -dimensional space takes the form

$$\Delta_{jk} = \left[\sum_{i=1}^n (x_{ij} - x_{ik})^2 \right]^{1/2}$$

Given that Δ_{jk} increases with the number of attributes an average distance is often computed. That is

$$d_{jk} = \sqrt{\Delta_{jk}^2/n}$$

Sneath and Sokal (1973) pointed out that this is actually a special case of the metric distance functions (the Minkowski metrics) whose general form is

$$d_{r(j,k)} = \left[\sum_{i=1}^n |x_{ij} - x_{ik}|^r \right]^{1/r}$$

The clustering technique chosen for this analysis falls into the category of sequential, agglomerative, hierarchic, nonoverlapping clustering methods. Most cluster analyses are sequential in that they apply a repeated sequence of operations on the set of OTU's.

Agglomerative techniques begin with the separate individuals and progressively fuse these into a smaller number of groups until all OTU's are contained in a single set. In contrast, divisive techniques begin with all OTU's in one set and progressively subdivide it into subsets.

Hierarchic classifications are equivalent to those used in classical biological taxonomy, so that any member of a lower ranking taxon is also a member of the higher ranked taxon. The combination of the hierarchic and the nonoverlapping method, in which taxa at any one rank are mutually exclusive, results in a nested classification analogous to that of conventional taxonomy.

Program HIERAR of the CLUSTAN package includes a choice of eight clustering strategies, all of which involve combinatorial transformations of the similarity matrix. A combinatorial strategy derives all measures subsequent to the initial set by manipulation of the similarity matrix without further reference to the original data set.

The clustering strategy chosen here is that based on average linkage outlined by Sokal and Michener (1958) and known as the unweighted pair-group method using arithmetic averages (UPGMA). The pair-group method is that in which only one OTU or cluster may be admitted for membership of an extant cluster at any one time.

Arithmetic average clustering computes the arithmetic average of the similarity (or dissimilarity) coefficients between an OTU which is a candidate for admission to an extant cluster and the members of that cluster, or between the members of two clusters which are about to fuse. This method does not account for the similarity (or dissimilarity) coefficients between members within the cluster. In contrast to centroid clustering, in which the centroid of the OTU's forming an extant cluster is located and the dissimilarity of any candidate OTU or cluster is measured from that centroid point, arithmetic average clustering does not consider the density of OTU's constituting the extant cluster.

Weighted clustering was introduced by Sokal and Michener (1958) to give fusing clusters or merging branches of a dendrogram equal weight regardless of the number of entities in each cluster or branch. This means that the most recently admitted member of a cluster is weighted equally with all previous members, and so this procedure must result in a distortion of the overall taxonomic relationships in favour of the last member of a cluster. Sneath and Sokal (1973) have shown that the weighted clustering method increases the distance between the clusters. In presenting this alternative Sokal and Michener (1958) were attempting to give equal importance to phyletic lineages, but with the present phenetic approach to numerical taxonomy use of a weighted clustering strategy seems undesirable. Unweighted clustering, on the other hand, gives equal weight to each OTU in a cluster whose resemblance with another OTU or cluster is being evaluated.

Thus, the UPGMA algorithm computes the average similarity or dissimilarity of a candidate OTU to an extant cluster, with each OTU in that cluster being weighted equally. This is the equivalent of Lance and Williams' (1967) group-average method which they define as:

$$U_{L,JK} = \frac{t_J}{t_{(J,K)}} U_{L,J} + \frac{t_K}{t_{(J,K)}} U_{L,K}$$

where - $U_{L,JK}$ is the average similarity between clusters L and JK, i.e. the dissimilarity coefficient;

- $U_{L,J}$ and $U_{L,K}$ are the average similarities between clusters (or OTU's) L and J and L and K respectively; and

- t_J , t_K and $t_{(J,K)}$ relate to the sample size, i.e. the number of individuals in clusters J, K and (J,K) respectively.

When examining some of the problems associated with cluster analysis Everitt (1979) concluded that this group-average clustering method is probably the most meaningful technique, especially in comparison with single-linkage clustering.

6.531 Cluster analysis with 17 selected variables (CLUSA)

One of the disadvantages of CLUSTAN is that the classification systems cannot handle mixed data. To include both binary and numeric (continuous) data it is required that the data of one mode be transferred to that of the other. The selected character set, as discussed in section 6.42 and listed in table 6.7, contains 18 continuous variables and one binary, i.e. ATEM - the presence or absence of a mucronate apex. Given that this one binary character was not shown to contribute significantly to either the discriminant functions, as derived in the discriminant analysis (section 6.51), or the principal components extracted using PCA, it was decided to mask ATEM from the data set in the cluster analysis instead of transforming it to a numeric form. For reasons discussed above (section 6.43), LTOBR was also excluded from the cluster analysis.

The remaining 17 variables were standardised to zero mean and unit variance and program CORREL of the CLUSTAN package was used to compute the similarity matrix with squared Euclidean distance as the similarity distance coefficient. The variables should be standardised when using continuous data to avoid bias of the similarity coefficient towards those variables with large variances.

This similarity matrix is then used by program HIERAR which employs the UPGMA method in an attempt to cluster the OTU's into closely related groups considered to be differentiated from other clusters by particular properties relating to the data set.

The results of the cluster analysis are represented here in the form of a phenogram. While it is recognised that phenograms result in information loss and that they can distort relations of distant OTU's (Clifford and Williams, 1973), the classification is presented in this form as it is conceptually simple and readily interpretable for comparison with a conventional

taxonomic hierarchy. The use of other graphical techniques such as linkage diagrams and contour maps has recently increased. Everitt (1978) discussed such techniques in relation to multivariate data.

A significant problem in interpreting the results of a cluster analysis is that of determining the most appropriate number of clusters for the set of data. The importance and difficulty of this problem has been discussed by several authors including Sneath and Sokal (1973) and Everitt (1979), who concluded that no satisfactory solution is available. He postulated that the problem may be insoluble in a general sense simply because there is no universally accepted definition of a cluster. Everitt suggested that any rigid inference of an optimal number of clusters in relation to the observed value of a numerical index of goodness of fit (as resulting from significance tests) may not be productive.

In view of this unresolved problem, and given that this analysis is concerned with individuals (the OTU's) of a species complex, in which broad scale structure is sought, only the last twenty clusters of the results are presented in the phenogram. Inclusion of the fusions of OTU's and clusters in the earlier stages of the cluster analysis adds little extra information and probably serves to confuse interpretation. It is the relationships of the members of the three species groups and the overall placement of the Intermediate individuals which is of interest.

The results of the cluster analysis using the 17 selected variables are presented in the phenogram in figure 6.28. Table 6.19 lists the individuals of each of the 20 clusters as represented in the phenogram. The main leaf type of each cluster is shown on the diagram and to aid in interpretation reference will be made to the leaves plotted in Appendix B. This cluster analysis will be referred to as CLUSA.

Table 6.19. Component OTU's of Clusters in CLUSA. (cf. fig.6.28).

(Groups: C = *D. cuneata*, A = *D. angustissima*,
V = *D. viscosa*, I = Intermediate.)

<u>Cluster number</u>	<u>Total no. of OTU's</u>	<u>Group</u>	<u>Population</u>	<u>Individuals</u>
1	4	C	GRAMP MDC	3541, 3547, 3551 1826
2	4	C	GRAMP MDC	3550 1832
		I	BLACKMT	Jgw1, Jgw3
3	17	C	MDC COLMON FINIS CWS COBAR	1828, 1829, 1831 814, 817, 820 Tind1621
4	25	A	SIMDES	Dmb16
		V	FRGAM SHERARB TAS MARION	Kuc3142 Whi8326 1545, 1546
		I	YASS BLACKMT ONGERUP MUBRAEN MTGREEN SINTON GRIFF	1688 Jgw5, Mc1132, Mc1133 3067, 3072, 3073, 3079 1886 Cov075, Cov652 Mc1344, Mc1345
5	2	I	SESA HYDEN	439 1023
6	1	C	CWS	Tind1622
7	1	I	ONGERUP	3078
8	29	C	GRAMP	3546
		A	SIMDES QULAFF STBLDS LINKI KVR	Dmb14 Bee1135 1299, 1301-1303 350, 353, 355-357

Table 6.19 (Cont'd)

<u>Cluster number</u>	<u>Total no. of OTU's</u>	<u>Group</u>	<u>Population</u>	<u>Individuals</u>
8 (cont'd)		I	YASS BLACKMT MUBRAEN REMARK SUGBUG GRIFF	1687, 1691 Jgw4 1885 1174, 1176 Mc1343
9	10	A	SIMDES QULAFF LINKI KVR LINWASX	Dmb17 Stb6793, Bee1437 1300 352
10	7	A I	LINREDR SESA REMARK	 432 1181
11	22	C A V I	COLMON CWS SIMDES FRGAM SHERARB QLANG SESA ONGERUP MUBRAEN REMARK HYDEN	815,819 Const350 Dmb15, Rhyko Roh1673, Whibgam, Eich636, Eich605 Evt741 Bri662, Wil14 437, 442, 443 3071 1887 1175 1019-1022
12	21	V	SLWAIT SLWATIP SHERARB WAMAG K WALL MARION	418, 422, 423, 425 Hub5101 3577 1541, 1542, 1548, 1549

Table 6.19 (Cont'd)

<u>Cluster number</u>	<u>Total no. of OTU's</u>	<u>Group</u>	<u>Population</u>	<u>Individuals</u>
12 (cont'd)		I	YASS MUBRAEN REMARK	1685 1883 1173
13	8	V	SLWAIT K WALL NZ	421 3576, 3578
		I	YASS	1686, 1689
14	1	V	QLANG	Mik2979
15	4	V	PALMV	
16	3	V	SHERARB	Francis, Evt1825, Whi9503
17	1	C	GRAMP	3548
18	5	V	QLREP QLBURM	Mori760
19	7	V	QLBURM QLANG K WALL	Gitt872, Sharp58, Sharp59, Shdurr, Poolman Bailey 3580
20	1	I	SINTON	Cov651

The phenogram (fig.6.28) indicates the general clustering of OTU's belonging to the three species groups. In particular the *D. cuneata* and *D. angustissima* individuals have formed reasonably distinct clusters. While those members of the *D. viscosa* group are seen as distinct from the other two species, the relations within the group are less satisfactory. Details of composition of the clusters and placement of particular individuals will now be discussed in preparation for the taxonomic interpretation as presented in section 6.6.

The first seven clusters form a group which appears to be distinct from the remaining OTU's. The phenogram indicates that this group corresponds to the *D. cuneata* species group, with only five *D. cuneata* individuals being placed outside of cluster numbers 1 to 7. Several OTU's from the Intermediate group, seven from *D. viscosa* and one *D. angustissima* individual are clustered with *D. cuneata*. Examination of leaves of these reclassified individuals helps to determine the basis on which the clusters are formed. Cluster 4 is composed of a combination of individuals from *D. viscosa*, *D. angustissima* (one only) and the Intermediate group. These leaves are more elongate than *D. cuneata* leaves and, since they share such features as the obovate shape and obtuse, truncate or rounded apices they have been clustered with *D. cuneata* and distinguished from other members of their respective groups. The morphological features of leaf shape and apex shape, which appear to be the most obvious common attributes of these clusters, correspond with the first two principal components as extracted in PCA (section 6.44). While single representatives of some populations are classified with the *D. cuneata* group, in other cases whole populations are transferred, e.g. the TAS population of *D. viscosa* and MTGREEN of the Intermediate group.

Clusters 6 and 7 are each composed of single individuals, which may be separated from other members of the group on apex shape and leaf size. ONGERUP 3078 (cluster 7) of the Intermediate group was similarly classified

into *D. cuneata* with the discriminant analysis (fig.6.24), as was BLACKMT Jgw1 (cluster 2 here).

Apart from three individuals, all *D. angustissima* OTU's are distinctly clustered into clusters 8, 9 and 10. Intermediate group individuals in clusters 8 and 10 have linear or oblong leaves mostly with acute apices. Cluster 8 also includes one of the reclassified *D. cuneata* individuals - GRAMP 3546. The results here again correlate with those of the discriminant analysis, in which GRAMP 3546 and members of the Intermediate population SUGBUG (for example) were classified into *D. angustissima*.

Classification of *D. viscosa* OTU's in this cluster analysis is more complex than that of either of the other two species. This is not unexpected since both the discriminant analysis and principal components analysis indicated weaker clustering of OTU's of this species. Table 6.19 reveals that clusters 11 and 12 contain the majority of the *D. viscosa* group and appear to represent those oblanceolate to lanceolate leaves with attenuate, acute apices. The leaves of this group are all of approximately the same size, i.e. c. 1cm wide and 5-7cm long. The fusion of clusters 11 and 12 with *D. angustissima* at a similarity coefficient of 1.524 reflects the affinity of these two groups.

Clusters 13 and 14 together contain 9 individuals, all of which have larger leaves than in the main *D. viscosa* cluster discussed above. Although these individuals have leaves of similar shape, the apex is broader (less attenuate) and in some cases is obtuse, e.g. the NZ population. Clusters 18 and 19 also contain large *D. viscosa* leaves. Since these last mentioned clusters include individuals with leaves of various shapes (cf. QLANG Bailey with QLREP Scarjon), some with long acute apices and others almost obtuse, it appears that their distinction is mainly on a factor of size. The variance in the data set as accounted for by the third principal component is probably responsible for this separation.

The remaining *D. viscosa* individuals are grouped together (clusters 15 and 16) on the basis of the presence of a petiole and the tendency towards spatulate-shaped leaves.

Two clusters remain, namely 17 and 20, both of which contain single individuals. The separation of *D. cuneata* GRAMP 3548 is difficult to explain when examining the leaf plot only. Ordination plots (fig.6.23) also separated this OTU from the centre of the *D. cuneata* group. With principal component two this individual received the highest score of all OTU's, indicating an extremely acute apex. Examination of the raw data matrix shows GRAMP 3548 to have a low AQB2 value (AQB2 = -0.266) and a relatively low SIA3 score. Other leaves have negative values for the apex quadratic term and correspondingly high scores for the second principal axis (implying the apical margins are concave), but the classification of this individual seems to be the result of a number of variables acting together.

The Intermediate OTU SINTON Cov651 (cluster 20) is the only individual with emarginate leaves in the data set. Given that the leaf parameter program was not designed to handle these leaves, as was discussed in section 6.22 above, the upper part of the leaf was omitted from the sectoring, as illustrated in figure 6.29. This accounts for the large values of such variables as AANG and SIA3 obtained for this OTU. The principal component ordination plots (fig.6.23) also single out SINTON Cov651. The position of this individual in the classification produced in this study must therefore be disregarded and further consideration of its position with respect to the rest of the complex considered independently.

The relative percentage of the Intermediate populations allocated to each of the *D. cuneata* (clusters 1 to 7), *D. angustissima* (clusters 8 to 10) and *D. viscosa* (clusters 13 to 16) groups are shown on the phenogram. The individuals of several populations are classified into different species, e.g. SESA, again reflecting the discriminant analysis results.

Knowing the composition of the clusters allows consideration of their interrelationships and the dissimilarities between them as indicated in the phenogram. The *D. cuneata* group appears to be a relatively distinct cluster. The morphological overlap of *D. viscosa* and *D. angustissima* is evident in the relatively early fusion of these two groups ($d = 1.524$) and the similar coefficients for the fusion of the *D. angustissima/D. viscosa* group ($d = 1.868$) and the *D. cuneata* group ($d = 1.774$), the latter being considered to be a relatively coherent group of OTU's.

Dissimilarity of the petiolate-spathulate leaves (clusters 15 and 16) and the large-leaved *D. viscosa* individuals (clusters 18 and 19) from the core of the *D. viscosa* group may be partly due to the recognised cluster analysis distortion of the distances among members of the larger or more distant clusters. These two groups will be further considered in the next section.

Comparison of cluster analysis and discriminant analysis results reveals similar classifications. The detailed classification of particular individuals can be determined from figures 6.24 and 6.28. Each of the four individuals misclassified in the discriminant analysis, i.e. GRAMP 3546, COLMON 819 of *D. cuneata* and SIMDES Dmb16 and Rhyko of *D. angustissima*, have also been classified into different groups (from which they were originally allocated) in the cluster analysis. In general terms cluster analysis shows a similar disjunction of *D. cuneata* from the other two species, which together form one large cluster, as was found with discriminant analysis. At this broad scale cluster analysis also shows general agreement with the ordination plots (fig.6.23) resulting from PCA.

6.532 Cluster analysis with non-computational variables (CLUSB)

A cluster analysis was carried out on all OTU's using only non-computational variables (table 6.7) in order to assess the potential of those

characters derived from the digitised leaves and which could not be measured by hand. This analysis, which will be referred to as CLUSB, can be compared with the second discriminant analysis (section 6.512 above), which was also based on non-computational variables only.

The results of this cluster analysis are presented in the phenogram in figure 6.30, and the constituents of the 20 clusters are given in table 6.20. Even a brief examination of this phenogram indicates considerable differences in the classification from that in the previous cluster analysis (CLUSA) (fig.6.28). Some of the differences and similarities of the two cluster analyses will be briefly discussed.

The most obvious difference in this cluster analysis is the distinction of the *D. angustissima* individuals into a separate group (clusters 14 to 17). In addition, this group includes only five Intermediate individuals. This *D. angustissima* group does not fuse with the combined *D. cuneata*/*D. viscosa* cluster until $d = 2.483$.

Another important feature of CLUSB is the apparent overlap between the *D. cuneata* and *D. viscosa* groups. For example, cluster 7 contains almost equal numbers of individuals of typical forms of these two species. Clusters 1 to 3 appear to be differentiated from other *D. cuneata* individuals on size, (both leaf length and breadth), and leaf shape features, such as AANG. Clusters 4 to 7 form a diverse group of *D. cuneata* and *D. viscosa* OTU's, which are clustered here, i.e. with the reduced set of variables, to indicate reasonably close affinity.

Clusters 8, 9 and 10 include all OTU's of clusters 13 and 14 in CLUSA. However, these two clusters also include individuals from more typical *D. viscosa* populations, part of which have been classified with *D. cuneata* in clusters 4 to 7. Again, the core of clusters 11 and 12 is the group of petiolate and spathulate leaves (cf. clusters 15 and 16 of CLUSA).

Table 6.20. Component OTU's of Clusters in CLUB. (cf. fig.6.30)

(Groups: C = *D. cuneata*, A = *D. angustissima*,
V = *D. viscosa*, I = Intermediate.)

<u>Cluster number</u>	<u>Total no. of OTU's</u>	<u>Group</u>	<u>Population</u>	<u>Individuals</u>
1	3	C	GRAMP	3541, 3547, 3551
2	3	I	BLACKMT	Jgw1, Jgw3
			HYDEN	1023
3	1	C	GRAMP	3548
4	33	C	GRAMP	3546
			COLMON	819
		A	SIMDES	Dmb14, Dmb15, Dmb17, Rhyko
			STBLDS	Borm029, Shod162
			LINKI	1300
			KVR	350, 356
		V	FRGAM	Roh1673, Whibgam, Eich605
			SHERARB	Evt741
			KWALL	3577
		I	SESA	437, 442, 443
			BLACKMT	Jgw4
			ONGERUP	3071
			MUBRAEN	1887
			REMARK	1174-1176
			HYDEN	1019-1022
			SUGBUG	2589, Carol, Emc2770
			GRIFF	Mc1343
5	2	I	YASS	1687, 1691
6	8	C	MDC	1828
			COLMON	815
			CWS	
			COBAR	Abram672
		V	FRGAM	Eich636
		I	ONGERUP	3078
7	50	C	GRAMP	3550
			MDC	1826, 1829, 1831, 1832
			COLMON	814, 817, 820

Table 6.20 (Cont'd)

<u>Cluster number</u>	<u>Total no. of OTU's</u>	<u>Group</u>	<u>Population</u>	<u>Individuals</u>
7 (cont'd)			FINIS	
			COBAR	Abram673-Abram675, Boorm676
		A	SIMDES	Dmb16
		V	FRGAM	Kuc3142
			SLWAIT	418, 423
			SLWATIP	1242
			SHERARB	Hub5101, Whi8326
			TAS	
			MARION	1541, 1545, 1546, 1548
		I	SESA	439
			YASS	1685, 1688
			BLACKMT	Jgw5, Mc1132, Mc1133
			ONGERUP	3072, 3073, 3077
			MUBRAEN	1886
			MTGREEN	2043, 2046, 2048
			REMARK	1173
			SINTON	Cov075, Cov652
			GRIFF	Mc1344, Mc1345
8	9	V	SLWAIT	421, 422, 425
			SLWATIP	1243, 1244, 1246, 1247
			MARION	1542, 1549
9	4	V	QLANG	Mik2979, Bri662, Will14
10	7	V	KWALL	3576, 3578
			NZ	
		I	YASS	1689
			MTGREEN	2049
11	6	V	PALMV	
			SHERARB	Francis, Whi9503
12	5	V	SHERARB	Evt1825
			WAMAG	
		I	MUBRAEN	1883

Table 6.20 (Cont'd)

<u>Cluster number</u>	<u>Total no. of OTU's</u>	<u>Group</u>	<u>Population</u>	<u>Individuals</u>
13	1	I	SINTON	Cov651
14	16	A	QULAFF	Stb6793, Bee1135
			STBLDS	Borm378, Hog8560, Eva2613
			LINKI	1299, 1301-1303
			KVR	353, 355, 357
		I	SESA	432
			MUBRAEN	1885
			SUGBUG	2588, 2590
15	7	A	QULAFF	Bee1437
			LINWASX	3370
			LINREDR	757, 758, 760, 761
		I	REMARK	1181
16	4	A	LINWASX	3365, 3367-3369
17	2	A	LINREDR	759
			KVR	352
18	5	V	QLREP	
			QLBURM	Mori760
19	6	V	QLBURM	Gitt872, Sharp58, Sharp59, Shdurr, Poolman.
			KWALL	3580
20	1	V	QLANG	Bailey

Table 6.20. Component OTU's of Clusters in CLUSB.
(cf. fig.6.30)

(Groups: C = *D. cuneata*
A = *D. angustissima*
V = *D. viscosa*
I = Intermediate)

The composition of the large-leaved *D. viscosa* clusters, i.e. 18, 19 and 20 of CLUSB, corresponds exactly with clusters 18 and 19 of CLUSA. The dissimilarity coefficients for the fusion of these OTU's with the remainder of the data set are very similar in both analyses.

The classification produced in CLUSB has not only split up individuals from Intermediate populations, but it has also separated OTU's from populations considered to be representative of the species. For instance, two individuals of the *D. angustissima* population KVR are clustered with *D. cuneata* in clusters 4 to 7, while the other three are included in the main *D. angustissima* grouping (clusters 14 to 17). *D. viscosa* SLWAIT is clustered in part with *D. cuneata* in cluster 7 and partly in cluster 8, and these two groups do not fuse until considerably later in the classification.

The two single individual clusters of CLUSA, namely SINTON Cov651 and GRAMP 3548 again occur as individual clusters, i.e. cluster 13 and 3 respectively. However, in this case GRAMP 3548 is grouped with the *D. cuneata* population to which it belongs. Given that the main character thought to be responsible for this OTU's misclassification in CLUSA was a computer derived variable (AQB2), which is omitted from this analysis, it is not unexpected that this individual is more sensibly classified here.

The Intermediate individual SINTON Cov651 probably remains separate in CLUSB because, although the variables used are non-computational, they were calculated in this analysis using the digitised and sectorised leaves. Since the sectors missed the emarginate part of the leaf (fig.6.29), characters such as AANG and A2OW would still be affected.

Classification of the Intermediate OTU's is indicated with the relative percentages on the phenogram. The close clustering of *D. cuneata* and *D. viscosa* has resulted in 75% of the Intermediate individuals being classified into those clusters.

Comparison of CLUSB with the discriminant analysis using non-computational variables indicates general agreement of the two analyses. The discriminant analysis also shows greater overlap of *D. viscosa* and *D. cuneata*.

Detailed examination of the leaf plots (Appendix B) suggests that the separation or clustering of OTU's in CLUSB is based largely on a combination of leaf shape and size variables. Leaf apex features appear to be less important here. This observation is supported by the results of the principal components analysis based on non-computational variables (section 6.44), which found the first two components related to a combination of leaf shape and size features.

6.533 Conclusion

Cluster analysis using 17 of the selected variables classified *D. cuneata* to form a distinct group from the more polymorphic cluster of *D. angustissima* and *D. viscosa*. These clusters appear to be differentiated on the basis of leaf shape and in particular leaf apex shape. Two other clusters are distinguished, both of which consist of *D. viscosa* individuals only. One includes the petiolate, spathulate leaves, while the other is formed primarily on leaf size and includes leaves of variable shapes from lanceolate to ovate to elliptic.

The variation of leaf morphology indicated by the close affinity of *D. angustissima* and *D. viscosa* is further emphasised with the classification of the Intermediate group OTU's into all three species clusters. Members of some potentially intrabreeding populations are placed widely apart in this analysis.

Cluster analysis using only non-computational variables results in a much less satisfactory classification. In this analysis *D. angustissima* is recognised as a distinct cluster, but a large amount of overlap exists

between *D. cuneata* and *D. viscosa*. The clusters are distinguished on a combination of leaf shape and size characters.

Use of computational characters derived from the digitised leaves results in stronger clustering within the three species. *Although these more defined indicators of shape present more realistic relationships between the taxa still no definite regular and reliable partitions are located in the data set.*

6.6 TAXONOMIC INTERPRETATION

Results of the multivariate analyses presented in the previous sections will now be interpreted in relation to the taxonomy of the whole *Dodonaea viscosa* complex in Australia. It is important to remember that the OTU's used in the analyses are a selection from a much larger collection of specimens and populations. The amount and variability of the populations that the OTU's represent must be taken into account when applying the numerical results to the taxonomic treatment of the group.

Analyses used in this study present classifications of considerable similarity. It has been shown that each of the three taxa involved in the *Dodonaea viscosa* complex includes a degree of uniformity or consistency when it is studied from the strict sense of that taxon. However, these taxa also exhibit a range of leaf morphology, which extends to the point of taxonomic overlap between species.

Cluster analysis, in which all OTU's are treated independently and without *a priori* judgement, classified individuals into relatively distinct groups corresponding to *D. cuneata*, *D. angustissima* and *D. viscosa*. The important fact in considering these clusters is that they contain members of the populations belonging to the Intermediate group. Separation of individuals from a single potentially intrabreeding population and their classification into different species indicates the range of leaf morphology within a population. Given the reasons for the initial forced formation of the Intermediate group of populations it is not surprising that members of those populations are clustered into different species.

Individuals of the Intermediate group exhibiting intermediate morphology break down the species limitations and are shown to lie between species clusters.

One of the aims of this study was to attempt to form a natural classification system of the *D. viscosa* complex. A natural classification should

be based on correlations of characters and discontinuity of variation, both for the assessment of relationships and the delimitation of taxa.

Considering that leaf morphology is the only area of variation in the complex it must be recognised that it is not possible, given this data set, to reliably and accurately separate the three species of the complex as they have been previously defined. I believe therefore, that the three taxa *Dodonaea cuneata*, *D. angustissima* and *D. viscosa* should be combined into one recognised polymorphic species, which must be known by the earliest published name *Dodonaea viscosa* Jacq. (Stafleu et al., 1978, Art. 11). Nevertheless, some status must be given to the components within this species. The results indicate that typical individuals can be classified into *D. cuneata* and *D. angustissima*, and on practical and convenience grounds alone these should be recognised. The taxonomic circumscription of these two infraspecific taxa i.e. *D. viscosa* ssp. *cuneata* (Sm.) West and *D. viscosa* ssp. *angustissima* (DC.) West is given in Chapter 7.

Problems associated with recognition of infraspecific taxa have been under discussion for many years and will remain controversial while taxonomists continue to classify organisms. Van Steenis (1957) in a thorough examination of specific and infraspecific delimitation emphasised the distinction and description of well-defined infraspecific taxa. He believed infraspecific taxa should be distinguishable on morphological characters, although with subspecies he accepted the existence of intermediary specimens.

Given that taxonomists are in part attempting to categorise natural organisms into convenient and artificial classification systems it is not unexpected that in many groups individuals and populations do not fall into well defined units. The use of infraspecific categories then can be seen as a compromise. While recognising that a considerable segment of a species may be more or less distinct it also allows for intergradation and natural overlap between the infraspecific taxa.

The actual infraspecific rank that is applied in a classification is also a topic of controversy. Davis and Heywood (1963) noted that a 'sub-species' is often distinguished on a very small number of characters, many of which are quantitative. Individually any of these characters can break down as discriminators.

The category of 'variety' has been used in many senses. It is commonly employed for local biotypes of species, which are morphologically distinct and occupying a restricted geographical or ecological area. Heywood (1959) emphasised the smaller scale and more localised nature of a variety compared with the larger regional basis of a subspecies. Application of the varietal rank is variable, but it is often used to indicate geographical, ecological or cytological disjunctions.

Populations (and individuals) within the *Dodonaea viscosa* complex exhibit some correlation of leaf morphological variation with environmental and geographical variables. A map of leaf outlines of only the OTU populations used in this numerical analysis (fig.6.31) indicates some geographical and ecological delimitation of populations. Although the large leaved members of the complex are mostly found in north-eastern Queensland and there appears to be a decrease in leaf size with an increase in latitude, there is actually no definite geographical cline of either leaf shape or leaf size. The Intermediate populations, which incidentally are restricted to southern Australia, contain individuals of variable morphology.

The location of OTU's relative to certain environmental variables appears however to be more highly correlated with leaf shape. For instance, typical linear leaves of the *D. angustissima* group are mostly found in arid habitats and primarily in hot arid regions of Australia. *D. cuneata sensu stricto* specimens are mainly restricted to dry locations of New South Wales, Victoria and South Australia. There was not sufficient time during this study to include environmental variables in the multivariate analyses, but

I believe rainfall, temperature, soil characteristics and even humidity data would be useful variables to test the relationship of the components of the *D. viscosa* complex with ecological aspects. Habitat details, such as vegetation density and associated species may also yield information on the presence of ecotypes within the complex. This apparent correlation of leaf morphology of the *D. viscosa* complex and certain environmental variables is discussed in a speculative manner in Chapter 5.

Apart from the two infraspecific taxa already mentioned other morphological forms can be recognised in the complex. These will be discussed in relation to the three *D. viscosa* "populations" which were included in the analysis, but which are not intrabreeding populations, i.e. QLBURM, QLREP and SHERARB. These groups, which occur in Queensland, were included in the analysis because Sherff (1947) had recognised them on leaf morphological characters as infraspecific taxa of *D. viscosa*, and it was of interest to determine their position in the classification derived by multivariate analysis. QLBURM, which was classified as *D. viscosa* var. *vulgaris* f. *burmaniana* by Sherff, and QLREP, a representative of *D. viscosa* var. *vulgaris* f. *repanda*, are the largest leaves of the complex with leaf shape ranging from lanceolate to ovate or elliptic and leaf apex from acute to obtuse.

To determine the contribution of size to the distinction of clusters 18 and 19 in CLUSA a cluster analysis was carried out excluding all variables relating to absolute size, i.e. LENA, WIDX and AREA were excluded. The two populations QLBURM and QLREP were still clustered separately from the remaining individuals, although the dissimilarity coefficient was not as large. This suggests that this large-leaved cluster is not partitioned from the data set on a size factor alone.

The geographical position (fig.6.31), relationships to *D. viscosa* outside of Australia and leaf morphology emphasise the validity of the two taxa as recognised by Radlkofer (1933) and later confirmed by Sherff (1947). The

taxonomic treatment of these subspecies to which rank they are now raised, is included in Chapter 7.

The other morphologically distinct group which was recognised in the cluster analysis and also in the PCA, is the petiolate-spathulate leaves of *D. viscosa* populations PALMV and SHERARB. In CLUSB the WAMAG population is also included in this cluster. The PALMV population is representative of a number of populations, which collectively may be considered to form an ecotype in that they are only found on rocky ranges, hills or outcrops in arid Australia. Given that these individuals are classified separately from the core of *D. viscosa* and considering their specific habitat requirements, it seems desirable to recognise them at the rank of subspecies. These populations have previously been classified into *D. viscosa* var. *spatulata*, a taxon which included a vast range of the complex both morphologically and geographically. This form is here described as ssp. *mucronata*; its taxonomic circumscription is given in Chapter 7.

In conclusion, the morphological multivariate analysis employed in this study together with consideration of some environmental and geographical parameters have enabled recognition of a polymorphic species *Dodonaea viscosa* Jacq. The taxonomic treatment presented in this thesis recognises this species as comprising seven infraspecific taxa, of the rank of subspecies:

- Dodonaea viscosa* Jacq. ssp. *viscosa*
- D. viscosa* ssp. *angustissima* (DC.) West
- D. viscosa* ssp. *cuneata* (Sm.) West
- D. viscosa* ssp. *angustifolia* (L.f.) West
- D. viscosa* ssp. *burmanniana* (DC.) West
- D. viscosa* ssp. *spatulata* (Sm.) Benth.
- D. viscosa* ssp. *mucronata* West

6.7 THE POTENTIAL OF THE DIGITISER

The second basic objective of this study was to assess the potential of a digitiser as a tool to be used in the data collection stage of multivariate analyses.

The digitiser has proven to be an extremely useful device in this analysis. Many advantages have been mentioned previously, but these together with the disadvantages will now be briefly discussed.

The major reason for using an electronic device such as a digitiser in an analysis of this kind is because it reduces the time taken to collect the data by a significant amount. In this case it took five minutes to measure only the non-computational variables by hand compared with one minute to digitise each leaf. Computation of the leaf parameters to produce the final data set occupied insignificant computer processing time.

This more rapid method of character measurement and computation enabled a larger sample of the group to be included. This is a great advantage when dealing with a common polymorphic complex of broad morphological and geographical range.

Since the digitised leaf images are stored on computer (in the form of regular sectors) they are available for computer analyses and they can be recalled at any stage to compute another leaf parameter, or to check the accuracy of the outline or to plot the leaves.

The precision and range of characters selected for the analysis can be increased simply because the leaf image is stored in the computer. The derivation of characters such as the quadratics, form factor and the symmetry of the leaf increases the information being used and therefore adds to the extent of the analysis. Leaf area meters have been used to obtain leaf areas in the past, but that is a tedious task compared with computing areas via the digitiser. The increased precision of characters proved to be useful in this analysis. The less satisfactory results obtained in the

discriminant analysis and cluster analysis, in which only non-computational variables were used are evidence of this.

Computation of the leaf parameters from the leaf images stored on file enabled the characters to be analysed for correlations, redundancy and power of discrimination over the whole data set rather than biased subsets of the data.

The interpretation phase was considerably enhanced through the use of plots of the leaves (Appendix B). This is an advantage not only to the analyst, but it also gives others a clearer conceptual image of the relationships between individuals. Use of the leaf plots in interpreting the results saved unnecessary handling of the dried leaves which the images represent.

My initial concern relating to sensitivity and accuracy of the digitiser appears to be unwarranted. These problems were either tested by measuring the same parameter by a different method, all of which resulted in very similar results, or by counteracting the digitising errors through the use of correcting factors, e.g. the regression line used in PERPM to "smooth" any discrepancies in the midrib.

This analysis has shown that the digitiser can be employed to great advantage in multivariate analyses, and the increasing availability at lower costs makes this technique a feasible proposition for future use.

CHAPTER 7

TAXONOMY OF *DODONAEA* IN AUSTRALIA

INTRODUCTION

The basis of earlier classifications (Bentham, 1863 and Radlkofer, 1933) has been discussed in relation to the taxonomic history of the genus (refer Chapter 2). Both systems recognised a similar number of groups, at the level of series or below, within *Dodonaea*.

Despite considerable vegetative polymorphism several natural groups clearly exist in the genus. The adaptive significance of floral and particularly fruit characters has led to natural disjunctions, and these discontinuities and correlations of characters are sufficient to delimit groups of practical use. The system proposed by Radlkofer (1933) fails to recognise these natural groups since it relies heavily on fruit and seed characters without correlation with other features, such as leaves.

The infrageneric structure proposed here is similar to that of Bentham (1863) in that it is based on combinations of the most variable and yet reliable characters, mainly of capsules and leaves. Constituent species of the groups are largely comparable to Bentham's, with two additional groups being delimited. While it is realised that a different infrageneric classification based primarily on fruit and seed characters and less on combinations of characters as used here may be feasible, I have argued in Chapter 5 that the approach taken here is more justified. Examination of various alternative systems resulted in unlikely biogeographic trends and more artificial groupings. The treatment as presented here is not only favoured by Wagner tree methods of estimating phylogeny, but also appears to provide the most practical and useful classification of *Dodonaea*.

It is proposed to raise the level of the seven groups to that of section in recognition of the significance of their consistency and naturalness. I feel the infrageneric category of series is more applicable to those genera which seem to have no natural taxa between the genus and species. In this case the level of series does not give the distinctions of the different groups within *Dodonaea* the status they deserve.

Capsule and seed morphology is fairly constant within the species, while leaf characters vary considerably in some taxa. It is the combination of a small number of consistent and significant characters which contribute to reliable discontinuities between the sections and the formation of natural groups within the genus.

KEYS

The key to sections within *Dodonaea* and keys to species are based as much as possible on vegetative characters. Features of flowers, capsules and seeds are used as secondary characters and/or in those cases in which no reliable leaf characters differentiate the taxa. Given that most species are dioecious, reliance on capsule or certain flower characters as the primary distinguishers theoretically implies only half the individuals of any population could be reliably identified, and then only in a limited period of the year. For this reason an attempt has been made to include as many reliable characters as possible. Where two species are readily separated by capsule or flower characters, vegetative features are included in the key as secondary characters if at all possible.

Dodonaea Miller, Gard. Dict. Abr. edn 4. (1754); Jacq., Enum. Pl. Ins. Carib. 19 (1760); L., Syst. Veg. edn 13. 299 (1774); Schreber, Gen. Pl. 1:257 (1789); Lamarck, Encyclop. 2:439 (1797); Smith in Rees, Cyclop. 12 (1809); DC., Prodr. 1:616 (1824); G. Don, Gen. hist. 1:673 (1831); Blume, Rumphia 3:188 (1857); Grisebach, Fl. Brit. W. Ind. Isl. 127 (1859); Bentham & Hooker f., Gen. Pl. 1:410 (1862); Bentham, Fl. Aust. 1:472 (1863); Bailey, Syn. Qld. Fl. 81 (1883); Tate, Fl. Extratrop. S. Aust. 27 (1890); Moore, Fl. N.S. Wales 93 (1893); Radlkofer in Engler et Prantl, Nat. Pflanzenfam. III. 5:356-357 (1895); Bailey, Fl. Qld. 1:311 (1899); Radlkofer in Martius, Fl. Bras. 13(3):637-639 (1900); Rodway, Fl. Tasm. 30 (1903); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:344-345 (1904); Ewart & Davies, Fl. N. Terr. 173 (1917); Black, Fl. S. Aust. edn 1. 362 (1926); Ewart, Fl. Vic. 736 (1931); Radlkofer, Pflanzenreich IV. 165:1350-1352 (1933); Black, Fl. S. Aust. edn 2. 540 (1952); Curtis, Fl. Tasm. 118 (1956); Blackall & Grieve, W. Aust. Wildfls. 2:322 (1956); Galbraith, Wildfls. Vic. edn 3. 88 (1967); Burbidge & Gray, Fl. A.C.T. 248 (1970); Beadle et al., Fl. Syd. Reg. 386 (1972); Willis, Hdbk. Pl. Vic. 2:356-357 (1972).

TYPE SPECIES: *Dodonaea viscosa* Jacq.

Carpinus J. Burm., Thes. zeylan. 55 (1737).

TYPE SPECIES: *C. betulus* L. (lectotype).

Ptelea L., Sp. Pl. 1:118 (1735), (see *D. viscosa*).

TYPE SPECIES: *P. trifoliata* L.

Triopteris P. Browne, Civ. nat. hist. Jamaica 191 (1756).

TYPE SPECIES: *T. jamaicensis* L.

Serjania Spreng., Syst. 2:248 (1825), (see *D. pinnata*).

TYPE SPECIES:

Thouinia Miq. in Lehm., Pl. Preiss. 1:224 (1845), (see *D. adenophora*).

TYPE SPECIES: *T. simplicifolia* Poiteau

Empleurosma Bartl. in Lehm., Pl. Preiss. 2:228 (1848), (see *D. pinifolia*).

TYPE SPECIES: *E. virgata* Bartl.

DESCRIPTION:

Perennial, dioecious or polygamo-dioecious shrubs or small trees, 0.1-5(-8)m high. Branches prostrate, ascending, erect or divaricate, rarely rooting at the nodes; branchlets often angular, sometimes terete, ribbed or flattened, usually with sessile or verruculose glands, glabrous, puberulent, pubescent with various types of simple hairs, or sometimes hirsute or pilose. Leaves scattered or spirally arranged, rarely opposite (*D. ericoides*), simple or pinnate, sessile or petiolate, exstipulate, usually viscous, usually with sessile or verruculose, convex, multicellular, resinous glands, venation eucamptodromous. Flowers actinomorphic, inconspicuous, unisexual or bisexual, pedicellate, axillary or terminal, arranged in monads to compound frondo-bracteose panicles, bracts leaf-like, small. Sepals 3-6(-7), at anthesis in male flowers free, in female flowers usually free, rarely fused near the base, valvate or narrowly imbricate towards the base, usually viscous, caducous or persistent. Petals 0. Disk small, rudimentary, in female & bisexual flowers a short gynophore enlarges at anthesis. Stamens in male & bisexual flowers 6-12(-16), inserted at disk margin or at gynophore base; filaments 0.1-2(-3.5)mm long, glabrous; anthers 2-lobed, basifixed between the lobes,

usually oblong, sometimes linear or linear-oblong, 4-angled, laterally dehiscent; connective usually extended into apical appendage, rarely absent; stamens in female flowers usually absent, sometimes rudimentary. Ovary in female & bisexual flowers (2-)3-5(-6)-carpellate, usually angled, sometimes rounded, usually glabrous, sometimes pubescent, usually viscous, often surrounded by layer of resin; ovary slightly raised on a short gynophore-like disk; placentation axile; ovules 2 per locule, superposed, anacampylotropous, upper one ascending & apotropous, lower one pendulous & epitropous, funicle thickened at the base; styles (2-)3-5(-6), connate & 2-6 grooved, filiform, often twisted spirally, separating usually unequally near the apex or in upper $\frac{1}{3}$, the free parts short & lobe-like, or arms 0.2-5mm long, usually recurved; ovary in male flowers usually rudimentary, sometimes absent. Capsule 2-6-angled or 2-6-winged, membranous, coriaceous or crustaceous; carpels usually laterally compressed, navicular or lunate, the dorsal face usually extended into an appendage; appendage a broad, rounded or obliquely elongated wing, horn-like, lobe-like, or rarely absent; dehiscence usually septifragal, sometimes septicidal, rarely finally irregularly dehiscent (*D. petiolaris*, *D. physocarpa*). Seeds 1 or 2 per locule, hilum surrounded by small amount of callose, or infundibular aril present; testa crustaceous or coriaceous, covered with hyaline membrane which sometimes lifts over entire seed or sometimes lifts at the margin only. Embryo circinnate.

DISTRIBUTION:





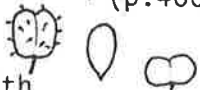


Dodonaea is primarily an Australian genus, with 60 endemic species and one (*D. viscosa*) which is pan-tropical. Two other species recognised outside of Australia, *D. eriocarpa* and *D. stenoptera* in Hawaii, appear to be closely

related to the type species. *D. madagascarensis* is a pinnate species restricted to Madagascar. *D. viscosa* is widespread throughout tropical Asia, Africa and the Americas.

ECOLOGY:

In Australia *Dodonaea* species grow in a vast range of habitats. They are shrubs or small trees of woodland, forest or shrubland associations, and are absent only from true dense rainforest, dense heath and alpine communities.

KEY TO SECTIONS OF *DODONAEA*

- 1a. Leaves simple 2
- 1b. Leaves compound 5
- 2a. Capsule winged, wing usually extending from apex to base of carpel, (in *D. bursariifolia* rarely above middle of capsule only), membranous or coriaceous, usually prominent & > 2mm broad (\leq 1mm broad in *D. bursariifolia*); dehiscence septifragal, or septicial in *D. bursariifolia*; seed exarillate, sometimes with hyaline membrane lifting at the margin 3
- 2b. Capsule angled & globose, not prominently winged, appendage at capsule apex only, crustaceous, usually lobe-like or horn-like, sometimes absent; dehiscence septifragal; seed arillate or exarillate & with hyaline membrane lifting at the margin 4
- 3a. Capsule in lateral view oblong to obovate, to transversely broad-elliptic or broad-oblong, carpel membranous or coriaceous, wing rounded, approx. equal width from apex to base, extending to central axis at capsule apex & base; seed sometimes with hyaline membrane lifting at the margin I. Sect. *Dodonaea* (p. 184) 
- 3b. Capsule in lateral view transverse-oblong, -elliptic or -obovate, carpel crustaceous or coriaceous, wing rounded or pointed, oblique, longer than broad & longer at capsule apex, rarely extending right to central axis at capsule apex & base; seed lacking hyaline membrane lifting at the margin . . II. Sect. *Platypterae* (p. 326) 
- 4a. Capsule appendage usually lobe-like & \leq 2.5mm long, rarely a narrow wing \leq 1mm broad (in *D. baueri*), sometimes absent; seed usually arillate, or with enlarged funicle, or with hyaline membrane lifting at the margin III. Sect. *Apterae* (p. 352) 
- 4b. Capsule appendage narrow & horn-like, 1-3(-6)mm long; seed arillate, lacking hyaline membrane lifting at the margin . . IV. Sect. *Cornutae* (p. 400) 
- 5a. Capsule without appendage; leaflets either 1.8-3(-4)mm long, with glandular hairs or hirsute, lacking sessile, verruculose or sunken glands, or (3-)4-7(-8)mm long & > 3.5mm broad, glabrous or rarely with hairs on midrib below VII. Sect. *Inappendiculatae* (p. 519) 
- 5b. Capsule prominently winged; leaflets without glandular hairs, if \leq 4mm long then glabrous to pubescent, not hirsute, with verruculose or sunken glands, if > 4mm long & glabrous then < 3mm broad 6
- 6a. Capsule in lateral view oblong to obovate, to transversely broad-elliptic or broad-oblong, carpel membranous or coriaceous, wing rounded, approx. equal width from apex to base; leaflets usually < 12mm long, apex usually toothed or lobed, shape various, if linear to lanceolate, then terminal leaflet short, lobe-like, less than half as long as laterals, or absent V. Sect. *Pinnatae* (p. 422) 
- 6b. Capsule in lateral view transverse-oblong to -obovate, carpel crustaceous, wing rounded or pointed, oblique, longer than broad & longer at capsule apex; leaflets usually > 12mm long, linear to lanceolate, apex acute to obtuse, terminal leaflet long & similar to laterals VI. Sect. *Plagiopterae* (p. 505) 

I. Sect. *Dodonaea*

Sect. *Eu-Dodonaea* Miq. in *Linnaea* 18:94 (1844).

Ser. *Cyclopterae* Benth., *Fl. Aust.* 1:474 (1863).

Ser. *Cyclopterae* subser. *Cyclopermae* Radlk., *Pflanzenreich* IV.165:1352 (1933).

Subser. *Oospermae* Radlk., loc.cit. 1352 (1933), p.p.

[Ser. *Apterae* auct. non Benth.: Benth., *Fl. Aust.* 1:481 (1863), p.p. (as to *D. bursariifolia*)].

[Ser. *Aphanopterae* subser. *Inappendiculatae* auct. non Radlk.: Radlk., *Pflanzenreich* IV.165:1357 (1933), p.p. (as to *D. procumbens*)].

TYPE SPECIES: Holotype: *D. viscosa* Jacq.

DIAGNOSIS:

Leaves simple, sessile or petiolate, margin entire to regularly serrate; capsule in lateral view oblong to obovate to transversely broad-elliptic or broad-oblong, rarely \pm orbicular, apex usually obcordate, rarely emarginate, carpel membranous or coriaceous, wing membranous or coriaceous, rounded, approx. equal width from apex to base, extending to central axis at apex & base of capsule; seed exarillate, sometimes with hyaline membrane lifting at the margin.

TYPIFICATION:

Since *D. viscosa* Jacq. is the type species of the genus it is automatically the type of this section (Stafleu et al., 1978, Art.22).

DISTRIBUTION:

Species within section *Dodonaea* occur in almost all parts of Australia. Several show restricted distributions in the east or southwest, while others are widespread across the continent.

- | | |
|--|---------------------------------------|
| <i>D. amblyophylla</i> Diels | <i>D. lobulata</i> F. Muell. |
| <i>D. bursariifolia</i> F. Muell. | <i>D. peduncularis</i> Lindl. |
| <i>D. camfieldii</i> Maiden et Betche | <i>D. petiolaris</i> F. Muell. |
| <i>D. coriacea</i> (Ewart et Davies)
D. McGillivray | <i>D. polyandra</i> Merrill et Perry |
| <i>D. falcata</i> West | <i>D. procumbens</i> F. Muell. |
| <i>D. filifolia</i> Hook. | <i>D. ptarmicaefolia</i> Turcz. |
| <i>D. filiformis</i> Link | <i>D. rigida</i> West |
| <i>D. hackettiana</i> W.V. Fitzg. | <i>D. serratifolia</i> D. McGillivray |
| <i>D. hirsuta</i> (Maiden et Betche)
Maiden et Betche | <i>D. triquetra</i> Wendl. |
| <i>D. intricata</i> West | <i>D. viscosa</i> Jacq. |
| <i>D. lanceolata</i> F. Muell. | |

KEY TO SPECIES OF SECTION *DODONAEA*

- 1a. Leaves subfiliform, terete, or rarely narrow-linear, < 0.2cm broad, 4-ribbed, or channelled above, rarely flat, entire 23
- 1b. Leaves various, never subfiliform or terete, if linear then > 0.2cm broad & sinuate, flat, entire to regularly toothed or lobed 2
- 2a. Leaves viscous, shiny, with sessile or verruculose glands, or pubescent; capsule usually with membranous carpels; seed lacking hyaline membrane lifting at the margin 3
- 2b. Leaves not viscous, dull, without glands, glabrous; capsule with coriaceous or crustaceous carpels; seed with hyaline membrane lifting at the margin 19
- 3a. Leaves \geq 1cm broad 4
- 3b. Leaves < 1cm broad 7
- 4a. Capsule greatly inflated, not readily dehiscent, wing usually < 4mm broad, carpels membranous with conspicuous venation; sepals 5, \leq 2.5mm long 3. *D. petiolaris*
- 4b. Capsule not inflated, septifragal, wing \geq 4mm broad, carpels usually coriaceous without visible venation; sepals 3-4(-5), if 5 then > 2.5mm long 5
- 5a. Leaves elliptic, usually > 2cm broad with length: width 3-4:1; capsule 2(-3)-winged, in lateral view \pm orbicular 6
- 5b. Leaves variable, not elliptic, usually < 2cm broad, with length:width usually > 4:1, if < 4:1 then leaves < 2cm broad; capsule 3-4-winged, in lateral view broad-elliptic to transversely broad-elliptic 1. *D. viscosa*
- 6a. Stamens \leq 10 (usually 8), filaments 0.3-0.5mm long; capsule carpel \geq 7mm broad, membranous, wing 4-4.5mm broad; leaves thin & chartaceous, isobilateral 1. *D. viscosa* ssp. *viscosa*
- 6b. Stamens > 10, filaments 0.9-1.2mm long; capsule carpel usually < 7mm broad, crustaceous & thickened, wing (4-)6-9mm broad; leaves thick & coriaceous, darker above than below 2. *D. polyandra*
- 7a. Leaves > 3.5cm long with length:width > 5:1 8
- 7b. Leaves \leq 3.5cm long with length:width \leq 5:1 11
- 8a. Inflorescence terminal, compound & > 4-flowered; leaves entire, or irregularly sinuate to irregularly denticulate, never lobed or toothed, usually > 0.25cm broad, linear, lanceolate to obovate; capsule carpels usually > 6mm long 9
- 8b. Inflorescence axillary, a 2-4-flowered botryoid; leaves lobed or toothed in upper $\frac{2}{3}$, usually < 0.25cm broad, linear; capsule carpels \leq 6.5mm long 10

- 9a. Branchlets with 2-3 rows of dense, white villous hairs; seeds compressed towards the margin; stamen apical appendage \pm absent or a lobe $< 0.1\text{mm}$ long, filaments pubescent above the middle, $0.2-0.3\text{mm}$ long
 4. *D. hackettiana*
- 9b. Branchlets glabrous to puberulent, never with villous hairs; seeds not compressed towards the margin; stamen apical appendage triangular, $0.2-0.3\text{mm}$ long, filaments glabrous, $0.3-0.5\text{mm}$ long 1. *D. viscosa*
- 10a. Leaves serrate, the teeth acute, midvein sinuate; ovary pubescent; capsule $\leq 10.5\text{mm}$ long 5. *D. ptarmicaefolia*
- 10b. Leaves irregularly 2-10(-12)-lobed, the lobes obtuse to rounded, midvein straight; ovary glabrous; capsule $\geq 10.5\text{mm}$ long 6. *D. lobulata*
- 11a. Leaves $< 0.25\text{cm}$ broad, linear, lobed or toothed in upper $\frac{2}{3}$ of leaf . . 18
- 11b. Leaves $\geq 0.25\text{cm}$ broad, oblong, obtriangular, angular-obovate to obovate, usually entire, if lobed or toothed then irregularly so & at apex or above the middle only 12
- 12a. Leaves usually $\leq 0.5\text{cm}$ broad, if > 0.5 then decurrent at base, if toothed then at apex only; flowers solitary or in compound inflorescences, axillary or terminal; stamen filaments $\leq 0.3\text{mm}$ long 15
- 12b. Leaves usually $> 0.5\text{cm}$ broad, if $< 0.5\text{cm}$ broad then with 1-2 irregular teeth above the middle, not at apex, base cuneate or attenuate, not decurrent; flowers in compound, terminal inflorescences; stamen filaments $> 0.3\text{mm}$ long 13
- 13a. Branchlets orange, sparsely pubescent, with verruculose glands; leaves with verruculose glands, apex truncate & irregularly dentate; sepals persistent; capsule membranous, carpel $\leq 7.5\text{mm}$ long . . . 7. *D. coriacea*
- 13b. Branchlets green or brown, glabrous or puberulent, never pubescent, with sessile glands; leaves with sessile glands, apex acute to obtuse, if truncate then also mucronate & not dentate; sepals caducous; capsule coriaceous, carpel $> 7.5\text{mm}$ long 14
- 14a. Erect shrubs; capsules $\geq 11\text{mm}$ broad, wing $\geq 3\text{mm}$ broad; pedicels glabrous; stamen filaments $< 0.7\text{mm}$ long; styles $< 8\text{mm}$ long 1. *D. viscosa*
- 14b. Prostrate shrubs; capsules $< 11\text{mm}$ broad, wing 0.5mm broad; pedicels puberulent; stamen filaments $\geq 0.7\text{mm}$ long; styles $\geq 8\text{mm}$ long
 8. *D. procumbens*
- 15a. Leaves obtriangular, angular-obovate to obovate; sepals persistent; fruiting pedicels filiform, usually $\geq 5\text{mm}$ long 16
- 15b. Leaves linear to oblong; sepals caducous; fruiting pedicels thick, $2-5\text{mm}$ long 17
- 16a. Leaves hirsute, petiolate, usually $< 0.5\text{cm}$ long, margin revolute; capsule hirsute; flowers axillary 9. *D. hirsuta*
- 16b. Leaves glabrous, sessile, usually $> 0.5\text{cm}$ long, margin not revolute; capsule glabrous; flowers terminal 10. *D. peduncularis*

- 17a. Leaves sessile, with sessile glands, base decurrent, apex acute; branchlets pubescent, winged or ribbed 11. *D. camfieldii*
- 17b. Leaves petiolate, with verruculose glands, base attenuate, apex truncate-emarginate, obtuse or irregularly toothed, never acute; branchlets puberulent, angular 12. *D. intricata*
- 18a. Leaves serrate, the teeth acute, midvein sinuate; ovary pubescent; capsule ≤ 10.5 mm long 5. *D. ptarmicaefolia*
- 18b. Leaves irregularly 2-10(-12)-lobed, the lobes obtuse to rounded, midvein straight; ovary glabrous; capsule ≥ 10.5 mm long 6. *D. lobulata*
- 19a. Leaves usually ≥ 4 cm long & > 0.8 cm broad, apex acuminate to obtuse, petiolate, rarely subsessile; capsule septifragal, usually > 11 mm long, or if < 11 mm long then leaves > 1 cm broad with long acuminate to acute apex 20
- 19b. Leaves usually < 4 cm long & < 0.7 cm broad, apex obtuse, rounded, rarely mucronate, sessile; capsule septifragal or septicidal, ≤ 11 mm long 22
- 20a. Leaves irregularly serrulate, usually < 1 cm broad; inflorescence a 3-6-flowered botryoid; pedicels ≤ 2.5 mm long . . . 13. *D. serratifolia*
- 20b. Leaves entire or sinuate, never serrulate, usually > 1 cm broad; inflorescence a panicle composed of monads to metabotryoids; pedicels > 4 mm long 21
- 21a. Capsules ≥ 14 mm broad, carpel < 12 mm long, wing membranous; leaves usually ≥ 2 cm broad, darker above than below; sepals broad-triangular, < 1.4 mm long, caducous; stamen filaments 1-1.5mm long 14. *D. triquetra*
- 21b. Capsules usually < 14 mm broad, carpel > 12 mm long, wing coriaceous; leaves usually < 2 cm broad, isobilateral; sepals lanceolate to ovate, ≥ 1.4 mm long, persistent; stamen filaments 0.2-0.3mm long 15. *D. lanceolata*
- 22a. Capsule septicidal, wing 0.5-1mm broad, rarely above middle of capsule only; leaves obovate; pedicels < 3 mm long; stamen filaments ≥ 0.6 mm long 16. *D. bursariifolia*
- 22b. Capsule septifragal, wing (1-)3-4mm broad, extending from apex to base of carpel; leaves linear to oblanceolate; pedicels ≥ 4 mm long; stamen filaments ca. 0.2mm long 17. *D. amblyophylla*
- 23a. Branchlets puberulent; leaves falcate, not rigid, usually ≤ 4 cm long 24
- 23b. Branchlets glabrous; leaves straight, usually erect, often rigid, usually > 4 cm long 25
- 24a. Leaves ≥ 2.5 cm long, scattered; stamens 8; sepals ≥ 1.5 mm long; seeds > 2.2 mm long, compressed towards the margin 18. *D. falcata*

- 24b. Leaves < 2.5cm long, very dense & obscuring the branches; stamens 5(-6); sepals \leq 1mm long; seeds < 2.2mm long, not compressed towards the margin 19. *D. filiformis*
- 25a. Leaves flat, usually > 0.1cm broad, with sessile glands; compound inflorescence of monads to botryoids . . . 1. *D. viscosa* ssp. *angustissima*
- 25b. Leaves 4-ribbed, or grooved above, \leq 0.1cm broad, with sessile or verruculose glands; inflorescence a few-flowered botryoid 26
- 26a. Leaves terete or 4-ribbed, rigid, apex acute, usually pungent-pointed; sepals broad-ovate, \geq 0.8mm broad; inflorescence axillary; seed not compressed towards the margin 21. *D. rigida*
- 26b. Leaves filiform, grooved above, not rigid, apex obtuse, never pungent-pointed; sepals lanceolate, \leq 0.6mm broad; inflorescence terminal; seed compressed towards the margin 20. *D. filifolia*

1. *Dodonaea viscosa* Jacq., Enum. Pl. Ins. Carib. 19 (1760); DC., Prodr. 1:617 (1824); Mueller, Pl. indig. Col. Vic. 1:85-86 (1862), (pertaining to ssp. *spatulata*, ssp. *burmanniana*, ssp. *cuneata*); Bentham, Fl. Aust. 1:475-477 (1863), p.p. (excl. Endeavour R. specimens - see *D. polyandra*), (ssp. *viscosa*, ssp. *angustifolia*, ssp. *spatulata*); Mueller, Fragm. 9:89 (1875), Native Pl. Vic. 1:120-121 (1879); Bailey, Fl. Qld. 1:313 (1899), (ssp. *viscosa*, ssp. *angustifolia*, ssp. *spatulata*); Radlkofer in Martius, Fl. Bras. 13(3):639-648 (1900), (ssp. *viscosa*, ssp. *burmanniana*, ssp. *angustifolia*); Rodway, Fl. Tasm. 30 (1903), (ssp. *spatulata*); Maiden, Proc. Linn. Soc. N.S. Wales 28:701 (1904); Black, Trans. R. Soc. S. Aust. 39:833 (1915), (ssp. *mucronata*); Ewart & Davies, Fl. N. Terr. 175 (1917), (ssp. *mucronata*); Black, Fl. S. Aust. edn 1. 362, fig.160E-K (1926); Domin, Biblioth. Bot. 22(89⁴):911 (1927), p.p. (excl. ref. to J. Britten - see *D. polyandra*); Ewart, Fl. Vic. 737, fig.290 (1931); Radlkofer, Pflanzenreich IV.165:1363-1374 (1933), (ssp. *viscosa*, ssp. *burmanniana*, ssp. *angustifolia*, ssp. *spatulata*); Sherff, Field Mus. Nat. Hist., Bot. Ser. 23:269-317 (1947), (ssp. *viscosa*, ssp. *burmanniana*, ssp. *angustifolia*, ssp. *spatulata*); Black, Fl. S. Aust. edn 2. 541, fig.693E-K (1952); Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956), (ssp. *mucronata*, possibly ssp. *spatulata*); Curtis, Fl. Tasm. 118, fig.35 (1956), (ssp. *spatulata*); Beard, W. Aust. Pl. edn 1. 61 (1965), edn 2. 81 (1970); Burbidge & Gray, Fl. A.C.T. 248, fig.247 (1970); Beadle et al., Fl. Syd. Reg. 387 (1972); Chippendale, Proc. Linn. Soc. N.S. Wales 96:246 (1972), (ssp. *mucronata*); Willis, Hdbk. Pl. Vic. 2:359 (1972).
- TYPE: leg. Sloane in Jamaica, ?BM, or illustration: Sloane, Nat. Hist. Jamaica 2: t.162 f.3 (1725), n.v. (see ssp. *viscosa* typification).

Carpinus forte viscosa, salicis folio integro oblongo J. Burm., Thes. zeylan. 55, t.23 (1737). [Here regarded as ssp. *burmanniana*].

TYPE: leg. Ceylon. ?Institut de France, Paris (Stafleu & Cowan, 1976), n.v.

Dodonaea sp. L., Hort. Cliff. 144 (1737).

TYPE: "Crescit in America". G. Clifford s.n., BM, n.v.

Ptelea viscosa L., Sp. Pl. 1:118 (1753).

TYPE: "India", n.v. (see ssp. *viscosa* typification).

Triopteris erecta fruticosa, foliis oblongis acuminatis, ramulis gracilibus
P. Browne, Civ. nat. hist. Jamaica 191, t.18 f.1 (1756). [Here regarded as ssp. *angustifolia*].

TYPE: leg. Browne in Jamaica. ?LINN, n.v.

Dodonaea angustifolia L.f., Suppl. Pl. 218 (1781); Swartz, Obs. bot. 150 (1791); Smith in Rees, Cyclop. 12 (1809); Lamarck, Encyclop. 2:439, t.304, f.2 (1797); Grisebach, Fl. Brit. W. Ind. Isl. 128 (1859). [Here regarded as ssp. *angustifolia*].

TYPE: "in India australi. H.U." ?S n.v. (see ssp. *angustifolia* typification).

D. spatulata Sm. in Rees, Cyclop. 12 (1809). [Here regarded as ssp. *spatulata*].

TYPE: "Brought by Mr. Archibald Menzies from the Sandwich Islands".

Syntype: A. Menzies s.n., topmost shrubs on the Sandwich Islands, alt. 6000 feet, s.dat. (K), n.v. (see ssp. *spatulata* typification).

D. cuneata Sm. in Rees, Cyclop. 12 (1809); DC., Prodr. 1:617 (1824); G. Don, Gen. hist. 1:674 (1831); Bentham, Fl. Aust. 1:477-478 (1863); Bailey, Fl.

Qld. 1:314-315 (1899); Black, Fl. S. Aust. edn 1. 363 (1926); Ewart, Fl. Vic. 737 (1931); Radlkofer, Pflanzenreich IV.165:1375-1376 (1933); Black, Fl. S. Aust. edn 2.541 (1952); Galbraith, Wildfls. Vic. edn 3. 88, t.94 (1967); Beadle et al., Fl. Syd. Reg. 386 (1972); Willis, Hdbk. Pl. Vic. 2:358 (1972); Leigh & Mulham, Telopea 1:264 (1977). [Here regarded as ssp. *cuneata*].

TYPE: "Native of New South Wales", n.v.

D. ovata Dum. Cours., Bot. Cult. edn 2. 6:327 (1814)

TYPE: "La Nouvelle - Hollande" (cult.), n.v.

D. asplenifolia Rudge, Trans. Linn. Soc. 11:297, t.20 (1815) - basionym for *D. viscosa* var. *asplenifolia* (Rudge) Hook. f.; DC., Prodr. 1:617 (1824). [Here regarded as ssp. *spatulata*].

TYPE: "prope Port Jackson in Nova Hollandia." Holotype: Hurst s.n., (Herb. Rudge), New Holland, s.dat./m.fl. (BM).

D. oblongifolia Link, Enum. Pl. Hort. Berol. 1:381 (1821); Lindley, Bot. Reg. 13:1051, t.1051 (1827); Radlkofer, Pflanzenreich IV.165:1396-1397 (1933).

TYPE: "Hort. angl." Type: B - probably destroyed, Radlkofer (1933): "Hort. Berol.! (fl. ♂; Hb. Link, nunc Hb. Berol.)", n.v. [Here regarded as ssp. *spatulata*].

D. burmanniana DC., Mém. Soc. Phys. Hist. Nat. 1:447 (1822), Prodr. 1:616-617 (1824); Grisebach, Fl. Brit. W. Ind. Isl. 127-128 (1859). [Here regarded as ssp. *burmanniana*].

TYPE: "croît à Ceylan et à Timor". Syntypes: M.D. ?Delefert s.n., Ceylon, 1818. st. (G-DC); Anon. s.n., Zeyl., s.dat. fr. (G-DC); Br. Leschenault s.n., Bengal, 1821. immat.fr. (G-DC); Museum de Paris, Timor, 1821. fr. (G-DC), (see ssp. *burmanniana* typification).

D. salicifolia DC., Mém. Soc. Phys. Hist. Nat. 1:447 (1822), Prodr. 1:617 (1824). [Here regarded as *ssp. angustifolia*].

TYPE: "cultivé jadis dans le jardin de Paris, sous le nom de Bois de reinette ... et d'après sa ressemblance avec un échantillon en feuilles de la Nouvelle-Hollande je la soupçonne originaire de ce pays". Syntypes: Anon. s.n., Bois de Reinette, Par., s.dat. st. (G-DC); Museum de Paris, Nouvelle Hollande côte orient, 1821. ?fl. (G-DC).

D. angustissima DC., Mém. Soc. Phys. Hist. Nat. 1:448 (1822), Prodr. 1:617 (1824); Willis, Hdbk. Pl. Vic. 2:358 (1972). [Here regarded as *ssp. angustissima*].

TYPE: Hort. Lectotype (here designated): Williams s.n., s.loc., s.dat. st. (G-DC), (see *ssp. angustissima* typification).

D. attenuata A. Cunn. in Field, Geogr. Mem. N.S. Wales 353-354 (1825); G. Don, Gen. hist. 1:673 (1831); Bentham, Fl. Aust. 1:477 (1863); Turner, Forage Pl. Aust. 19 (1891); Bailey, Fl. Qld. 1:314 (1899); Black, Fl. S. Aust. edn 1. 362-363 (1926); Domin, Biblioth. Bot. 22(89⁴):911 (1927); Ewart, Fl. Vic. 739 (1931); Radlkofer, Pflanzenreich IV.165:1377-1379 (1933); Black, Fl. S. Aust. edn 2.541 (1952); Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970); Burbidge & Gray, Fl. A.C.T. 250 (1970); Beadle et al., Fl. Syd. Reg. 387 (1972); Chippendale, Proc. Linn. Soc. N.S. Wales 96:246 (1972); Leigh & Mulham, Telopea 1:264 (1977). [Here regarded as *ssp. angustissima*].

TYPE: "Channel of Cox's River". Syntype: A. Cunningham 65, Cox River, 1822. m.fl. (BM, CGE, W).

D. repanda Schum. et Thonn., Beskr. Guin. Pl. 194 (1827). [Here regarded as *ssp. viscosa*].

TYPE: "Almindelig ved Bredderne af Volta", n.v.

D. scabra Lodd. ex Loudon, Hort. Brit. 154 (1830).

TYPE: "N. Holl." (cult.), n.v.

D. umbellata G. Don, Gen. hist. 1:674 (1831). [Here regarded as ?ssp. *angustifolia*].

TYPE: "Native of New Holland (v.s. herb. Lamb.)", n.v.

D. kingii G. Don, Gen. hist. 1:674 (1831). [Here regarded as ?ssp. *angustifolia*].

TYPE: "Native of New Holland (v.s. herb. Lamb.)", n.v.

D. conferta G. Don, Gen. hist. 1:674 (1831). [Here regarded as ssp. *spatulata*].

TYPE: "Native of Van Diemen's Land (v.s. herb. Lamb.)", n.v.

D. asplenifolia Rudge var. *arborescens* Hook., J.Bot. (Hooker) 2:415 (1840). [Here regarded as ssp. *spatulata*].

TYPE: "Mr Lawrence (n.221). Mr Gunn (n. 377)." Lectotype (here designated): R.C. Gunn 377, Hobart, V.D.Land, 27.xi.1840. fr. (K). Isolectotypes: BM, CGE, NSW (ex BM). Syntype: Gunn 377, V.D.'s Land, s.dat. f.fl./m.fl. (K).

D. preissiana Miq. in Lehm. Pl. Preiss. 1:226 (1845); Mueller, Fragm. 1:72 (1859). [Here regarded as ssp. *angustissima*].

TYPE: "Crescit inter rupium fissuras montis Hardy, reg. York. 11 Sept. 1839, sp. masc. et fem. Herb. Preiss. No. 2437; et in rupestribus montis Currie [Preiss 2436]." Lectotype (here designated): L. Preiss 2437, In Nova Hollandia ora occ. inter rupium fissuris montis Hardy (York), 11.ix.1839. immat.fr./m.buds. (U91932). Isolectotypes: G, P, L908.269-953, W150710, MEL(2 sheets). Syntype: L. Preiss 2436, In Nova Hollandia ora occ. in rupestribus montis Currie, 10.iv.1840. fr. (U91931).

- D. viscosa* var. *asplenifolia* (Rudge) Hook. f., Fl. Tasm. 1:55 (1856), based on *D. asplenifolia* Rudge. [Here regarded as ssp. *spatulata*].
- D. denticulata* F. Muell., Fragm. 1:97 (1859). [Here regarded as ssp. *angustissima*].
- TYPE: "In valle Kogoneerup Novae Hollandiae austro-occidentalis."
Holotype: Anon. 423, Kogoneerup Valley, s.dat. f.fl., fr. (MEL).
- D. viscosa* var. *vulgaris* Benth., Fl. Aust. 1:476 (1863); Radlkofer in Martius, Fl. Bras. 13(3):646 (1900), Pflanzenreich IV.165:1368-1369 (1933), p.p. (excl. F.3 *burmanniana* subf. *laurina* - see *D. polyandra*, and subf. *excisa*); Sherff, Field Mus. Nat. Hist., Bot. Ser. 23:271-285 (1947), p.p. (excl. f.4. *eriocarpoidea*, & ? f.2 *schiedeana*). [Here regarded as ssp. *viscosa* & ssp. *burmanniana*].
- TYPE: "tropical Australian species as well as some from Hastings River, Beckler." Syntype: Dr. Beckler s.n., Hastings R., N.S.W., s.dat. fr., bisex. fl. (G).
- D. viscosa* var. *angustifolia* (L.f.) Benth., Fl. Aust. 1:476 (1863); Radlkofer in Martius, Fl. Bras. 13(3):646 (1900), Pflanzenreich IV.165:1368-1369 (1933). [Here regarded as ssp. *angustifolia*].
- D. viscosa* var. *spatulata* (Sm.) Benth., Fl. Aust. 1:476-477 (1863); Radlkofer, Pflanzenreich IV.165:1368-1370 (1933), p.p. (excl. subf. *eriocarpa*). [Here regarded as ssp. *spatulata*].
- D. attenuata* A. Cunn. var. *linearis* Benth., Fl. Aust. 1:477 (1863); Bailey, Fl. Qld. 1:314 (1899); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:345, fig.42A (1904); Black, Fl. S. Aust. edn 1. 363 (1926); Radlkofer, Pflanzenreich IV.165:1378-1379, fig.43A (1933); Black Fl. S. Aust. edn 2. 541 (1952); Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956). [Here regarded as ssp. *angustissima*].

- TYPE: "New England, C. Stuart; Mitta Mitta, Genoa and Buchan rivers in Victoria, F. Mueller; Kangaroo Island, Waterhouse, Sealy; Swan River, Drummond, n.203." Syntypes: C. Stuart s.n., New England, s.dat. fr. (MEL); Mueller s.n., Mitta Mitta River, i.1854. fr. (MEL); Mueller s.n., Buchan River, i.1855. m.fl. (MEL); Mueller s.n., Genoa River, ix.1860. f.fl. (MEL); Waterhouse s.n., Kingscote, Kangaroo Island, s.dat. fr. (MEL); Sealy s.n., Kangaroo Island, s.dat. st. (MEL); Drummond 203, Swan River, 1844. fr. (BM (2 sheets), CGE, G, MEL, P, W92004). Possible syntype: Anon. s.n., New England, N.S. Wales, s.dat. m.fl. (BM ex MEL).
- D. cuneata* Sm. var. *coriacea* Benth., Fl. Aust. 1:477 (1863); Radlkofer, Pflanzenreich IV.165:1375-1376 (1933). [Here regarded as ssp. *cuneata*].
 TYPE: "Wimmera and Murray river, F. Mueller." Probable syntypes: F. Mueller s.n., Murray River, s.dat. fr. (CGE); F. Mueller s.n., Wimmera, s.dat. fr. (G).
- D. cuneata* Sm. var. *rigida* Benth., Fl. Aust. 1:477 (1863); Radlkofer, Pflanzenreich IV.165:1375-1376 (1933); Willis, Hdbk. Pl. Vic. 2:358 (1972) in obs. [Here regarded as ssp. *cuneata*].
 TYPE: "Grampians and Buffalo ranges". Probable syntypes: F. Mueller s.n., Buffalo Ranges, ii.1853. m.fl. (MEL); F. Mueller s.n., Mt. Abrupt, xi.1853. fr. (MEL).
- D. ptarmicaefolia* Turcz. var. (?) *subintegra* Benth., Fl. Aust. 1:479 (1863), basionym for *D. attenuata* var. *subintegra*. [Here regarded as ssp. *angustissima*].
 TYPE: "W. Australia, Drummond, n.204. and 205." Syntypes: J. Drummond 204 & 205, Swan River, 1844. m.fl./f.fl. (BM (2 sheets of each), CGE, G, MEL, W92014).

- D. viscosa* var. *vulgaris* Benth. f. *repanda* (Schum. et Thonn.) Radlk. in Martius, Fl. Bras. 13(3):646 (1900); Radlkofer, Pflanzenreich IV.165:1368 (1933); Sherff, Field Mus. Nat. Hist., Bot. Ser. 23:272-277 (1947). [Here regarded as ssp. *viscosa*].
- D. viscosa* var. *vulgaris* f. *schiedeana* (Schltdl.) Radlk. in Martius, Fl. Bras. 13(3):646 (1900), see TAXON OF UNCERTAIN STATUS, p.
- D. viscosa* var. *vulgaris* f. *burmanniana* (DC.) Radlk. in Martius, Fl. Bras. 13(3):646 (1900); Radlkofer, Pflanzenreich IV.165:1368-1369 (1933), p.p. (excl. subforms); Sherff, loc. cit. 272,277-284 (1947). [Here regarded as ssp. *burmanniana*].
- D. attenuata* A. Cunn. var. *denticulata* (F. Muell.) Radlk., Pflanzenreich IV.165:1378-1379 (1933). [Here regarded as ssp. *angustissima*].
- D. attenuata* var. *subintegra* (Benth.) Radlk., Pflanzenreich IV.165:1378-1379 (1933). [Here regarded as ssp. *angustissima*].
- D. viscosa* var. *linearis* (Harv. & Sond.) Sherff, Amer. J. Bot. 32:214 (1945); Sherff, loc. cit. 285-287 (1947). [Here regarded as ssp. *angustifolia*].
- D. viscosa* var. *linearis* f. *angustifolia* (L.f.) Sherff, Amer. J. Bot. 32:214 (1945); Sherff, loc. cit. 287-295 (1947). [Here regarded as ssp. *angustifolia*].
- D. viscosa* var. *arborescens* (Hook.) Sherff, Amer. J. Bot. 32:214 (1945); Sherff, loc. cit. 297-299 (1947). [Here regarded as ssp. *spatulata*].
- D. viscosa* var. *arborescens* f. *spatulata* (Sm.) Sherff, Amer. J. Bot. 32:214 (1945); Sherff, loc. cit. 299-303 (1947). [Here regarded as ssp. *spatulata*].

D. nematoidea Sherff, Amer. J. Bot. 33:499 (1946), syn. nov. [Here regarded as ssp. *burmanniana*].

TYPE: "C.T. White 7679, large shrub 2 meters tall, flowers greenish, common in rocky gorge base of Biggenden Bluff, Biggenden, South Burnett District, Queensland, May 17, 1931." Holotype: C.T. White 7679, loc. cit., 17.v.1931. f.fl. (A), n.v. Isotypes: NY n.v., BRI128492.

D. cuneata Rudge, Trans. Linn. Soc. 11:296, t.19 (1813), nom. illeg. (Stafleu et al., 1978, Art.64).

D. dioeca Roxb., Hort. Beng. 28 (1814), nom. nud.

D. angustifolia Roxb., Hort. Beng. 28 (1814), nom. nud.

D. neriifolia A. Cunn. ex A. Gray, U.S. Expl. Exped., Phan. 15 Bot. 1:262 (1854), nom. nud.

[*D. lanceolata* auct. non F. Muell.: Bentham, Fl. Aust. 1:475 (1863), p.p. (as to "Clarence river, Beckler." only); Mueller, Fragm. 9:77 (1875), p.p. (as to Lord Howe Is.); Hemsley, Ann. Bot. 10:234 (1896); Maiden, Proc. Linn. Soc. N.S. Wales 28:701 (1904), p.p. (as to Lord Howe Is. specimens).]

[*D. petiolaris* auct. non F. Muell.: Mueller, Fragm. 9:89 (1875), p.p. (as to "in montibus Musgravei"), Mueller, Cens. Aust. Pl. 1:25 (1882), p.p. (as to "S.A." only), Sec. Cens. Aust. Pl. 1:42 (1889), p.p. (as to "S.A." only); Tate, Hdbk. Fl. Extratrop. S. Aust. 28 (1890); Black, Fl. S. Aust. edn 1. 363 (1926), p.p. (as to "Far north and westward to Musgrave Range"), edn 2. 541 (1952), (as in preceding).]

DESCRIPTION (Fig. 7.1, 7.2 & Appendix B):

Dioecious or polygamo-dioecious shrub or small tree, 1.5-5(-8)m high, from spreading, dense shrubs to erect, multistemmed shrubs to single-stemmed,

small trees. Branches dense, spreading (e.g. *ssp. cuneata*) or erect (e.g. *ssp. angustissima*); branchlets angled to flattened, usually slightly ribbed, puberulent to glabrous. Leaves simple, sessile or petiolate; petiole (when present) 2.5-4mm long to 10-18mm long, usually glabrous, sometimes puberulent; lamina variable, linear to narrow-oblong, or linear-lanceolate, or lanceolate to obovate-elliptic, or obovate to spatulate, rarely narrow-obovate, or obtriangular to angular-obovate, 1-15 x 0.1-4cm (see subspecies for details), bright green, sometimes darker above, usually coriaceous, sometimes chartaceous (*ssp. viscosa*), usually viscous, usually with sessile glands, glabrous, base narrow-attenuate to cuneate, margin entire to irregularly sinuate to irregularly denticulate, sometimes repand, apex obtuse to acute, acuminate, sometimes rounded and mucronate, rarely emarginate, rarely irregularly 3-toothed, midvein prominent, lateral venation conspicuous, sometimes more so above than below, or obscure. Flowers unisexual and bisexual, in compound inflorescences composed of monads to botryoids, terminal; pedicels (3-)4-7.5(-9)mm long, viscous, glabrous. Sepals 3-4, lanceolate to ovate, often lanceolate in females and ovate in males, (1.3-)1.5-2.5(-3) x (0.5-)0.8-1.5(-2)mm, acute to obtuse, viscous, outer surface usually glabrous, inner surface villous, sometimes almost tomentose, rarely glabrous, caducous; at anthesis the sepals in male flowers are recurved, in female flowers they are free and erect, surrounding the ovary, in bisexual flowers they are initially as in females, later recurved. Stamens in male & bisexual flowers (6-)8(-10), usually exceeding the sepals, divergent; filaments 0.3-0.5mm long, glabrous; anther lobes oblong 1.8-2.4(-3) x 0.8-1mm, glabrous; apical appendage triangular, broad-acute, 0.2-0.3mm long, glabrous; in female flowers stamens absent.

Ovary in female and bisexual flowers (2-)3-4-carpellate, globose to obovoid, angled, 1-1.2(-1.5) x (0.9-)1-1.3mm, viscous, with sessile glands, pubescent or glabrous; styles 3-4, connate, twisted, 2.5-6.5(-8)mm long, glabrous, separating near the apex, each free arm 0.2-1mm long, recurved; in male flowers rudimentary ovary usually present. Capsule (2-)3-4-winged, in lateral view from broad-elliptic to transversely broad-elliptic to \pm orbicular (ssp. *viscosa*), (8.5-)10-20(-28) x (11-)13-22(-28)mm, coriaceous or membranous, glabrous, dark red-brown or purple to pink or yellow or light brown, base cordate, sometimes deeply so, apex deeply obcordate, sometimes with wings overlapping, rarely emarginate, carpel excluding wing depressed-ovate to transverse-elliptic, (5.5-)6-12(-16) x 3.5-5(-7.5)mm; wing (3-)4-6(-10)mm broad, extending from apex to base of carpel, broadest at the capsule apex, usually broader than the valve, usually membranous, sometimes coriaceous; dehiscence septifragal. Seeds 2-4, lenticular, 2-3.1 x 1.8-3mm, black, dull; aril absent. Seedling glabrous; hypocotyl (5-)8-16(-20)mm long; cotyledons lanceolate, (20-)22-28(-37) x (1.5-)2.3-3.5(-4.2)mm, acute, glabrous; epicotyl 0.5-1.5(-2)mm long; first 3-4 leaves simple, alternate, sessile, usually obovate, sometimes oblong-ob lanceolate, irregularly 3-5-lobed or-toothed above the middle, the teeth or lobes acute, base attenuate to cuneate, otherwise as in mature foliage.

Chromosome number: see subspecies.

TYPIIFICATION:

Jacquin (1760) gave no detailed description in the protologue for *D. viscosa*, but cited "Sloane Jam. t.162.f.3". This illustration of material presumably collected in Jamaica by Sloane was published in

1725. I have not seen the plate, but the description given by Sherff (1945,p.269) indicates it is definitely of a plant belonging to ssp. *viscosa*. Investigations have been made at BM in an attempt to locate any specimens in the Sloane herbarium which could be the type material. If none is found the Sloane plate should be selected as the lectotype.

One undated W sheet labelled "Hb.Jacq." contains a specimen of ssp. *viscosa* collected in the West Indies. Since this specimen is not dated and Jacquin makes no reference to it in the protologue, it cannot be considered part of the type collection.

Many workers have considered the combination *Dodonaea viscosa* to be based on Linnaeus' *Ptelea viscosa* (1753) from India. However, Jacquin makes no mention of Linnaeus' *Ptelea viscosa*, of which he was probably aware. The two names are based on different types and are therefore nomenclaturally independent. The earliest combination of *Dodonaea viscosa* is that of Jacquin, and to regard Linnaeus as the author would be to create a later homonym (Stafleu et al., 1978, Art. 64). The one specimen in the Linnaean herbarium labelled *Ptelea viscosa* (in Linnaeus' handwriting) may not be the type material of this name (Stearn, 1957). Further enquiries will be made in an attempt to locate the Linnaean type.

Typification of the various subspecies is considered as each is discussed. The types of several synonymous names in *D. viscosa* have not been located. Placement of these names is based on the protologue and concepts of previous workers, e.g. Radlkofer (1900, 1933) and Sherff (1947). Material either cited or determined by Radlkofer and Sherff has been examined for each taxon recognised by them.

Lectotypes have not been selected from among the syntypes for some synonymous names. In some cases it has not been possible to determine

if there is another specimen of the type collection in the herbarium in which the author worked, e.g. those taxa described by Bentham at K. Lectotypes will be designated once the information and/or specimen(s) are obtained.

NOTES:

1. *D. viscosa* is a polymorphic species, with a world-wide distribution. Variability in leaf morphology in the Australian material has been the subject of a numerical taxonomic analysis (Chapter 6). The results of that analysis form the basis of the classification proposed here. Two species, *D. angustissima* DC. and *D. cuneata* Sm., are reduced to subspecies of *D. viscosa* and five other subspecies are recognised.

The classification is based primarily on leaf characters. Flowers are morphologically relatively constant throughout the complex. Apart from ssp. *viscosa*, which has a distinctive capsule shape (and usually only two wings), the size and shape of fruits vary slightly throughout the subspecies and are similar to other members of Sect. *Dodonaea*. Plants from a particular locality may show some constancy in capsule morphology, but when examined on a broad scale the variation seems to be continuous.

Plants typical of each of the seven subspecies can be found in many discrete populations. However, there are instances of populations with individuals showing intermediate leaf morphology between the subspecies (Chapter 6). These intergrading populations break down the classification proposed here in approximately 30% of the material examined. Nevertheless, I feel the disjunctions between the forms which do exist within the species to be of sufficient significance to warrant formal recognition. Since some of the subspecies appear to be ecotypes, a classification is useful from a practical point of view alone.

Intergradation of subspecies is discussed within each and under INTERGRADATION OF SUBSPECIES (p.225). The typical form of the species (ssp. *viscosa*) is the most constant morphologically, while ssp. *spatulata* is the most variable.

2. The synonymy included in this treatment relates mainly to Australian material. Some names based on extra-Australian specimens are included in order to clarify the position of another name or to place a particular combination in context.

3. A copy of the recent treatment of *Dodonaea* in the Americas by Lippold (1978) was received too late for it to be fully assessed (or for specimens to be borrowed), in relation to Australian *Dodonaea viscosa*. Initial examination of this classification indicates a rather narrow species concept compared with that adopted here for the genus in Australia.

4. The leaves, fruits and wood of *Dodonaea viscosa* are used by man for various purposes. In Australia, where the genus is known as 'native hops', the capsules were used by the early colonists as a substitute for true hops in making yeast and beer.

Horticulturally *D. viscosa* is probably the best known member of the genus. In Australia a purple-leaved form, originating in New Zealand's South Island, is grown extensively in gardens. In Africa *D. viscosa* is used as a hedge, being especially successful in dry areas (Dale & Greenway, 1961). In some countries it is used as a sand binder and in marshland reclamation. The wood is very hard and close-grained and is used (e.g. in India) for engraving, turning and for tool handles.

Medicinal usage of various parts of *D. viscosa*, particularly the leaves, was discussed by Watt & Breyer-Brandwijk (1962). The leaves are bitter and contain an alkaloid. They are used in various regions to control fevers, colic, rheumatism, venereal diseases and even as an anaesthetic (Standley, 1923).

KEY TO SUBSPECIES OF *D. VISCOSA*

(This key should be used in conjunction with
the representative leaf outlines shown opposite)

- 1a. Leaves elliptic, rarely obovate-elliptic, usually > 2cm broad, with length:width 3-4:1, chartaceous; capsules 2(-3)-winged, \pm orbicular, membranous, carpel (excluding wing) \geq 7mm broad 1. ssp. *viscosa*
- 1b. Leaves variable, rarely elliptic, usually < 2cm broad, with length:width usually > 4:1, if < 4:1 then leaves < 2cm broad and not elliptic, coriaceous; capsules 3-4-winged, broad-elliptic to transversely broad-elliptic, coriaceous or membranous, carpel (excluding wing) < 6mm broad 2
- 2a. Leaves linear, lanceolate to narrow-elliptic or rarely oblanceolate, with length:width 5-15(-30):1, apex long-acute to acuminate or acute, rarely rounded or obtuse with a mucronate tip 3
- 2b. Leaves obovate to spatulate or obtriangular to angular-obovate, with length:width usually < 6:1, apex truncate or rounded with a mucronate tip or short-acute to obtuse, rarely emarginate (ssp. *cuneata*) 6
- 3a. Leaves lanceolate to narrow-elliptic, > 1cm broad, apex long-acute, usually not viscous 2. ssp. *burmanniana*
- 3b. Leaves linear-lanceolate, linear to narrow-oblong, or rarely oblanceolate, < 1cm broad, apex long-acute to acuminate, acute, rounded with short acute to mucronate tip, or obtuse, usually viscous 4
- 4a. Leaves linear-lanceolate, narrowly tapered at apex & base, apex long-acute to acuminate, tapering to petiole (6.5-)10-15(-18)mm long, lateral venation conspicuous 3. ssp. *angustifolia*
- 4b. Leaves linear to narrow-oblong, rarely oblanceolate, not narrowly tapered at apex, apex acute, rounded with acute to mucronate tip or obtuse, sessile or with petiole (1-)4-7(-10)mm long, lateral venation usually obscure. 5
- 5a. Leaves < 0.6cm (rarely 0.6cm) broad, with length:width > 7.5:1, linear to narrow-oblong, rarely oblanceolate, viscous or if oblanceolate not viscous (arid sand dune form), sessile 4. ssp. *angustissima*
- 5b. Leaves > 0.6cm broad, with length:width < 7.5:1, usually obovate to spatulate, sometimes oblanceolate, not linear to narrow-oblong, viscous, sessile or tapering to petiole < 10mm long 7. ssp. *spatulata*
- 6a. Leaves obtriangular to angular-obovate, or narrow-obovate, usually < 3cm long & with length:width < 3.5:1, apex truncate or obtuse, rarely emarginate, usually with a short, acute tip or sometimes irregularly 3-toothed 5. ssp. *cuneata*
- 6b. Leaves obovate to spatulate, usually > 3cm long & with length:width > 3.5:1, apex rounded & mucronate, or obtuse to short-acute 7
- 7a. Leaves (1-)1.2-2(-2.5)cm broad, apex rounded & mucronate, rarely obtuse, with petiole (3.5-)5-15(-20)mm long 6. ssp. *mucronata*
- 7b. Leaves (0.5-)0.6-1(-1.6)cm broad, apex obtuse to short-acute, rarely mucronate, sessile or with petiole (1-)4-7(-10)mm long 7. ssp. *spatulata*

1. ssp. *viscosa*

Ptelea viscosa L. (1753); *Dodonaea repanda* Schum. et Thonn. (1827);
D. viscosa var. *vulgaris* Benth. (1863), p.p.; *D. viscosa* var. *vulgaris* f.
repanda (Schum. et Thonn.) Radlk. (1900).

FIGURES: Sloane, Nat. Hist. Jamaica 2: t.162 f.3 (1725); Plumier, Cat. Pl.
 Amer. ed. Burman 10:245, t.247 f.2 (1760); Capuron, Mém. Mus. Natl. Hist.
 Nat., Ser.B, Bot. 19:25, t.4. f.12-16 (1969).

DESCRIPTION (Fig. 7.1 ; Appendix B, *D. viscosa* group, population QLREP):

Dense, spreading shrub 1-2m high, branchlets glabrous; leaves with
 petiole 2.5-4(-6)mm long; lamina elliptic or rarely obovate-elliptic,
 (7-)8.5-11(-12.5) x (2-)2.2-3(-4)cm, chartaceous, sometimes viscous, base
 broad-attenuate, margin irregularly sinuate, apex obtuse or broad-acute,
 lateral venation conspicuous; capsule 2(-3)-winged, ± orbicular,
 15-23 x 20-25mm, membranous, carpel (excluding wing) transverse-elliptic,
 11.5-15 x 7-7.5mm, wing 4-4.5mm broad.

Chromosome number: not known for Australian material.

DISTRIBUTION (Fig. 7.2):

In Australia ssp. *viscosa* occurs primarily along the coast of north-
 east Queensland, and on the offshore islands, extending across Torres
 Strait to New Guinea. Collections have also been made at Port Macquarie
 and on the Hastings River in north-eastern New South Wales.

Beyond Australia ssp. *viscosa* is found in tropical America, Africa
 and Asia. It occurs in Florida, West Indies and in South America (e.g.
 Venezuela, Brazil), in the Philippines, Celebes, Java and Borneo, on
 Madagascar and in southern tropical Africa (Radlkofer, 1933; Sherff, 1947).

ECOLOGY:

This form of *D. viscosa* occurs mainly as a small, dense shrub in coastal situations. It is usually associated with sand and often on dunes close to the foreshore.

NOTES:

This is the most distinctive subspecies in the species and shows little intergradation. The orbicular capsules and the larger, thinner leaves serve to distinguish it from the other subspecies.

SPECIMENS EXAMINED: selection only (37 collections examined).

NEW SOUTH WALES:- Anon. s.n., Port Macquarie, xii.1897. bisex.fl., fr. (NSW 140934). - Evans 2268, nr. Port Macquarie, 25.viii.1927. fr., bisex.fl. (CANB).

QUEENSLAND:- Banfield s.n., Dunk Is., xii.1906. fr. (BRI73035). - Lawrie s.n., Dauan Is., Torres Strait, 9.ix.1971. bisex.fl. (BRI140720). - Scarth-Johnson 756A, Weary Bay, v.1978. fr. (BRI). - L.S. Smith 11013, Bloomfield Reach, 1.6km E of Bloomfield R., 4.ix.1960. fr. (BRI, CANB). - L.S. Smith & Pedley 10013, Port Douglas Beach, 25.viii.1957. fr. (BRI). - Specht & Specht 236, Lizard Is., 24.xii.1974. fr. (BRI). - Thorsbourne s.n., Hinchinrook Is. at S end of Ramsay Beach, 19.viii.1970. fr. (BRI109408).

2. ssp. *burmanniana* (DC.) West, stat. nov.

Carpinus forte viscosa, salicis folio integro oblongo J.Burm. (1737); *D. burmanniana* DC. (1822), basionym; *D. viscosa* var. *vulgaris* Benth. (1863), p.p.; *D. viscosa* var. *vulgaris* f. *burmanniana* (DC.) Radlk. (1900); *D. nematoidea* Sherff (1946).

FIGURES: J.Burm., Thes. zeylan. 55, t.23 (1731); Rumph., Hb. Amboin. 4: t.50 (1743); Lamarck, Encyclop. 2:439, t.304 f.1 (1797); Capuron, Mém. Mus. Natl. Hist. Nat., Ser.B, Bot. 19:25, t.4 f.17 (1969).

DESCRIPTION (Fig. 7.1 ; Appendix B, *D. viscosa* group, population QLBURM):

Large shrub or small tree 2-6m high, branchlets usually glabrous, sometimes puberulent; leaves with petiole (6-)10-12(-18)mm long; lamina lanceolate to narrow-elliptic, (6.5-)7.5-10(-15) x (1.4-)1.6-2(-2.3)cm, coriaceous, base attenuate, margin entire to irregularly sinuate, apex long-acute, lateral venation conspicuous; capsule 3-4-winged, in later view broad-elliptic to transversely broad-elliptic, (8.5-)10-20(-28) x (11-)13-22(-28)mm, coriaceous or membranous, carpel (excluding wing) depressed-ovate to transverse-elliptic, (5.5-)6-12(-16) x 3.5-5(-6)mm, wing (3-)4-6(-10)mm broad.

Chromosome number: not known for Australian material.

TYPIIFICATION:

A.P. de Candolle (1822) validly published *D. burmanniana* by referring to J. Burman's Thesaurus zeylanicus (1737), which contained a short description and illustration. de Candolle's Prodrômus (1824) herbarium contains four specimens, three of which originated in Ceylon or Timor, and which bear dates prior to 1822. Although these herbarium specimens were not cited in the protologue they were almost certainly available to de Candolle in 1822, and are therefore regarded as syntypes in preference to Burman's illustration (Stafleu et al., 1978, p.75 4b).

DISTRIBUTION (Fig. 7.2):

In Australia ssp. *burmanniana* occurs on the east coast from the Grafton area of north-eastern New South Wales, through southern Queensland to Cairns in the north-east. This subspecies also occurs in tropical America, Africa and Asia. It extends from Mexico through Central America to South America (e.g. in Peru, Brazil, Argentina). In Africa it is found in Kenya and Tanzania, while in Asia it has been collected in China, India, Malaya, the Philippines and Indonesia (Radlkofer, 1933; Sherff, 1947).

ECOLOGY:

This subspecies is a shrub or small tree of wet sclerophyll forest or woodland associations. It is often on rocky slopes and hills and sometimes in sandy soils.

NOTES:

Misapplications of the name *Dodonaea lanceolata* have been made for Lord Howe Island material belonging to ssp. *burmanniana* (e.g. Maiden, 1904).

SPECIMENS EXAMINED: selection only (87 collections examined).

NEW SOUTH WALES:- Crisp 4482 & Telford, Lord Howe Is., track from Old Settlement to North Bay, 21.x.1978. fr.(AD, CGE). - McGillivray 2306, 5m1 S of Wooli, 5.vii.1966. st. (NSW). - Pickard 1487, Lord Howe Is., Far Flats, W foot of Mt.Lidgbird, 20.v.1971. st. (NSW). - Poolman s.n., Tabulam, xi.1904. fr. (BRI134906, NSW106393). - Thurtell & Coveny 3861, Glenugie Peak, 16km SE of Grafton, 9.xii.1971. fr. (NSW). - Williams s.n., Pye's Creek, SW of Tenterfield, 17.xii.1966. fr. (NSW140814).

QUEENSLAND:- Gittins 864, Rockland Springs, W side of Blackdown Tableland, 25ml WSW of Duaringa, vii.1964. m.fl. (NSW, BRI). - Gittins 872, Stanage Point, vii.1964. f.fl (NSW). - Sharpe 58-59, Townsville rd., 14km N of Bowen, 28.xi.1971. fr. (BRI). - Telford 5327, Mt.Walsh, 6km S of Biggenden, 28.v.1977. m.fl.(CBG).

3. ssp. *angustifolia* (L.f.) West, stat. nov.

Triopteris erecta fruticosa, foliis oblongis acuminatis, ramulis gracilibus P.Browne (1756); *D. angustifolia* L.f. (1781), basionym; *D. salicifolia* DC. (1822); ?*D. umbellata* G.Don (1831); ?*D. kingii* G.Don (1831); *D. viscosa* var. *angustifolia* (L.f.) Benth. (1863); *D. viscosa* var. *linearis* (Harv. & Sond.) Sherff (1945); *D. viscosa* var. *linearis* f. *angustifolia* (L.f.) Sherff (1945).

FIGURES: P.Browne, Civ. nat. hist. Jamaica t.18 f.1 (1756); Lamarck, Encyclop. 2:439, t.304 f.2 (1797); Cavanilles, Icon. IV.14, t.327 (1797); Capuron, Mém. Mus. Natl. Hist. Nat., Ser.B, Bot. 19:25, t.4 f.18 (1969).

DESCRIPTION (Fig. 7.1; Appendix B, *D. viscosa* group, populations QLANG, KWALL):

Compact shrub, 1.5-3(-5)m high, branchlets glabrous, sometimes puberulent; leaves with petiole (6.5-)10-15(-18)mm long, triquetrous; lamina linear-lanceolate, narrowly tapered at apex and base, (5.5-)7.5-10(-14) x (0.5-)0.7-0.85(-1)cm, coriaceous, viscous, base narrow-attenuate, margin entire to irregularly sinuolate, apex long-acute to acuminate, lateral venation conspicuous; capsule as in ssp. *burmanniana*.

Chromosome number: not known.

TYPIFICATION:

Linnaeus *filius* based *D. angustifolia* on material from Hortus Uppsalensis (HU), of which most material is now held at S. It has not been possible to locate any specimen which may belong to the type collection. Since Lippold (1978) did not find any type material either, it may be necessary to choose a neotype for this name. However, this has not been done here as *ssp. angustifolia* has not been studied on a world-wide basis and I have not examined sufficient Indian material. Further investigations will be made in European herbaria in an attempt to locate Linnaeus *filius*' type specimen(s).

DISTRIBUTION (Fig. 7.2):

D. viscosa ssp. angustifolia occurs in the Darling Downs region of south-eastern Queensland, on the slopes and tablelands of the Great Dividing Range in New South Wales and in far-eastern Victoria.

Beyond Australia *ssp. angustifolia* occurs in the Americas, Africa and Asia. It has been extensively collected in Florida and Mexico, in Peru, Ecuador and Bolivia in South America and in the West Indies. It occurs in South Africa, through the Middle East to India, China, the Philippines and Fiji (Radlkofer, 1933; Sherff, 1947).

ECOLOGY:

This subspecies usually grows as a shrub of dry sclerophyll forest or woodland associations, often in rocky situations.

NOTES:

1. Several workers have interpreted *D. angustifolia* Swartz, Obs.bot. 150 (1791) as a later homonym of *D. angustifolia* L.f. (1781). As Sherff

(1949) correctly pointed out, Swartz referred to Murray's Syst. Veg. edn 14. (1784), which in turn referred to *D. angustifolia* of L.f. Swartz was correctly applying L.f.'s name to a Jamaican plant.

2. Sometimes ssp. *angustifolia* intergrades with ssp. *spatulata* (e.g. McGillivray 3046-3048) and ssp. *angustissima* (e.g. Adams 697).

One *D. viscosa* population from Kanangra Walls in the Blue Mountains of N.S.W. (Burgess CBG34792, West 3585-3586) appears to be a form of this subspecies. It differs from typical ssp. *angustifolia* in having broader, entire leaves which are relatively thick, and tend towards ssp. *burmanniana*. Geographically this population is within the distribution of ssp. *angustifolia*, while the closest ssp. *burmanniana* population is in north-eastern N.S.W. near Grafton.

SPECIMENS EXAMINED: selection only (103 collections examined).

NEW SOUTH WALES:- Boorman s.n., Narrabri West, vi.1907. f.fl. (NSW140906).

- Crisp 2155, south coast, 2 km N of Central Tilba, foot of Mt. Dromedary, 26.ix.1976. immat.fr. (AD, CBG). - Dunlop 582-583, Warrumbungles N. P.

21.viii.1969. f.fl./m.fl. (CBG). - Maiden s.n., Boggabri, xi.1899. fr.

(NSW140912). - Shoobridge 277, Pilliga Scrub, 23ml from Narrabri towards Bingara, 25.x.1967. fr. (CBG). - Simmons, per Copley 5085, Silent Grove N of Torrington, 18.x.1977. fr. (AD).

QUEENSLAND:- Anon. s.n., Leyburn, 1.x.1978. fr. (BRI242662). - Bailey s.n.,

Highfield, s.dat. f.fl. (BRI71232). - Michael 2979, Porter's Gap, vii.1945.

fr. (BRI, CANB). - Williams 4, 24ml W of Warwick on rd. to Goondiwindi, 16.ix.1968. fr. (BRI).

VICTORIA:- West 838-839, S side of Lake Mallacoota on Lakeside Dve.,

11.ii.1975. m.fl./f.fl. (AD).

4. ssp. *angustissima* (DC.) West, comb. et stat. nov.

D. angustissima DC. (1822), basionym; *D. attenuata* A.Cunn. (1825);
D. preissiana Miq. (1845); *D. denticulata* F.Muell. (1859); *D. attenuata*
 var. *linearis* Benth. (1863); *D. ptarmicaefolia* Turcz. var. (?)
subintegra Benth. (1863); *D. attenuata* var. *denticulata* (F.Muell.) Radlk.
 (1933); *D. attenuata* var. *subintegra* (Benth.) Radlk. (1933).

FIGURES: Turner, Forage Pl. Aust. t.19 (1891); Diels in Engler's Bot.
 Jahrb. 35:346, fig.42A (1904); published again in Radlkofer, Pflanzenriech
 IV.165:1362, fig.43A (1933); Blackall & Grieve, W.Aust. Wildfls. 2:324
 (1956).

DESCRIPTION (Fig. 7.1 ; Appendix B, *D. angustissima* group):

Erect, multistemmed shrub, 2-4m high, branchlets glabrous; leaves
 sessile, linear to narrow-oblong, sometimes oblanceolate (in arid sand
 dune form), (3-)4.5-8(-9.5) x (0.1-)0.15-0.4(-0.6)cm, coriaceous, usually
 viscous (arid sand dune form not viscous), base narrow-attenuate, margin
 irregularly sinuate to irregularly denticulate, apex acute to obtuse,
 sometimes obtuse with very short acute or \pm mucronate tip, lateral venation
 obscure; capsule as in ssp. *burmanniana*.

Chromosome number: $n = 14$ (West 1081, 1149, 1189, 1254, 1644, 1714, 1899,
 1902, 1923, 1927, 2111, 2176)

TYPIIFICATION:

A.P. de Candolle described *D. angustissima* from horticultural
 material in Geneva botanic gardens. The only specimen of this taxon in
 G-DC is one collected by Williams. This agrees with the protologue and,
 although it relates to the 'Prodromus' (1824), it is here chosen as the
 lectotype.

DISTRIBUTION (Fig. 7.2):

D. viscosa ssp. *angustissima* is restricted to Australia and is widespread in the southern and central parts of the continent. It occurs in the south-west of Western Australia extending through the Great Victoria Desert into South Australia and Northern Territory. It is found throughout arid regions of the Northern Territory and extends into the south-west and the central Mitchell district of Queensland. This subspecies has an extensive distribution in South Australia, where it is absent only from the far south-east. Apart from the coastal regions it is common in all areas of New South Wales and is also found in northern Victoria.

ECOLOGY:

Ssp. *angustissima* occurs in arid and semi-arid areas and is usually associated with open woodland and sand plain country, occasionally occurring on the margins of sand dune systems. In areas such as the Flinders Ranges of South Australia it is found in rock crevices and at the base of rocky outcrops, and in south-west Western Australia it is often associated with granite outcrops.

This subspecies is one of several inedible shrub species being studied in north-west N.S.W. to assess its regeneration potential in the pastoral lands (Booth & Barker, 1979). It appears that the past high domestic stocking rates of this region has resulted in a change of dominant species of the arid shrublands. Some unpalatable woody shrub species are showing considerable regeneration and are regarded as "weed problems" by those concerned with the pastoral industry.

NOTES:

1. This subspecies shows similarities with ssp. *mucronata* and ssp. *cuneata* in exhibiting consistent morphology and appearing as a distinct

taxon in arid areas, but at the margins of its distribution in higher rainfall areas it intergrades with other subspecies. The intergrading populations appear to involve mainly ssp. *spatulata*, but occasionally, and especially in N.S.W. and Victoria, ssp. *cuneata* seems to be involved (see INTERGRADATION OF SUBSPECIES p.225).

2. A very narrow-leaved form (<2mm broad) of *D. viscosa* (e.g. LINREDR, LINWASX of Appendix B, *D. angustissima* group), previously recognised as *D. attenuata* var. *linearis* Benth., is here included in ssp. *angustissima* without further formal taxonomic recognition. Although there are populations consisting of this narrow-linear form only, many contain individuals with both narrow and broader leaves. The total intergradation is such that no natural break occurs and it seems impracticable to separate the narrow form from ssp. *angustissima*. Some plants have narrow leaves in the younger shoots and broader subtending leaves, implying developmental gradation.

3. Included in this narrow-leaved form is a small number of populations in central Queensland with more rigid leaves with thickened margins (QULAFF in Appendix B, *D. angustissima* group). This form was clustered with ssp. *angustissima* in the numerical analysis, but it may have slightly different fruits and sepals from most material belonging to this species. Its placement in the cluster analysis is not unexpected since only leaf morphological characters were considered. Field studies on a population basis are needed to establish its position in the complex.

SPECIMENS EXAMINED: selection only (more than 700 collections examined)
 NEW SOUTH WALES:- Briggs 2748, Mootwingee, NE of Broken Hill, 22.v.1969. f.fl. (NSW). - Gittins 1909A & B, 138ml from Broken Hill towards Tibooburra, viii.1969. m.fl./f.fl., fr. (NSW). - Mullins s.n., Molonglo Gorge, 12km NE of Canberra, x.1972. m.fl. (CBG57316).

NORTHERN TERRITORY:- Ball 14-17, Simpson Desert, x.1977. m.fl./fr. (AD). - Lazarides 6154, 8ml ENE of Mt. Olga, 7.x.1956. fr. (AD,BRI,CANB,NSW).

QUEENSLAND:- Blake 6793, Mitchell distr., between Yalleroi & Jericho, 15.vii.1934. f.fl. (BRI,CANB). - Purdie 1143, Gregory South distr., 35km WNW of Birdsville, 17.ix.1977, mature f.fl., immat.fr. (BRI).

SOUTH AUSTRALIA:- Lothian 3390, Lake Torrens Basin, 8km W of Yadlabenna Dam, NW of Leigh Creek, 11.xi.1964. fr. (AD). - West 1299-1304, Kangaroo Is., Vivonne Bay, 0.5km NW of Point Ellen, 26.xii.1975. m.fl./f.fl., fr. (AD). - West 1896-1905, Eyre Pen., 41km E of Kimba on Whyalla-Kimba rd., 17.viii.1977. m.fl./f.fl., fr. (AD).

VICTORIA:- West 1714-1717, 13km W of Ouyen on rd. to Pinnaroo, 29.x.1976. m.fl./f.fl. (AD).

WESTERN AUSTRALIA:- Beard 3383, NE end of Lake Lefroy, 26.v.1964. fr. (PERTH). - West 3365-3370, 2.8km N of Southern Cross on rd. to Bullfinch on edge of Lake Koorkardine, 11.xii.1978. fr./m.fl. (AD).

5. ssp. *cuneata* (Sm.) West, comb. et stat. nov.

D. cuneata Sm. (1809), basionym; *D. cuneata* var. *coriacea* Benth. (1863); *D. cuneata* var. *rigida* Benth. (1863).

FIGURES: Rudge, Trans. Linn. Soc. 11:296, t.19 (1813); Galbraith, Wildfls. Vic. edn 3. t.94 (1967).

DESCRIPTION: (Fig. 7.1 ; Appendix B, *D. cuneata* group):

Compact, spreading shrub, 1-3m high, branchlets glabrous or puberulent; leaves sessile or shortly petiolate; petiole (when present) ca.1mm long; lamina obtriangular to angular-obovate to narrow-obovate, (1.2-)1.5-2.5(-3) x (0.4-)0.5-0.85(-1.2)cm, coriaceous, sometimes viscous, base cuneate,

margin entire to irregularly sinuate, apex truncate or obtuse, rarely emarginate, usually with a very short, central, acute or mucronate tip, sometimes irregularly 2-3-toothed, lateral venation obscure; capsule as in ssp. *burmanniana*.

Chromosome number: $n = 14$ (West 1355, West 1661, West 2540).

TYPIFICATION:

Smith described *D. cuneata* from specimens originating in New South Wales. Material from the Smith herbarium, now held at LINN, has not been seen. Further attempts will be made to locate type material of this taxon or to examine a microfiche copy of the Smith herbarium, in order to clarify the typification.

DISTRIBUTION (Fig. 7.2):

D. viscosa ssp. *cuneata* occurs primarily in semi-arid areas of south-eastern Australia. It grows in the Murray mallee areas of South Australia, in north-western Victoria and on the western slopes and plains of New South Wales. The subspecies also extends into the tablelands in the Hunter Valley region (N.S.W.) and in Queensland it is found in the Wide Bay and Moreton districts.

ECOLOGY:

This subspecies grows in mallee scrub communities in semi-arid areas, and in open forests in high rainfall regions. It is normally in sandy loams, but also occurs on rocky hillsides, e.g. in several Queensland populations.

NOTES:

1. The typical form of *ssp. cuneata*, like *ssp. mucronata* and *ssp. angustissima*, appears to be an arid ecotype with relatively consistent morphology. In higher rainfall areas, such as in eastern Victoria and in the central coast and tablelands of N.S.W., *ssp. cuneata* exhibits integradation with other subspecies, particularly *ssp. spatulata*.

2. Most of the Queensland specimens seen during this study have leaves with definite emarginate apices, e.g. Carroll 1115-1116. In all other features they clearly belong to *ssp. cuneata*.

SPECIMENS EXAMINED: selection only (256 collections examined).

NEW SOUTH WALES:- Crisp 1518, Western plains, 4km W of Kamarah, 50km E of Griffith, 13.xi.1975. fr. (CBG). - Webb s.n., Wiseman's Ferry - St.Albans, 7.x.1967. fr. (NSW140656). - West 814-817, 6.4km W of Matong & 25.6km E of Narrandera on Narrandera-Coolamon rd., 30.i.1975. immat.fr. (AD).

QUEENSLAND:- Carroll 1115-1116, Blackall Ra., 6ml from Mapleton towards Cooloolabin, 25.v.1967. m.fl./f.fl. (CBG, NSW). - Telford 721-722, Blackall Ra., 6ml from Mapleton towards Cooloolabin, 22.v.1969. f.fl./m.fl. (CBG). - C.T. White s.n., Moreton distr., Enoggera, s.dat. fr. (BRI72455).

SOUTH AUSTRALIA:- Sharrad 514, Cooke Plains, 40km SSE of Murray Bridge, 23.ii.1960. m.fl. (AD). - West 1659-1661, on outskirts of Mannum, 25km N of Murray Bridge, 15.ix.1976. m.fl./f.fl. (AD). - West 1826-1833, Monarto, 12km W of Murray Bridge, 15.v.1977. m.fl./f.fl. (AD).

VICTORIA:- Phillips s.n., between Inglewood & Wedderburn, 21.ix.1961. immat.fr. (CBG). - West 1718-1719, 3km NE of Walpeup, 25km WSW of Ouyen, 29.x.1976. fr. (AD).

6. ssp. *mucronata* West, ssp. nov.

[*D. viscosa* var. *spatulata* auct. non (Sm.) Benth.: Bentham, Fl. Aust. 1:476-477 (1863), p.p.; Radlkofer, Pflanzenreich IV.165:1368-1370 (1933), p.p.; Chippendale, Proc. Linn. Soc. N.S.Wales 96:246 (1972)].

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956).

Folia petiolo (3.5-)5-15(-20)mm longo, lamina plerumque spatulata, interdum obovata, (2.5-)3-5.5(-6) x (1-)1.2-2(-2.5)cm, basi late attenuata, apice plerumque rotundato mucronatoque, raro solum obtuso, venis lateralibus conspicuis.

TYPE: Holotype: M. Lazarides 5302, Northern Territory, Palm Valley, 12mi SW of Hermannsburg Mission, 24° 04' S 132° 45' E, 15.v.1955. fr. (AD95915080). Isotypes: BRI18211, CANB82402, NSW, PERTH.

The subspecific epithet refers to the leaf apex.

DESCRIPTION (Fig. 7.1 ; Appendix B, *D. viscosa* group, populations: PALMV, WAMAG, SHERARB (Francis, Evt1825, Whi9503):

Erect to spreading shrub, 1.5-4m high, branchlets glabrous; leaves with petiole (3.5-)5-15(-20)mm long; lamina usually spatulate, sometimes obovate, (2.5-)3-5.5(-6) x (1-)1.2-2(-2.5)cm, coriaceous, viscous, base broad-attenuate, margin entire to irregularly sinuate, apex rounded and mucronate, rarely obtuse, lateral venation conspicuous, at least on the upper surface; capsule as in ssp. *burmanniana*.

Chromosome number: n = 14 (West 3329)

DISTRIBUTION (Fig. 7.2):

D. viscosa ssp. *mucronata* is widespread in arid central Australia. It occurs in Western Australia from north of Kalgoorlie to the Hamersley

Ranges and east into the Rawlinson Ras. and hills of the Great Victoria Desert. Its distribution extends into the Northern Territory, where it is common in the Petermann and MacDonnell Ras., extending as far as Mt Isa in north-west Queensland, and into the Musgrave and Everard Ras. of north-west South Australia. The sand dune areas of north-east South Australia and the Simpson Desert appear to cause a disjunction between the latter populations and those on the plains and western slopes of New South Wales.

ECOLOGY:

This subspecies appears to be restricted to rocky hills and ranges and associated rocky creeks and gullies in arid areas.

In central Australia increased seen germination follows most fires (G. Griffin, pers. comm., 1979). The discontinuous rocky nature of the habitat in which ssp. *mucronata* grows does not encourage a large amount of fuel, and so wild fire intensities are usually low and plants often regenerate by coppicing.

NOTES:

1. Ssp. *mucronata* was previously included in var. *spatulata* (Sm.) Benth. (=ssp. *spatulata* (Sm.) West), but in its typical form it is quite distinct from the latter taxon. It appears to associate with a specific habitat and to form an ecotype within *D. viscosa*. In the centre of its distribution, i.e. in Northern Territory and north-west South Australia, ssp. *mucronata* is very consistent morphologically, whereas on the margins of its distribution (e.g. western New South Wales and western Western Australia) some plants show intergradation with ssp. *spatulata* (see INTERGRADATION OF SUBSPECIES p.225).

SPECIMENS EXAMINED: selection only (237 collections examined).

NEW SOUTH WALES:- Morris s.n., Broken Hill, 28.xi.1919. fr. (NSW140791).

NORTHERN TERRITORY:- Donner 4277, Mount Cavenagh, 17km SW of Kulgera H.S., 20.viii.1973. fr. (AD). - Gittins 2023, Heavitree Ra., nr. Stuart's Pass, ix.1969. fr. (NSW, BRI). - Perry 5383, Stanley's Chasm, nr. Alice Springs, 4.ix.1955. fr. (AD, BRI, CANB, NSW, PERTH).

QUEENSLAND:- Gittins 740, Burke distr., N of Mt Isa, v.1963. fr. (BRI, NSW).

SOUTH AUSTRALIA:- Eichler 17411, Musgrave Ras., Cave Hill, 8.ix.1963. fr. (AD, W). - Symon 2546, Mt. Lindsay, 6.viii.1962. fr. (AD, ADW). - Turvey s.n., Musgrave Ra., vii.1968. immat.fr. (NSW140749).

WESTERN AUSTRALIA:- Carolin 6015, S side of Cavenagh Ra., 31.vii.1967. m.fl. (NSW). - George 12173, 137km E of Warburton, 26.vii.1974. fr. (PERTH). - West 3328-3330, 6.8km N of Mt Magnet on rd. to Meekatharra, 9.xii.1978. m.fl./immat.fr./fr. (AD).

7. ssp. *spatulata* (Sm.) West, stat. nov.

D. spatulata Sm. (1809), basionym; *D. asplenifolia* Rudge (1815); *D. oblongifolia* Link (1821); *D. conferta* G. Don (1831); *D. asplenifolia* var. *arborescens* Hook. (1840); *D. viscosa* var. *asplenifolia* (Rudge) Hook. f. (1856); *D. viscosa* var. *spatulata* (Sm.) Benth. (1863); *D. viscosa* var. *arborescens* (Hook.) Sherff (1945); *D. viscosa* var. *arborescens* f. *spatulata* (Sm.) Sherff (1945).

FIGURES: Rudge, Trans. Linn. Soc. 11:297, t.20 (1815); Lindley, Bot. Reg. 13: t.1051 (1827); Black, Fl. S. Aust. edn 1. 361, fig. 160E-K (1926), edn 2. 539, fig.693E-K (1952); Curtis, Fl. Tasm. 118, fig.35 (1956).

DESCRIPTION (Fig. 7.1 ; Appendix B, Intermediate group, populations: HYDEN, MTGREEN; *D. viscosa* group: TAS, MARION, FRGAM, SLWAIT, SLWATIP, SHERARB (Hub5101, Evt741, Whi8326); *D. cuneata* group: GRAMP):

Erect to spreading shrub, 1.5-4m high, branchlets glabrous to puberulent; leaves sessile or petiolate; petiole (when present) (1-)4-7 (-10)mm long; lamina usually obovate, sometimes spatulate, rarely elliptic, (2.3-)3-5.5(-7.5) x 0.6-1(-1.6)cm, coriaceous, viscous, base narrow-attenuate to attenuate, margin entire to irregularly sinuate or irregularly denticulate, apex obtuse to short-acute, sometimes obtuse or rounded with a very short acute or mucronate tip, lateral venation usually conspicuous on lower surface; capsule as in ssp. *burmanniana*.

Chromosome number: n = 14 (West 1023, 1186, 1219, 1679, 1764, 2001, 2039, 2463, 2472)

TYPIFICATION:

Smith described *D. spatulata* from a specimen collected by Menzies in Hawaii (Sandwich Islands). No material of this type collection has been seen to this time, but Sherff (1947) cited a syntype now held at K. Attempts will be made to locate further type material, e.g. at LINN, where Smith's herbarium is housed, and to examine a microfiche copy of Smith's herbarium.

DISTRIBUTION (Fig. 7.2):

D. viscosa ssp. *spatulata* is widespread in temperate and semi-arid southern Australia. It is found in southern Queensland, in almost all areas of New South Wales, south-eastern and southern Victoria and in Tasmania. Ssp. *spatulata* is widely distributed in southern South Australia and, with a disjunction on the Nullarbor Plain, also in south-west Western Australia.

ECOLOGY:

Ssp. *spatulata* occurs in various habitats usually in temperate, high rainfall areas. It is a shrub of open forest or woodlands and mallee scrublands, and grows mostly in sandy loams.

This subspecies appears to have high powers of regeneration following various disturbances. After significant rains plants of some populations have been observed shooting from the base following total leaf loss during a drought period (West 1741-1744). Others coppice after heavy grazing, such as by feral goats in the Flinders Ranges of South Australia.

Initial studies carried out in western New South Wales on the effect of fire on mortality of this subspecies indicate it is sensitive to fires, especially when the shrubs are under water stress (K.C. Hodgkinson, pers. comm., 1979). Low intensity fires may result in loss of 50% of the population, rising to approx. 70% for high intensity fires. Regeneration occurs through coppicing and seed germination.

NOTES:

1. Ssp. *spatulata* shows the greatest amount of leaf morphological variation of the seven subspecies here recognised. It is widespread in temperate southern Australia and occupies a wide variety of habitats. This subspecies intergrades with ssp. *angustissima*, ssp. *cuneata* and ssp. *mucronata* in the temperate areas in which they are sympatric (see INTERGRADATION OF SUBSPECIES, p.225).

The variation shown by ssp. *spatulata* is mainly in leaf shape, including variation in both apex and base. The leaves of Appendix B, Intermediate group: HYDEN, MTGREEN and *D. viscosa* group: TAS, MARION, FRGAM,

SLWAIT, SLWATIP, SHERARB (Hub5101, Evt741, Whi8326) illustrate the polymorphic nature of this subspecies. In some regions, such as in Tasmania and in the northern Flinders Ras. and Mt Lofty Ras. of South Australia the leaf shape remains relatively constant. On the other hand, in southern and eastern New South Wales and in the south-east of South Australia ssp. *spatulata* is very variable and often intergrades with other subspecies.

2. Populations of ssp. *spatulata* from the Grampians and surrounding ranges in western Victoria show some morphological distinction from most material of this subspecies. The majority of plants from this region have obovate, slightly thicker, broader and more rigid leaves with irregularly denticulate margins. It is this form which was recognised by Bentham (1863) as *D. cuneata* var. *rigida* and which was included in the numerical analysis of *D. viscosa* (Chapter 6) as population GRAMP of group *D. cuneata* (Appendix B). It was clustered in that analysis mainly with material belonging to ssp. *cuneata*, but it is here placed in ssp. *spatulata* primarily on leaf size, shape and the margin. This form is not recognized at any formal taxonomic level, as it varies greatly within populations and intergrades extensively with other subspecies.

SPECIMENS EXAMINED: selection only (more than 500 collections examined).
 NEW SOUTH WALES:- Cleland s.n., Dubbo, 29.ix.1911. immat.fr. (AD96234019).
 - Crisp 4385, Warrumbungle Ra., 21.5km WSW of Coonabarabran, 11.x.1978 f.fl.,fr. (AD,CBG). - Hoogland 11377, nr. Mulyandra, 12ml from Forbes towards Grenfell, 7.ix.1968. m.fl. (CANB, NSW). - Thurtell & Coveny 3899, 4ml NNE of Boonoo Boonoo, 24.2km NNE of Tenterfield, 12.xii.1971. m.fl. (AD, NSW).

QUEENSLAND:- Adams 1344, South Kennedy Distr., 4ml NNW of "Star Downs", 7.x.1964. fr. (CANB, BRI, NSW, AD, MEL). - Henderson 234, Leichhardt distr., 3ml S of Moura on rd. to Theodore, 4.iii.1967. fr. (CANB, BRI). - C.T. White 9503, Roma, 25.x.1933. fr. (BRI).

SOUTH AUSTRALIA:- West 1762-1767, Southern Lofty region, Torrens Gorge, 6.8km E of Kangaroo Ck.dam & 28.9km NE of Adelaide, 20.xii.1976. m.fl./f.fl.,fr. (AD). - West 2001-2007, Eyre Pen., Lincoln N.P., 1km W of Pillie Lake, 11km S of Port Lincoln township, 22.viii.1977. m.fl./f.fl.,fr. (AD).

TASMANIA:- Whinray 774, Bass Strait, Furneaux Grp., Prime Seal Is., 17.x.1972. fr. (AD). - C.T. White 8326, Bellerive, nr. Hobart, 9.ii.1932. m.fl./f.fl. (BRI).

VICTORIA:- Beaglehole 43083, Portland, nr. Swan Lake Falls, 1952. m.fl./f.fl. (AD). - Webb s.n., Mt.Arapiles, 23.viii.1965. immat.fr. (CBG12771). - West 3541-3555, Grampians, Mt.Sturgeon, 2km NW of Dunkeld, 28.xii.1978. fr./st./mature m.fl. (AD).

WESTERN AUSTRALIA:- Everist 9133, Coodardy, 33ml NW of Cue on Nondi rd., 6.ix.1969. fr. (BRI, CANB). - Filson 8758, 50ml E of Yalgoo, on Geraldton-Mt.Magnet rd., 11.ix.1966. fr. (MEL, PERTH). - West 3116-3119, 15.2km E of Newdegate on Lake King-Newdegate rd., 28.xi.1978. m.fl./f.fl., fr. (AD).

PUTATIVE HYBRIDS:

1. *D. boroniaefolia* X *D. viscosa* ?ssp. *cuneata*, see *D. boroniaefolia*.
2. *D. procumbens* X *D. viscosa*, see *D. procumbens*.

INTERGRADATION OF SUBSPECIES:

The morphological intergradation of subspecies involves those diagnostic characters which are used to separate them. The variable characters appear to have a broad genetic basis contributing to the extreme polymorphism of the species. Given the extensive geographical distribution within Australia and the range of habitats in which the species occurs, it is not surprising that it shows significant polymorphism. Intergradation is found only in higher rainfall, southern temperate areas and not in the arid region or in the north of Queensland.

Several of the subspecies are sympatric in parts of their distributions, and it is in these areas that intergradation occurs. However, each subspecies is also ecologically and geographically distinct for some part of its range. It appears from the discussion within each subspecies, that the morphological differences between the subspecies are correlated with the differences in their respective environments, although it has not been possible to determine whether the character differences expressed in the typical forms of the subspecies are of direct adaptive significance to the plants. In morphologically intergrading populations, individual plants superficially resembling different subspecies have been observed growing side by side (see Chapter 6 for further discussion of Intermediate populations). It would seem therefore, that the character variation in these higher rainfall, southern temperate, intergrade regions, is not an outward expression of basic physiological differences, although it may be when comparing arid subspecies (e.g. *ssp. mucronata*) with an east coast temperate subspecies (e.g. *ssp. burmanniana*).

Variability within the subspecies has been briefly discussed under each. In addition, reference is made to a number of other variants, which

are considered too variable or inadequately known to recognise as distinct taxa. In this section the leaf morphological characters showing intergradation between particular subspecies is discussed and a small number of specimens or populations of each intergrade are cited. Examples of most morphological variants along the intergrades are plotted in Appendix B. In some populations it seems as though the variation in leaf morphology is continuous from ssp. *cuneata* through ssp. *spatulata* to ssp. *angustissima*; examples are given under 4. below.

1. ssp. *spatulata* - ssp. *mucronata*

Intergrade populations between these two subspecies occur in western New South Wales, south-west Queensland and Western Australia. Leaves are variously obovate-spathulate, with or without a petiole and the apex ranges from acute to rounded and mucronate, to obtuse.

Specimens: selection only

NEW SOUTH WALES:- Crisp 4156, 40km NNW of Cobar, Bundella Stn., 7.ix.1978. f.fl. (AD, CBG). - Gardiner s.n., Mootwingee, 100km NE of Broken Hill, 8.viii.1962. fr. (AD). - Jensen s.n., 4ml WSW of Narrabri, viii.1911. m.fl. (NSW140739). - McGillivray 2742, 4ml N of Kenebri, xi.1967. m.fl. (NSW).
WESTERN AUSTRALIA:- Ashby 2526, Wooleen H.S. on Boolardy rd., SE of Carnarvon, 18.viii.1968. fr. (AD). - Wilson 7373, 5km NE of Bandya H.S., 100km N of Laverton, 27.viii.1968. fr. (PERTH).

2. ssp. *spatulata* - ssp. *angustissima*

(see Appendix B, Intermediate group, populations: MUBRAEN, REMARK, SUGBUG, YASS, SESA, ONGERUP).

Intergrades occur in southern South Australia, Victoria, New South Wales, southern Queensland and Western Australia. Plants have the more spreading habit of *ssp. spatulata* with leaves showing all gradations between the two subspecies. Populations are composed of plants with sessile or petiolate leaves of various shapes from linear-oblong to lanceolate to obovate, with the apices varying from obtuse to acute.

Specimens: selection only

NEW SOUTH WALES:- Harvey s.n., Warrumbungle Mts., xi.1958. fr. (NSW140724).

- Pickard & Coveny 1083, Burning Mt., 13km SE of Murrurundi, vi.1969. f.fl.

(NSW). - West 1685-1691, 21km NW of Yass on rd. to Harden, 26.x.1976.

fr., f.fl./mature m.fl. (AD).

QUEENSLAND:- Tindale s.n., 25.5ml W of Warwick towards Karara, i.1969.

m.fl. (NSW140725).

SOUTH AUSTRALIA:- West 1173-1183, Mt Remarkable N.P., 2km SW of Black

Hill, 11.x.1975. fr./st. (AD). - West 1882-1888, Murray mallee,

Braendler's Scrub, 4.5km S of Monarto South, 13km SW of Murray Bridge,

7.viii.1977. fr. (AD). - West 431-443, South east, nr. Desert Camp C.P.,

42km S of Keith, 10.xi.1974. f.fl., immat.fr./m.fl. (AD).

VICTORIA:- Carroll s.n., 1.5ml from Suggan Buggan R., towards Wulgumerang,

18.xii.1965. fr. (CBG14747). - West 2587-2590, 7km N (by rd.) of Suggan

Buggan on rd. to Jindabyne, 7.v.1978. buds (AD).

WESTERN AUSTRALIA:- West 3066-3078, 14km SW of Gnowangerup on Ongerup-

Borden rd., 27.xi.1978. m.fl./f.fl., fr. (AD).

3. *ssp. spatulata* - *ssp. cuneata*

(see Appendix B, Intermediate group, populations BLACKMT, SINTON;

Burbidge & Gray, Fl. A.C.T. 249, fig.247 (1970)).

Populations showing intergradation between these two subspecies are composed of plants with obovate to obtriangular leaves, with apices varying from acute or obtuse to truncate, emerginate or 2-3-toothed. These intergradations occur in New South Wales and Victoria where the two subspecies are sympatric.

Specimens: selection only.

NEW SOUTH WALES:- Burbidge 7485, Black Mt., A.C.T. 5.v.1964. f.fl./fr. (CANB). - Constable s.n., Pinnacles Mt., 8ml NNW of Grenfell, iii.1956. m.fl. (NSW37904). - Coveny s.n., 4ml S of Bulga, 14ml SW of Singleton, 11.i.1968. f.fl./m.fl. (NSW140651, NSW140652). - Fagg 6, Mootwingee Ra., 110km NE of Broken Hill, 14.v.1964. m.fl. (AD).
VICTORIA:- Morrison s.n., Moonee Ponds, 13.iii.1891. m.fl. (AD, CANB).

4. *ssp. cuneata* - *ssp. spatulata* - *ssp. angustissima*

(see Appendix B, Intermediate group, population GRIFF).

Plants which intergrade between these three subspecies occur in some extremely variable populations mainly in New South Wales. These shrubs usually have long, oblanceolate or obtriangular leaves, & are truncate or 2-3-toothed at the apex.

Specimens: selection only.

NEW SOUTH WALES:- Crisp 1343-1345, Cocopara Ra., 1km W of Mt. Bingar, 25km NE of Griffith, 11.xi.1975. m.fl./f.fl. (CBG, AD).

TAXON OF UNCERTAIN STATUS:

D. viscosa var. *vulgaris* Benth. f. *schiedeana* (Schltdl.) Radlk.

Radlkofer (1933) cited specimens of this form from Norfolk Island and Queensland. Brazilian specimens determined by Radlkofer as f. *schiedeana* (from W) have been examined during this study and duplicates of specimens from New Guinea cited by Sherff (1947) (i.e. Brass 5053, Schlechter 19118) have also been seen.

Of the large amount of *D. viscosa* material examined, none of the Australian specimens appear to belong to this form. Several Norfolk Island specimens examined in this treatment have close affinities to the New Zealand material and show little resemblance to f. *schiedeana*. It probably does not occur in Australia, but is regarded as being of uncertain status with respect to Australian *D. viscosa* until a broader world-wide study of this species is undertaken.

2. *Dodonaea polyandra* Merrill et Perry, J. Arnold Arbor. 21:525 (1940);

McGillivray, *Telopea* 1:67 (1975).

TYPE: "BRITISH NEW GUINEA: Western Division, Wassi Kussa River, Tarara, Brass 8379 (TYPE), 8379A, December 1936, abundant in rainforest fringing streams (very slender tree 5-7m. high, dioecious)." Holotype: L.J. Brass 8379, New Guinea, Western Division, Tarara, Wassi Kussa R., xii.1936 (A), n.v. Isotype: F.fl., fr. (BRI8356).

D. viscosa Jacq. var. *laurina* J. Britten in Banks & Solander, Ill. Bot.

Cook's Voy. 1:16. t.42 (1900); [Radlkofer, *Pflanzenreich* IV.165:1369 (1933) pro syn., sub *D. viscosa* var. α *vulgaris* F.3. *burmanniana* subf. *laurina*; McGillivray, *Telopea* 1:67 (1975) pro syn.]

TYPE: "Cape Grafton". Lectotype: Banks & Solander s.n., Lookout Point ('Cape Grafton'), 1770. (BM). Isotype: MEL84152. Syntype: Cunningham 147, (K).

[*D. viscosa* var. *vulgaris* auct. non Benth.: Bentham, *Fl. Aust.* 1:476 (1863), p.p. (as to Endeavour river specimens only).]

FIGURES: Banks & Solander, Ill. Bot. Cook's Voy. 1:16, t.42 (1900).

DESCRIPTION (Fig. 7.3):

Dioecious shrub or small tree, 1.5-6(-8)m high, slender, erect. Branches spreading; branchlets acutely angled or flattened, viscous, glabrous. Leaves simple; petiole (3-)4-6(-10)mm long, glabrous; lamina narrow-elliptic to elliptic, rarely obovate, (5.5-)7-9.5(-10.5) x (1.6) 2.5-3.5(-4.2)cm, dark green on upper surface, paler below, coriaceous, thick, viscous, with sessile glands, glabrous, base attenuate, margin entire, weakly sinuate, thickened, apex obtuse-acuminate, midvein and lateral venation prominent. Flowers unisexual, in panicles composed of monads to botryoids, terminating branchlets; pedicels (4.5-)6.5-10(-14)mm long. Sepals 4(-5), linear-oblong, 2.5-3 x (0.9-)1.2-1.6mm, obtuse viscous, glabrous, caducous; at anthesis the sepals in male flowers are

spreading, in female flowers they are free, erect & surrounding the ovary. Stamens in male flowers (11-)12-14, exceeding the sepals, divergent; filaments 0.9-1.2mm long, glabrous; anther lobes oblong, 2.1-2.2 x 0.7-0.8mm, glabrous, apical appendage triangular-acute, to 0.3mm long, glabrous; stamens in female flowers absent. Ovary in female flowers 2-3-carpellate, ovoid, angled, 1.3-1.5 x 0.8-1.1mm, viscous, glabrous; styles 2-3, connate for almost entire length, 6-10(-13)mm long, glabrous, usually separating at the apex into very short lobes 0.1mm long, sometimes undivided; in male flowers rudimentary ovary usually present. Capsule 2(-3)-winged, in lateral view broad-oblong to transversely broad-oblong to suborbicular, 16-22(-28) x (15-)20-25(-30)mm, glabrous, purple-brown or purple tinged at maturity, base cordate, wings rarely overlapping, apex obcordate, wings sometimes overlapping; carpel excluding wing navicular, (10-)11.5-14 (-17.5) x (3.5-)4-6.5(-7)mm, crustaceous & thickened; wing (4-)6-9mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve, membranous; dehiscence septifragal. Seeds 2-4, lenticular-globose, 2.2-2.5 x 2.3-2.4mm, black, shiny; aril absent. Seedling not seen.

Chromosome number: not known.

DISTRIBUTION (Fig.7.3):

In Australia *D. polyandra* is confined to Queensland's Cape York Peninsula region, particularly on the east and north coasts and off-shore islands. Its distribution extends across Torres Strait into the Western Division of Papua New Guinea.

ECOLOGY:

This species is most commonly found as a shrub or small tree on the fringes of rainforest communities. It also occurs in *Acacia* or *Agonis* scrub, in open *Eucalyptus* woodlands and in *Callitris* woodlands. *D. polyandra* usually grows in sandy or gravelly soils and is often near a river or creek bank. In New Guinea it grows as a small tree in woodlands among species of *Melaleuca*, *Acacia* and *Tristania*.

D. polyandra flowers from May to October and fruits are usually present from October to December.

AFFINITIES:

D. polyandra is most closely related to the *D. viscosa* complex, with which it has been confused. It differs from members of that group in having larger, elliptic, dorsiventral leaves, 2(-3)-winged capsules with large wings surrounding thickened, rounded valves and a larger number of stamens.

In leaf morphology *D. polyandra* resembles *D. triquetra*, from which it is distinguished by the latter's smaller fruits with carpels which are not thickened, lenticular seeds with the hyaline membrane lifting at the margin and leaves lacking sessile glands, and each with a long-acuminate apex.

SPECIMENS EXAMINED: selection only (51 collections examined)

QUEENSLAND:- Brass 18410, Cape York Pen., Lockerbie, 10ml WSW of Somerset, 25.iv.1948. f.fl. (BRI,CANB).- Briggs 1983, 3ml W of Cooktown, on rd. to Endeavour R. bridge, 4.viii.1968. fr. (NSW).- Gittins 2188, 16km N of Hope Vale Mission, 24km NW of Cooktown, 4.ix.1970. fr. (BRI,NSW).- Hind 266, Cape York Pen., Browns Ck., Kennedy rd., 19.viii.1973. fr. (NSW).- Scarth-Johnson 527A, Cook distr., Hopevale, 22.vii.1977.

fr. (BRI).- L.S. Smith 11158, Hoop pine area, nr. McIvor area, 6.ix.1960.

fr. (BRI).- L.S. Smith 12646, Cook distr., nr. Somerset, 13km SE of Cape York, 30.x.1965. m.fl. (BRI); Stocker 825, Lankelly Creek, 23.xi.1971.

m.fl. (BRI).

NEW GUINEA:- Eddowes & Kumul s.n., Western Distr., 3ml W of Arufi village, Morehead sub-distr., 17.viii.1968. fr. (BRI115947, CANB185712, NGF36052,

NSW).- Ridsdale & Galore s.n., Western distr., nr. Weam, Bensbach sub-distr., 10.viii.1967. fr. (BRI132462, CANB185712, NGF33642, NSW).

3. *Dodonaea petiolaris* F. Muell., *Fragm.* 3:13 (1862); Bentham, *Fl. Aust.* 1:475 (1863); Mueller, *Fram.* 9:89 (1875), p.p. (excl. "in montibus Musgravei"), *Pl. coll. in Capric. W. Aust. by H.S. King 2* (1886) and published again in *Trans. & Proc. R. Soc. Vic.* 23:51 (1887), *Vic. Nat.* 8:93-94 (1891); Moore, *Fl. N.S.Wales* 94 (1893); Bailey, *Fl. Qld.* 1:313 (1899); Ewart & Davies, *Fl. N. Terr.* 175 (1917); Black, *Fl. S. Aust. edn 1.* 363 (1926), p.p. (excl. "Far North and westward to Musgrave Range"); Radlkofer, *Pflanzenreich IV.165*:1390-1391 (1933); Black, *Fl. S. Aust. edn 2.* 541 (1952), p.p. (excl. "Far North and westward to Musgrave Range"); Chippendale, *Trans. R. Soc. S. Aust.* 84:101 (1961); Beard, *W. Aust. Pl. edn 1.* 60 (1965), *edn 2.* 81 (1970); Chippendale, *Proc. Linn. Soc. N.S.Wales* 96:246 (1972).
 TYPE: "In eremo occidentali fluminis Darling. Neilson." Holotype: Neilson s.n., Darling River, s.dat. immat.fr. (MEL84120).

DESCRIPTION (Fig.7.4):

Dioecious shrub, 1-2m high, erect. Branches erect; branchlets angular, viscous, with verruculose glands, sometimes sparsely pubescent. Leaves simple; petiole 7.5-14mm long, channelled above, viscous, sometimes sparsely pubescent; lamina broad-lanceolate to ovate, often conduplicate & recurved, (2.5-)3-4.5(-6.6) x (0.8-)1-1.5(-2.5)cm, coriaceous, with sessile glands, viscous, glabrous, base attenuate to truncate, margin entire to sinuate, wavy or undulate, apex acute, midvein prominent, lateral venation prominent on lower surface, often obscure above. Flowers unisexual, in terminal compound inflorescences composed of monads to botryoids; pedicels (2.5-)3.5-5.5(-8)mm long, viscous, glabrous. Sepals 5, linear-lanceolate, channelled above, (1.2-)1.5-2(-2.5) x (0.3-)0.4-0.5(-0.7)mm, acute, thick, viscous, glabrous, persistent; at anthesis the sepals in male flowers are recurved, in female flowers they are free, erect & surround the ovary. Stamens in male flowers 6-10, exerted beyond sepals,

divergent; filaments 0.3-0.5mm long, glabrous; anther lobes oblong, (2-)2.3-3 x 0.7-1.2mm, glabrous; apical appendage broad-triangular, thick, 0.3-0.5mm long, glabrous; in female flowers rudimentary stamens sometimes present. Ovary in female flowers 3-carpellate, obovoid, angled, 1.5-2 x 1.2-1.5mm, viscous, with sessile glands & resin layer, glabrous; styles 3, connate, twisted in upper half, 4-6.6mm long, red, viscous, glabrous, separating unequally at apex, each free arm 0.5-1.6mm long, recurved; in male flowers rudimentary ovary usually present. Capsule 3-winged, in lateral view broad-oblong to ellipsoid, greatly inflated, (16-)21-30(-38) x (12-)15-25(-30)mm, membranous, venation obvious, glabrous, pink to purple-red & yellow at maturity, base cordate to truncate, apex truncate to emarginate, with persistent style base; carpel excluding wing transverse-ovate, (14-)20-26(-34) x (6.5-)7-10(-12.5)mm; wing 1.5-3.5(-4) mm broad, extending from apex to base of carpel, usually broadest at the capsule apex, much narrower than the valve; not readily dehiscent, carpel walls shred into transverse strips. Seeds 2-5, globose, (2.7-)3-3.4 x (2.5-)3-3.6mm, black, dull; aril absent. Seedling glabrous; hypocotyl (17-)20-23.5(-40)mm long; cotyledons lanceolate or narrow-oblong, (15.5-)17-20(-22) x 3.5-5(-5.5)mm, acute, glabrous; epicotyl 1-1.5mm long; first 2-6 leaves simple, alternate, petiolate, ovate, with sessile glands, base cuneate, margin entire to sinuate, wavy or undulate, rarely irregularly lobed, apex acute.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.4):

D. petiolaris occurs in a large area of central Western Australia, in central Northern Territory, south-western Queensland and north-western New South Wales. Two major disjunctions in its distribution occur between W.A. and the N.T. and between the latter and south-west Queensland.

In W.A. it is common in the Mt. Magnet area and extends to the north-west into the margins of the Gibson Desert at Mt. William Lambert. In the N.T. *D. petiolaris* occurs north of Alice Springs and further east on a sandstone hill at Lucy Creek Station, north of Jervois Range (Lazarides 5910). This shrub is common around Bourke in N.S.W., the most southern locality being the 'Lachlan River' (exact location uncertain). In Queensland it is found in the Grey Range and Thargomindah area extending in a north-easterly direction to Quilpie and the southern Warrego Range.

ECOLOGY:

D. petiolaris is found on rocky hills or ranges and on the gibber plains of arid and semi-arid areas. It often grows on the slopes or on top of hills, ridges or ranges of various rock types, including laterite, basalt, ironstone, quartz, granite and magnetite. In flatter situations it is often associated with mulga (*Acacia aneura*) shrublands.

D. petiolaris does not grow in deep sands and is therefore absent from the larger sand dune regions of Central Australia. Its preference for rocky outcrops and gibber plains partly explains the disjunctions in the distribution of this species. In the west the sand sheets of the Gibson and Great Victoria Deserts probably contribute to its absence in those areas, while the Simpson Desert and sand dunes of north-eastern South Australia would be major factors limiting its distribution in Central Australia.

Flowering occurs in autumn to winter (March to July), with fruit maturing in late August to October. Mature fruit may remain on the bushes until the next flowering season.

NOTES:

1. Previous records of *D. petiolaris* in South Australia appear to be misidentifications of *D. viscosa* ssp. *mucronata*. References to its occurrence in that state in the literature probably emanate from Mueller's (1875) reference ("in montibus Musgravei") to material collected on the Forrest expedition of 1874. Three specimens of *D. petiolaris* collected by Forrest, which are now housed at MEL, have labels with dates (but no locality data) corresponding to the time that Forrest was in the Gibson Desert of Western Australia (Forrest, 1875), and not in S.A. The material from the Musgrave Ras., to which Mueller (1875) refers is most probably *D. viscosa* ssp. *mucronata*, as are the Giles collections from the Macdonnell and Rawlinson Ranges which he also mentions. I have seen no specimens of *D. petiolaris* from S.A. during this study and it has not been found in neighbouring states in close proximity to the border. It is believed therefore that, this species does not occur in S.A.

2. *D. petiolaris* is the only member of the Sect. *Dodonaea* with an inflated capsule and a fruit which lacks a direct method of capsule dehiscence. The release of the seed in this species appears to depend on the eventual breakdown of the outer membranous carpel walls. Field observations suggest the whole fruit is wind blown and rolled around on the ground (or rocks) and that physical damage is the main factor initiating the transverse shredding of the capsule.

AFFINITIES:

D. petiolaris most closely resembles *D. viscosa* ssp. *mucronata* in leaf shape, but the leaves of the two species differ in several features. *D. viscosa* ssp. *mucronata* leaves are usually spatulate, lack a definite petiole, have a mucronate apex and obscure lateral venation on the upper surface.

The capsule of *D. petiolaris* is very distinct. The pinnate-leaved *D. physocarpa* is the only other species in the genus with an inflated capsule.

SPECIMENS EXAMINED: selection only (127 collections examined).

NEW SOUTH WALES:- Constable 4504, Mount Oxley, 20ml ESE of Bourke, 13.x.1963. fr. (AD,NSW,U).- Milthorpe & Cunningham 1739, 4.1ml N of Ledknapper Crossing, iii.1974. m.fl./f.fl. (NSW).- Noble s.n., "Tundulya", S of Louth, xi.1973. fr. (NSW140687).- Pickard 1819 & Benson, 24km E of Hungerford, Qld. border, 26.v.1972. m.fl. (BRI,NSW).

NORTHERN TERRITORY:- Lazarides 5910, 28ml NNE of Lucy Creek Stn., 6.ix.1956. fr. (AD,BRI,CANB,PERTH).- Lothian 506/54, Woodgreen Stn., 160km NNE of Alice Springs, 1954. f.fl. (AD).

QUEENSLAND:- Blake 6704, Mitchell distr., Bilbah Downs nr. Emmet, 10.vii.1934. f.fl./m.fl. (BRI,CANB).- Pedley 2443, Warrego distr, 15ml S of "Humburn", 9.ix.1967. fr. (BRI).- Trapnell & Williams 250, Warrego distr., 59km NW of Quilpie, 28.viii.1973. fr. (BRI).- K. Williams 105, Warrego distr., 46ml W of Cunnamulla, 26.ix.1968. fr. (BRI).

WESTERN AUSTRALIA:- Chinnock 3933-3934, 25.8km SE of Lander turnoff on Woodlands-Mt. Augustus rd., 11.ix.1977. fr. (AD).- George 5454, Gunbarrel Hwy., Mt. William Lambert, 26.vii.1963. f.fl.,fr./m.fl. (PERTH).- Mitchell 311, 8km W of Bulloo Downs H.S., Upper Ashburton, 13.iv.1977. m.fl. (PERTH).- Speck 1003, 10ml W of Mileura on Nookawarra rd., 17.vii.1958. fr. (CANB, PERTH).- Trudgen 335, Hamersley Ra. N.P., S side of Mt. Bruce, 7.viii.1963. fr. (PERTH).- West 3331-3335, Mt. Magnet, 2km NW of Mt. Magnet township, 9.xii.1978. mature m.fl./fr. (AD).

4. *Dodonaea hackettiana* W.V. Fitzg., J. W. Aust. Nat. Hist. Soc. 2:21-22

(1905); Radlkofer, Pflanzenreich IV.165:1377 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:323 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).

TYPE: "King's Park, Perth, among limestone.- J. Sheath, August 1904".

Holotype: ?J. Sheath s.n., King's Park, Perth, viii.1904. f.fl. (NSW 144256).

FIGURE: Blackall & Grieve, W. Aust. Wildfls. 2:323 (1956).

DESCRIPTION (Fig.7.5):

Dioecious shrub, 1.5-3(-4.5)m high, erect. Branches dense, spreading; branchlets ribbed or angular, with 2-3 rows of dense white, villous hairs extending to the branches. Leaves simple, sessile, narrow-elliptic (3-)3.5-4.8(-5.5) x (0.35-)0.45-0.7(-0.9)cm, bright green, coriaceous, thin, with sessile glands, sparsely pubescent on midrib & margin, base attenuate, margin entire, apex acute, midvein prominent, lateral venation usually obscure. Flowers unisexual, in compound inflorescences composed of monads to botryoids, terminal; pedicels (1.8-)2.5-4(-4.5)mm long, pubescent below the middle, rarely glabrous. Sepals 3, rarely 4 in male flowers, viscous, outer surface sparsely pubescent or glabrous, inner surface villous, caducous, in male flowers broad-ovate, 1.6-2.1 x 1.6-1.8mm, acute, in female flowers ovate, 1.6-2.1 x 1-1.2mm, acute; at anthesis the sepals in male flowers form a cup-shaped structure, they are free & imbricate at the base, in female flowers they surround the ovary, are free at the apex only, valvate below, recurved at apex. Stamens in male flowers 6(8), approx. equal in length to the sepals, erect to spreading; filaments 0.2-0.3mm long, sparsely pubescent above the middle; anther lobes oblong, 1.4-1.5 x 0.6-0.7mm, glabrous; apical appendage ±absent,

a broad lobe less than 0.1mm long, pubescent; stamens in female flowers absent. Ovary in female flowers 3-carpellate, oblong, angled, 0.7-0.9 x 0.8-1mm, with sessile glands, pubescent; styles 3, connate, straight, 3-4.5mm long, separating at the apex, each free arm 0.1-0.3mm long, recurved; in male flowers rudimentary ovary sometimes present. Capsule 3-winged, in lateral view transversely broad-elliptic, (9.5-)11-13 x (12.5-)14-17mm, membranous, glabrous, orange-brown at maturity, base cordate, apex obcordate, with the wings sometimes overlapping; carpel excluding wing navicular, (4.5-)5-6(-6.5) x 3-4.5mm; wing 3.5-5(-5.5)mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve; dehiscence septifragal. Seeds 3-4, lenticular, compressed towards the margin, 2.4-2.7 x 2.1-2.4(-2.6)mm, black, dull; aril absent. Seedling pubescent; hypocotyl 18-23mm long; cotyledons linear-lanceolate, 20-25(-30) x 2-3mm, acute, glabrous; epicotyl 4-6mm long; first 6 leaves simple, alternate, petiolate, irregularly deeply 3-lobed, the 2 lateral lobes linear, obtuse & entire, the central lobe obovate & 2-3-toothed, base cuneate.

Chromosome number: $n = 14$ (West 3253)

TYPIFICATION:

Although the holotype does not have any collector's name on it, the label, in Fitzgerald's handwriting, includes the locality and date of collection as in the protologue. Two other sheets (NSW144257, NSW144258), which were part of Fitzgerald's herbarium and are now held at NSW, contain specimens with male flowers and fruit. These are probably of the same collection and would have been available to Fitzgerald when he described *D. hackettiana*. However, these specimens were collected in July, 1904 and, are therefore not part of the type collection.

DISTRIBUTION (Fig. 7.5):

D. hackettiana appears to be confined to a very small area around Perth in Western Australia. One collection from 'Warriup Hills' (east of Albany) must be regarded as a doubtful locality.

ECOLOGY:

This species is known from a limited number of populations, which are all associated with limestone or with sands overlying limestone. In King's Park, Perth *D. hackettiana* grows on limestone cliffs in *Eucalyptus gomphocephala* open forest with *Casuarina* sp., *Pelargonium* sp., *Grevillea* sp. and *Dianella* sp., or in association with *Dryandra floribunda*. South of Perth it is found in *Eucalyptus marginata* open forests and tall *Banksia* sp. forest.

Baird (1977) included *D. hackettiana* with *Dryandra sessilis* and *Conospermum triplinervium* as shrubs which are killed by fire when burnt off to ground level.

D. hackettiana usually flowers in August, September or October. The fruit develops quickly and is usually mature by December or January.

NOTES:

The restricted distribution of this species to a very small number of populations in close proximity to a major capital city places it at risk in terms of survival in the wild. The King's Park population is the only one known to be within a reserve of any type. Hartley & Leigh (1979) classified *D. hackettiana* as an endangered endemic.

AFFINITIES:

D. hackettiana shows slight resemblance to some individuals of the *D. viscosa* complex and the capsules are typical of Sect. *Dodonea*. The

thin leaves with pubescent margins and midribs and the villous indumentum on the branches serve to distinguish this species.

SPECIMENS EXAMINED:

WESTERN AUSTRALIA:- Hb. Fitzgerald s.n., nr. Perth, vii.1904. fr./m.fl. (NSW144257).- Gardner s.n., ? Warriup Hills, x.1940. m.fl. (PERTH).- Green & Stokes 297, King's Park, nr. War Memorial, 23.ii.1955. fr. (PERTH).- Helms s.n., Swan R., 5.viii.1898. m.fl. (NSW98183, PERTH).- Maiden s.n., King's Park, Perth, x.1909. f.fl. (NSW), fr.(W).- Main s.n., Thomson's Lake Reserve, Jandakot, ix.1962. f.fl. (PERTH).- Sheath s.n., King's Park, Perth, vii.1904. m.fl. (NSW144258).- Sheath s.n., King's Park, Perth, x.1909. fr. (NSW).- Sheath s.n., Perth, xii.1910. fr. (NSW).- Sheath s.n., King's Park, Perth, 1911. fr. (AD97236247, NSW98182, PERTH).- Steedman s.n., South Perth Zoo, xi.1924. fr. (PERTH).- West 3251-3254, King's Park, Perth, above Stirling Hwy., 5.xii.1978. fr. (AD).- West 3262-3267, 20km S of Perth, 1km S of Bibra Lake, 5.xii.1978. fr. (AD).- West 3268-3271, 24km S of Perth, S of Thompson's Lake, 5.xii.1978. mature m.fl./fr. (AD).

5. *Dodonaea ptarmicaefolia* Turcz., Bull. Soc. Imp. Naturalistes Moscou 25.II: 155 (1852); Mueller, Fragm. 1:220 (1859), p.p. (excl. *D. denticulata* F. Muell. - see *D. viscosa* ssp. *angustissima*); Bentham, Fl. Aust. 1:479 (1863), p.p. (excl. syn. *D. denticulata* F. Muell. and *D. ptarmicifolia* var. (?) *subintegra* Benth. - see *D. viscosa*); Mueller, Fragm. 9:87 (1875); Radlkofer, Pflanzenreich IV.165:1379-1380 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:323 (1956); Beard, W. Aust. Pl. edn 1. 61 (1965), edn 2. 81 (1970).

TYPE: "Nova Hollandia. Drummond. coll. V. n. 248." Syntypes: J. Drummond 248, Western Australia, 1850. fr. (BM,G,MEL84134).

FIGURE: Blackall & Grieve, W. Aust. Wildfls. 2:323 (1956).

DESCRIPTION (Fig. 7.6):

Dioecious shrub, 1-3.5(-4)m high, erect. Branches erect & spreading; branchlets angular or ribbed, viscous, glabrous. Leaves simple, sessile or rarely petiolate; petiole (when present) 3-5(-8)mm long, viscous, glabrous; lamina linear, rarely oblong or lanceolate, (2-)2.5-5(-5.3) x 0.1-0.3(-0.55)cm, bright green, coriaceous, viscous, with sessile or brown verruculose glands, glabrous, base attenuate, tapering to petiole, margin serrate with serrations 1-1.5mm long, usually entire in lower 1/3 of leaf, apex acute & recurved, midvein prominent, often sinuous, lateral venation obscure. Flowers unisexual, in axillary 3-4-flowered botryoids; pedicels (3.5-)4-6.5(-7.5)mm long, shorter in male flowers, glabrous. Sepals 3(-4), ovate, 1.5-2 x 1-1.5mm, acute, viscous, outer surface with verruculose glands, glabrous or sparsely pubescent, inner surface densely villous to tomentose, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are free, erect, imbricate at the base & surrounding the ovary. Stamens in male flowers 6(-8), approx. same length as the

sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 1.6-2 x 0.6-0.7mm, glabrous; apical appendage absent or a very short lobe of 0.1mm long, glabrous; stamens in female flowers absent. Ovary in female flowers 3(-4)-carpellate, elliptic to globose, angled, 1-1.1 x 1-1.1mm, with sessile glands, pubescent; styles 3(-4), connate, 1.5-2.1mm long, glabrous, separating at the apex, each free arm usually less than 0.15mm long, recurved; in male flowers rudimentary ovary usually present. Capsule 3(-4)-winged, in lateral view transverse-elliptic or transverse-oblong, (6-)7.5-9(-10.5) x (10-)12-15(-16)mm, membranous, viscous, with sessile or verruculose glands, purple-red or red-brown at maturity, base cordate or rarely truncate, apex obcordate, wings sometimes overlapping; carpel excluding wing depressed-ovate & navicular, 4.5-5.5 x 2.5-3.5mm; wing 3-5mm broad, extending from apex to base of carpel, broadest in the upper half of the capsule, broader than the valve; dehiscence septifragal. Seeds 2-5, lenticular, 2-2.2(-2.5) x 2-2.1mm, black, shiny; aril absent. Seedling glabrous; hypocotyl 12-16mm long; cotyledons linear-lanceolate, 12-18 x 1.5-2mm, acute, glabrous; epicotyl 2-5mm long; first 4-8 leaves simple, alternate, sessile, oblanceolate, irregularly 5-6-lobed above the middle, base attenuate, apex irregularly 3-toothed, the teeth obtuse.

Chromosome number: not known.

TYPIFICATION:

Turczaninow designated the Drummond collection no.248 as the type. Three duplicates of this collection have been examined (BM,G,MEL84134), but it has not been possible at this stage to ascertain whether there is another specimen at KW, the herbarium housing Turczaninow's main herbarium. The typification of *D. ptarmicaefolia* will be clarified upon receiving information or material from KW.

DISTRIBUTION (Fig.7.6):

D. ptarmicaefolia is confined to south-west Western Australia in the Eyre district north of Hopetoun. It extends from the Tammin area in the north-west to Peak Charles on the eastern limit of its distribution.

ECOLOGY:

This species is most commonly found in sandy loams as a shrub of mallee scrub communities. Associated species include *Eucalyptus flocktoniana*, *E. aff. loxophleba*, *E. leptocalyx*, *Melaleuca uncinata*, *Dodonaea caespitosa* and *Acacia* spp. Occasionally, e.g. at Peak Charles, *D. ptarmicaefolia* grows in granitic sand at the base of a large granite outcrop amongst *Casuarina* sp. and *Olearia* sp.

D. ptarmicaefolia appears to be a successful coloniser of disturbed sites. It grows near creek and river crossings (e.g. Jackson 1405) and regenerates rapidly from seed after fire (e.g. West 3007-3010, Phillips R., 25.xi.1978).

Flowers are usually present in early winter, i.e. April to June, and capsules are mature in late spring to early summer (October to January).

NOTES:

1. Turczaninow's original spelling of the specific epithet has been retained rather than the commonly used 'ptarmicifolia'. It is believed that Turczaninow named this species because of the similarity of its leaves to those of *Achillea ptarmica* L. (Compositae), which is a common European species with serrate leaves (Clapham et al., 1962 and Keble Martin, 1974). (The genus *Ptarmica* (Tourn.) Neck. is a synonym of *Achillea* L. (Hooker & Jackson, 1895)). Stearn & Smith (1972) included 'Ptarmica' as a separate entry from *Achillea Ptarmica* in the gardener's

dictionary, indicating that this name may have been used as a common or garden name for this species. Assuming Turczaninow meant ptarmica-leaved, then the epithet should be 'ptarmicaefolia' (Stafleu et al., 1978, Rec. 73G.1(b)).

2. The majority of plants in a population at Peak Charles (Haegi 965, George 10619 & West 2913-2919), a Fitzgerald specimen from Cunderdin (NSW108324) and a Gardner collection from Tammin (PERTH) differ from most *D. ptarmicaefolia* material in having broader, shorter leaves and sometimes longer serrations. All other features of these individuals place them in this species.

AFFINITIES:

D. ptarmicaefolia is most closely related to *D. lobulata*, with which it shares a similar fruit shape. The two species can be distinguished by the irregular lobes on the usually narrower leaves of the latter species and its glabrous ovary and larger fruits.

SPECIMENS EXAMINED: selection only (50 collections examined).

WESTERN AUSTRALIA:- Ashby 1930, Tarin Rock, 20km W of Lake Grace, 2.ix.1966. fr. (AD).- George 10619, Peak Charles, 10.iv.1971. m.fl./f.fl. (PERTH).- Haegi 1046, Phillips R. crossing, 15km SW of Ravensthorpe on rd. to Ongerup, 18.ix.1976. fr. (AD).- Jackson 1405, Oldfield R. crossing on Ravensthorpe-Esperance rd., 13.x.1968. fr. (AD, PERTH).- Jefferies 641028, 79ml S of Coolgardie, x.1964. fr. (PERTH).- Kessell 2085, Cocanarup, nr. Ravensthorpe, 9.i.1924. m.fl. (PERTH).- West 2913-2919, Peak Charles, 100km SW of Norseman, 23.xi.1978. fr. (AD).- West 2983a-2988, 17.4km SE of Ravensthorpe on rd. to Hopetoun, 24.xi.1978. fr. (AD).- West 2989-2993, Ravensthorpe Caravan Park, 0.5km N of Ravensthorpe P.O., 24.xi.1978. fr. (AD).- West 3111-3115, 15.2km E of Newdegate, 47.8km W of Lake King township, 28.xi.1978. fr. (AD).

6. *Dodonaea lobulata* F. Muell. in *Linnaea* 23:372 (1853), Pl. indig. Col. Vic. 1:86 (1862); Bentham, *Fl. Aust.* 1:479 (1863); Mueller, *Fragm.* 9:87 & 197 (1875); Brown, *For. Fl. S.Aust.* t.17 (1882); Mueller, *Vic. Nat.* 8:94-95 (1891), p.p. (excl. "Kangaroo Island (J.E. Brown)"); Turner, *Forage Pl. Aust.* 20 (1891); Moore, *Fl. N.S.Wales* 94 (1893); Black, *Fl. S.Aust.* edn 1. 363 (1926); Radlkofer, *Pflanzenreich* IV.165:1380-1381 (1933), p.p. (excl. Queensland); Black, *Fl. S.Aust.* edn 2. 542, fig.697 (1952); Blackall & Grieve, *W.Aust. Wildfls.* 2:323 & 326 (1956); Beard, *W.Aust. Pl.* edn 1. 60 (1965), edn 2. 81 (1970); Willis, *Hdbk. Pl. Vic.* 2:359 (1972) in obs.

TYPE: "In collibus rupestribus virgultosis montium Flinders- et Elders-range." Lectotype (here designated): F. Mueller s.n., Flinders & Elders ranges, x.1851. fr. (MEL84108). Isolectotype: MEL84107.

FIGURES: Brown, *For. Fl. S.Aust.* t.17 (1882); Turner, *Forage Pl. Aust.* 20 (1891); Black, *Fl. S.Aust.* edn 2. 942, fig.697 (1952); Blackall & Grieve, *W.Aust. Wildfls.* 2:323 & 326 (1956).

DESCRIPTION (Fig. 7.7):

Dioecious shrub, 1-3m high, erect, multistemmed. Branches dense, slender and spreading; branchlets angled to slightly ribbed, viscous, with verruculose glands, glabrous or sparsely puberulent. Leaves simple, sessile, linear to linear-oblong, rarely almost pinnatifid, concave or channelled above, convex below, (1.5-)2-3.8(-5.5) x 0.05-0.2(-0.25)cm, coriaceous, thick, viscous, with verruculose glands, or rarely with sessile glands, glabrous to puberulent, base narrow-attenuate, apex obtuse, weakly recurved, midvein conspicuous, lateral venation obscure, margin irregularly 2-10(-12)-lobed in upper 2/3, entire in lower 1/3 of leaf, rarely whole leaf entire, the lobes elliptic to linear-oblong & usually concave above, 1-1.5(-5) x 0.5-1mm, obtuse to rounded. Flowers unisexual,

diadic or triadic, axillary; pedicels (3-)4-5.5(-6.5)mm long, viscous, with verruculose glands, glabrous, rarely sparsely pubescent at the base. Sepals 3-4, ovate, (1.6-)2-2.5(-2.7) x 1.2-1.6mm, acute, viscous, outer surface with verruculose glands, glabrous, inner surface villous, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are valvate & free at the apex only, surrounding the ovary. Stamens in male flowers 6-8, just exceeding or approx. equal in length to the sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, (1.2-)1.8-2.2 x 0.7-0.9mm, glabrous; apical appendage ±absent, or a very small broad, obtuse lobe, 0.5-1mm long, glabrous or pubescent; stamens in female flowers absent. Ovary in female flowers 3(-4)-carpellate, obovoid or ovoid, angled, 1-1.5 x 1-1.5mm, viscous, with resin layer, glabrous; styles 3(-4), connate, sometimes twisted above the middle, (3-)5-7mm long, glabrous, separating unequally at the apex, each free arm 0.1-0.3(-0.5)mm long, recurved; in male flowers rudimentary ovary present. Capsule 3(-4)-winged, in lateral view transversely broad-elliptic to broad-obovate, (10.5-)12-14(-15) x (14-)15-21mm, viscous, sometimes with verruculose glands, glabrous, red to red-brown at maturity, base cordate, apex deeply obcordate, with wings sometimes overlapping; carpel excluding wing depressed-ovate to depressed-oblong, navicular, 5-6.5 x (3.5-)4-5mm, coriaceous; wing 4-6(-7)mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve, coriaceous to membranous; dehiscence septifragal. Seeds 2-4, lenticular to flattened-lenticular, 2.5-3 x 2.6-3mm, black to dark brown, shiny; aril absent. Seedling glabrous or sparsely puberulent; hypocotyl 15-20mm long; cotyledons linear-lanceolate, (14-)18-20 x (1-)1.5-2mm, acute, glabrous; epicotyl (1-)2-2.5mm long; the first 3-5 leaves simple, sessile, linear to linear-oblongate, usually 3-5-lobed near the apex, the lobes obtuse, base narrow-attenuate, otherwise as in mature leaves.

Chromosome number: $n = 14$ (West 936, West 3416, West 3445)

TYPIIFICATION:

Two sheets of the type collection of *D. lobulata* have been examined (MEL84107, MEL84108). Both sheets contain fruiting specimens obviously of the same collection, and both bear labels in Mueller's handwriting. MEL84108 is here chosen as the lectotype because it contains the larger specimens in slightly better condition than the isolectotype MEL84107.

DISTRIBUTION (Fig. 7.7):

D. lobulata is found in arid areas in central and western New South Wales, in the east and south-west of South Australia and in southern Western Australia. In W.A. it is very common around Kalgoorlie and Coolgardie extending almost to Leonora in the north and to Mt. Ragged in the south. A few collections have been made in the Kellerberrin-Bruce Rock area also. Although *D. lobulata* does not occur on the Nullarbor Plain, it is found at Maralinga in the south-west of S.A. from whence its distribution shows a disjunction to the Gawler Ranges and Eyre Peninsula region further east. It is very common throughout the Flinders Ranges and continues eastwards as far as Broken Hill in western N.S.W. Another slight disjunction occurs in the distribution in N.S.W. between Broken Hill and the area around Cobar, where it is found from near Bourke in the north to West Wyalong in the south.

The location of two collections, namely Cranfield s.n., east of Ravensthorpe (PERTH) and Major 15, south of Birksgate Ra. (AD), must be regarded as doubtful and require verification.

ECOLOGY:

D. lobulata grows on rocky slopes, hills and ridges of various rock types including granite, quartzite, laterite and ironstone. It is also found in clay or sandy loams, usually with outcropping rocks or nodules at the surface, e.g. in the goldfields areas of W.A.

It appears that this habitat preference may explain some of the disjunctions in the distribution of this species. For instance, the sand-dune systems west of Lake Everard and north of Ceduna in S.A. and the limestone of the Nullarbor Plain probably form barriers to its continuous distribution in these areas. In eastern S.A. it is found only on rocky hills and ridges and not on any of the intervening shrubland plains. The lack of any rocky outcrops or ranges in western N.S.W. probably explains the disjunction between the Barrier Ranges near Broken Hill and the stony ridges and rocky outcrops of the Cobar area.

D. lobulata is a shrub of arid open woodland or shrubland with associated species varying over its distributional range. In N.S.W. it occurs in *Eucalyptus intertexta* or *E. populnea*, *Acacia aneura* woodlands with *Cassia* spp. and *Eremophila* spp. In the Flinders Ranges of S.A. it may be associated with *Eucalyptus morrisii*, *E. camaldulensis*, *Acacia notabilis*, *Eremophila freelingii*, *E. oppositifolia*, *Triodia irritans* and chenopods such as *Maireana sedifolia* and *Atriplex vesicaria*. In W.A., habitats in which *D. lobulata* occur include *Eucalyptus salmonophloia* and *E. lesouffii* woodlands, and open shrublands dominated by *E. clelandii* and *Maireana sedifolia* with *Ptilotus* sp. and *Bassia* spp. It is also found in mallee shrubland to the south of its distribution (east of Norseman) dominated by *Eucalyptus lesouffii*, *E. dundasii* and *Melaleuca pauperiflora*.

D. lobulata flowers from May to July and mature fruit is usually present from August to December.

PUTATIVE HYBRIDS:

1. *D. microzyga* x *D. lobulata*, see *D. microzyga*.
2. *D. adenophora* x *D. lobulata*, see *D. adenophora*.

NOTES:

1. Apart from the putative hybrids described above, a small number of W.A. specimens (e.g. Maiden NSW126047, Blackall 4064, West 1138-1145) have leaves that are almost pinnatifid with slightly longer lobes than the typical form. These lobes are not incised to the midribs of the leaf and do not appear to be true leaflets. In all other respects these plants belong to *D. lobulata* and are placed in that species.

2. In W.A. *D. lobulata* appears to be a species with a high degree of plasticity. In leaf morphology it intergrades with or forms putative hybrids with *D. adenophora* and commonly with *D. microzyga*, and there is some evidence (two collections only) of intermediates between *D. lobulata* and the latter species in western S.A., where they are also sympatric. In the eastern part of its distribution (i.e. in eastern S.A. and N.S.W) however, *D. lobulata* is very consistent morphologically and is a distinct taxon.

3. In western New South Wales *D. lobulata* has been regarded as an important forage plant for domestic animals (e.g. Turner, 1891). It appears that this grazing maintains the species at a population level so that it, unlike *D. viscosa*, has not become a "weed" problem on the western plains, where overgrazing has disturbed the balance of the associated native species.

Heavy grazing by goats of *D. lobulata* has been observed in the Flinders Ranges and by sheep in such areas as Afghan Rocks, east of Balladonia in W.A.

4. *D. lobulata* appears to be one of the most aromatic of all *Dodonaea* species. Dawson et al. (1966) in an analysis of the acidic constituents of the leaves and branchlets isolated three new diterpenes and a new flavone from *D. lobulata*.

5. Bailey (1899) included *D. lobulata* in the Queensland flora: "Has been obtained at a few inland western localities." No material of this species from Queensland has been seen during this study. Bailey's records were probably misidentifications of another species.

AFFINITIES:

In N.S.W. and S.A. *D. lobulata* is a distinct species and can be readily distinguished on its lobed leaves. However, in W.A. this species shows affinities with *D. microzyga* and *D. ptarmicaefolia*. It can be distinguished from the latter species by the regular, acute serrations of the slightly broader leaves of *D. ptarmicaefolia* which also has a pubescent ovary, and smaller capsules and seeds than *D. lobulata*.

In their typical forms *D. lobulata* and *D. microzyga* var. *acrolobata* are quite distinct. *D. microzyga* has pinnate leaves and solitary flowers, while *D. lobulata* has simple leaves and 2-3(-4) flowers per axil. However, these two species appear to intergrade in some areas in which their distributions overlap and these populations are composed of individuals with intermediate leaf morphology with certain features resembling either one of the two species (see PUTATIVE HYBRIDS under *D. lobulata*).

SPECIMENS EXAMINED: selection only (377 collections examined).

NEW SOUTH WALES:- Corn s.n., Nyngan, ix.1936. fr. (NSW108335).- Crisp 4153, 40km NNW of Cobar, Bundella Stn., 7.ix.1978. fr. (AD,CBG).- Moore 5689, "Tundulya", 25ml SE of Louth, 22.viii.1970. fr. (CANB).- Morris s.n., Broken Hill, i.1920. m.fl. (NSW108340).- Stevens s.n., Doradilla, 25ml N of Byrock, 8.ix.1969. fr. (NSW108329).

SOUTH AUSTRALIA:- Jackson 1818, Flinders Ras., Brachina Gorge, 18km WNW of Oraparinna H.S., 16.ix.1971. fr. (AD).- Jaegermann 177, Gawler Ras., NW side of Unalla Hill, 15km NE of Mt. Ive H.S., 3.x.1972. fr. (AD).- Turner s.n., nr. Maralinga, 7.v.1961. f.fl. (AD96232254).- West 382-385, Bibliando Stn., S side of the Bluff, 21.x.1974. fr. (AD).- West 1421-1424, Flinders Ras., Bunyeroo Ck., 16km N of Wilpena Chalet, 30.v.1976. mature f.fl./mature m.fl. (AD).

WESTERN AUSTRALIA:- Chinnock 1073, 10km S of Menzies, 16.ix.1973. fr. (AD).- George 7396, Pine Hill, NW of Mt. Ragged, 17.i.1966. f.fl./m.fl. (PERTH).- Jefferies 631013, 18ml NW of Coolgardie, x.1963. fr. (PERTH).- West 3441-3445, 3.9km S of Menzies on rd. to Kalgoorlie, 13.xii.1978. fr./m.buds. (AD).

7. *Dodonaea coriacea* (Ewart et Davies) D. McGillivray, *Telopea* 1:66-67 (1975).
D. peduncularis Lindl. var. *coriacea* Ewart et Davies, *Fl. N. Terr.* 175
 (1917) - basionym; Chippendale, *Proc. Linn. Soc. N.S.Wales* 96:246 (1972).
 TYPE: "70 miles N. of Camp IV, G.F. Hill (8/6/1911)". Holotype:
G.F. Hill 390, 70 miles N. of Camp IV, N.T. Survey, 28.vi.1911. fr.
 (MEL84119).

DESCRIPTION (Fig. 7.8):

Polygamo-dioecious shrub, 0.5-1.5m high, spreading. Branches intricate; branchlets angular or terete, light orange, viscous, with verruculose glands, sparsely pubescent. Leaves simple, sessile, oblanceolate to obovate, (1.4-)2-2.5(-3) x (0.4-)0.5-0.7(-0.9)cm, coriaceous, viscous, with verruculose glands, sparsely pubescent or glabrous, base attenuate, margin entire or unevenly serrate, apex truncate, irregularly dentate, midvein prominent, lateral venation obscure. Flowers predominantly bisexual, rarely unisexual (see Notes), in compound inflorescences composed of monads to botryoids, terminating branchlets; pedicels (6.5-)8-10(-11.5)mm long, viscous, with sessile glands, & simple hairs near the base. Sepals 4-5, lanceolate to ovate, (1.6-)1.7-2(-2.4) x (0.5-)0.7-1mm, acute, viscous, both surfaces sparsely pubescent, persistent; at anthesis the sepals in male flowers are spreading, in female & bisexual flowers they are ascending & free, in fruit usually recurved. Stamens in male flowers 4-5, exserted beyond sepals, spreading; filaments 0.4-1mm long, glabrous; anther lobes oblong, 1-1.4 x 0.5-0.7mm, glabrous; apical appendage triangular-acuminate, 0.2mm long, pubescent; stamens in bisexual flowers 4-5, approx. equal in length to the sepals, erect, filaments & anthers as in male flowers, but many are sterile (see Notes); in female flowers rudimentary stamens are sometimes present. Ovary in female & bisexual

flowers 3-carpellate, obovoid, 3-angled, 1-1.4 x 0.9-1.2mm, viscous, pubescent on dorsal face of each carpel; styles 3, connate & twisted in lower part, 1.5-3.5mm long, glabrous, viscous, separating unequally near the apex, each free arm 0.1-0.5mm long, recurved; in male flowers rudimentary ovary sometimes present. Capsule 3-winged, in lateral view transverse-elliptic, (11.5-)12.5-16(-18.5) x (13.5-)14.5-17(-18)mm, membranous, viscous, with sessile glands, sparsely pubescent or glabrous, creamy-yellow at maturity, sometimes tinged with purple, base cordate, apex emarginate to obcordate, wings often overlapping; carpel excluding wing lunate, (4.5-)5.5-7.5 x 3.5-4mm; wing 3.5-5.5mm broad, extending from apex to base of carpel, broadest near the capsule apex, usually broader than the valve, translucent; dehiscence septifragal. Seeds 2-4, lenticular, sometimes compressed towards the margin, 2.4-2.8 x 2-2.3mm, black, shiny; aril absent. Seedling glabrous, with sessile glands; hypocotyl 4mm long; cotyledons linear, 14 x 1.4mm, acute, glabrous epicotyl 3mm long; first 4-8 leaves simple, alternate, sessile, obovate, irregularly lobed, base cuneate to attenuate, margin irregularly toothed or lobed, apex acute, irregularly toothed.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.8):

D. coriacea occurs in eremian northern Australia between latitudes 18° and 24°S. It extends across the continent from the Hamersley Ranges in Western Australia to the Mt. Isa region of western Queensland.

ECOLOGY:

D. coriacea grows in deep red sands and on quartzite and laterite hills in semi-arid areas receiving less than 500mm annual rainfall. It

is commonly a shrub of *Triodia* and *Plectrachne* sandplain grasslands, and is also found in *Eucalyptus gamophylla* and *E. terminalis* woodland associations on quartzite and laterite hills.

Flowering occurs in autumn and winter (March to July), with fruit maturing late July to October. Most bushes flower continuously over a period of 2-3 months, and therefore exhibit a range of developmental stages from buds to almost mature fruit.

NOTES:

Individual plants of this species can produce male or female flowers, and true bisexual flowers as well as "false" bisexual flowers. These "false" bisexual flowers usually contain an apparently well developed ovary and stamens, but are often either male- or female-sterile, and therefore function reproductively as unisexual flowers. These plants are not considered to be polygamous as true male and female unisexual flowers do not occur on the same bush. (See Chapter 4 for further discussion).

AFFINITIES:

D. coriacea is most closely related to *D. peduncularis*, from which it can be distinguished on the smaller, 4-winged capsules and smaller leaves of the latter species. The light orange branchlets with verruculose glands are characteristic of *D. coriacea*. The capsules of this species closely resemble those of *D. filifolia* and several other species of Sect. *Dodonaea*.

SPECIMENS EXAMINED: selection only (93 collections examined).

NORTHERN TERRITORY:- Chippendale 5642, 34.7ml NE of Tanami, 11.iv.1959.

bisex.fl.,fr. (NSW,MEL,PERTH).- Lazarides 5827, 34ml NNE of Barrow

Creek Township, 24.viii.1956. fr. (AD,CANB,NSW,PERTH).- Must 192,

Gibsons Creek, 35ml N of Tennant Creek, 19.vii.1969. bisexual.fl. (AD,CANB,

MEL,NSW).- Parker 234, nr Chilla Well, 29.vii.1970. f.fl.,fr. (AD).

QUEENSLAND:- Farrel 706, Burke Distr., 16km NW of Yelvertoft Stn.,

20.ii.1977. fr. (BRI).- Trapnell & Williams 143, Gregory North Distr.,

68km N of Dajarra, 20.viii.1973. fr. (BRI).

WESTERN AUSTRALIA:- Ashby 4173, 41km from Roebourne turnoff at entrance

to Gorge, 5.viii.1971. bisexual.fl.,fr. (AD).- Beard 4251, Bohemia Downs,

105km SE of Fitzroy Crossing, 28.v.1965. fr. (NSW,PERTH).- George 14638,

McLarty Hills, Great Sandy Desert, 5.viii.1977. fr. (PERTH).- Trudgen 396,

Rhodes Ridge, Hamersley Ra., 10.viii.1973. bisexual.fl.,immat.fr. (PERTH).

8. *Dodonaea procumbens* F. Muell., Definitions of rare or hitherto undescribed Aust. pl. in Trans. Phil. Soc. Vic. 1:8 (1855), published again in Hooker's J. Bot. Kew Gard. Misc. 8:33 (1856), Pl.indig. Col Vic. 1:86-87 (1862); Bentham, Fl. Aust. 1:478 (1863); Mueller, Native Pl. Vic. 1:121 (1879), p.p. (excl. reference to South Australia); Moore, Fl. N.S.Wales 93 (1893); Black, Fl. S. Aust. edn 1. 363 (1926); Ewart, Fl. Vic. 737 (1931); Radlkofer, Pflanzenreich IV.165:1401-1402 (1933); Black, Fl. S.Aust. edn 2. 541 (1952); Burbidge & Gray, Fl. A.C.T. 250 (1970); Willis, Hdbk. Pl. Vic. 2:358 (1972).

TYPE: "In subsaline flats and peaty places at the foot of Mount Sturgeon and Mount Abrupt." Lectotype (here designated): F. Mueller s.n., at the foot of Mount Sturgeon, xi.1853. f.fl.,fr. (MEL84132). Isolectotypes: MEL84133, NSW140601. Probable isolectotypes: MEL84130, MEL84131.

DESCRIPTION (Fig. 7.9):

Dioecious or rarely polygamo-dioecious shrub, prostrate, to 1.5m diam. Branches dense, prostrate, often rooting at the nodes; branchlets angular or flattened, sometimes weakly ribbed, puberulent. Leaves simple, sessile, angular-obovate to oblanceolate, (0.75-)1-2.2(-3) x (0.35-)0.45-0.7(-0.85)cm, light green, coriaceous, viscous, with sessile glands, sparsely puberulent or rarely glabrous, base attenuate, margin thickened, revolute, usually with (1-)2(-4) irregular teeth or lobes up to 2.5mm long and mostly above the middle of the leaf, sometimes entire, apex acute, rarely acuminate, sometimes tri-dentate, midvein prominent, lateral venation usually obscure, sometimes visible below. Flowers unisexual, or rarely bisexual, monadic or diadic, sometimes forming compound inflorescences, terminating branchlets; pedicels 3.5-6(-7.5)mm long, usually longer in male flowers, ribbed, thick, erect, sparsely puberulent. Sepals 4-5(-7), linear-lanceolate, often unequal in size, (2-)2.3-3 x 0.5-0.9mm, acute, viscous, outer surface

glabrous, inner margin pubescent, caducous; at anthesis the sepals in male flowers are recurved, in female flowers they surround the ovary & are free, erect, recurved at the apex & imbricate below the middle. Stamens in male & bisexual flowers 8-10, exceeding the sepals, divergent; filaments 0.7-1.1mm long, glabrous; anther lobes oblong, 2-2.6 x 0.7-0.9mm, glabrous; apical appendage triangular, acute, 0.2-0.3mm long, glabrous; stamens in female flowers absent. Ovary in female & bisexual flowers (3-)4-carpellate, oblong, angled, 1-1.2 x 0.6mm, viscous, usually pubescent near the apex, sometime glabrous; styles (3-)4, connate, twisted, 8-25mm long (including free apical arms), glabrous or sparsely pubescent near the base, separating unequally above the middle, each free arm up to 2.5mm long, divergent; in male flowers rudimentary ovary usually absent. Capsule (3-)4-winged, in lateral view broad-oblong with undulate valves, 11-13 x (8-)9-10.5mm, crustaceous, with sessile glands, glabrous, red-brown at maturity, base cordate to truncate, apex emarginate; carpel excluding wing broad-lunate, undulate, 10.5-12 x 3.5-4.5mm; wing 0.5mm broad, extending from apex to base of carpel, approx. same width for its entire length, much narrower than the valve, crustaceous; dehiscence septifragal. Seeds 2-4, lenticular to lenticular-oblong, 2.5-3(-3.6) x 2.4-2.6(-3)mm, black, dull; aril absent. Seedling glabrous; hypocotyl 3.5-5mm long; cotyledons narrow-linear, 18-24 x 1.5-2mm, acute, glabrous; epicotyl 1-1.5mm long; first 2-4 leaves simple, alternate, petiolate, obovate or spatulate, base attenuate, margin entire, apex acute, irregularly 2-3-toothed.

Chromosome number: not known.

TYPIIFICATION:

Lectotypification was necessary for *D. procumbens* as six sheets of the type collection (MEL (4 sheets), AD and NSW) have been examined, and

there may be more sheets at MEL. Mueller did not nominate any one of these specimens as the type, and so it is necessary to choose a lectotype for this name. Three of the sheets seen (i.e. MEL84132, MEL84133, NSW 140601) bear labels in Mueller's handwriting and are dated '1853'. The other two MEL sheets and the AD one (MEL84130, MEL84131, AD96233019) do not contain Mueller's handwriting and the labels do not include information on the collector or date of collection. However, the specimen(s) on each of these 6 sheets contain both female flowers and fruit and almost certainly are of the one collection. Since the AD and NSW specimens were from Mueller's herbarium he probably had all six sheets available to him at the time of describing this species. Of the three sheets annotated by Mueller, MEL84132 contains the better specimens and is here selected as the lectotype. The three sheets which lack date and collector data are regarded as probable isolectotypes.

DISTRIBUTION (Fig. 7.9):

D. procumbens occurs near Burra in the Mt. Lofty Ranges of South Australia, in south-western Victoria and near Cooma in the Monaro region of south-eastern New South Wales. In Victoria it is mainly found as an undershrub in the Penola-Dergholm area just east of the South Australian-Victorian border and in the Grampians. In the past it has been collected at Castlemain and one isolated record exists from Sale in the Gippsland area.

ECOLOGY:

D. procumbens is a prostrate shrub which grows in open *Eucalyptus camaldulensis* or *E. fasciculosa* woodlands in flat, low-lying areas. Associated species include *Hakea rugosa*, *Melaleuca decussata*, *Astroloma humifusa* and several grasses. The grey sandy or clay loams in which *D. procumbens* grows are sometimes waterlogged during winter.

Flowering takes place in summer, i.e. November to February, and fruit are usually present at this time too. The fruits may take 10-12 months to mature.

NOTES:

The disjunctions in the distribution of *D. procumbens* from the northern Mt. Lofty Ranges to the Grampians area of western Victoria and then to the Monaro region of southern New South Wales probably reflect occurrences of a refugial nature. Other species, such as *Acacia melanoxydon* and *Eucalyptus goniocalyx*, show similar patterns of distribution associated with the isolated disjunct mountains and ranges in south-eastern Australia (Boomsma, 1972 & Specht, Brownell & Hewitt, 1961).

PUTATIVE HYBRIDS:

D. procumbens x *D. viscosa*

Intermediates have been found between these species in two different populations, one in South Australia, south of Burra (West 3596-3606) and the other in south-western Victoria (Beauglehole 38017-38019). *D. procumbens* is present in both of these populations and plants showing intermediate features grade through to a longer, narrow-leaved form of *D. viscosa*. The putative hybrids have linear-lanceolate to oblanceolate leaves, sometimes with sessile glands, puberulent branchlets, flowers in 3-4-flowered botryoids, terminating branchlets, pubescent ovaries and capsules similar to those of *D. procumbens* except that they are more elongate and have a broader wing. These individuals show some characteristics, such as habit and capsule shape and texture, that superficially resemble *D. viscosa* ssp. *cuneata*. However, no plants belonging to that subspecies were located at either site.

Specimens:

SOUTH AUSTRALIA:- Kuchel 2381, Northern Mt. Lofty Ras., N of Manoora, 30km NW of Eudunda, 22.x.1966. f.fl./m.fl./fr. (AD).- West 3595-3600, nr. "Holm Hill", 7.5km N of Manoora, 28.7km SSW of Burra, 15.ii.1980. fr./st./mature m.fl. (AD).

VICTORIA:- Beaglehole 38018 & 38019, 4m ENE of Dergholm P.O., 7.xii.1971. fr. (MEL).

AFFINITIES:

D. procumbens is a very distinct species showing most affinity to *D. humifusa* of Western Australia. The leaves of these two species are similar, they have the same prostrate habit and occupy similar habitats. *D. humifusa* has smaller capsules with lobe-like appendages, broader sepals and arillate seeds. *D. viscosa* ssp. *cuneata* is sometimes confused with *D. procumbens*, but apart from the differences in capsules, inflorescences and flowers, the former taxon does not have toothed oblanceolate leaves.

SPECIMENS EXAMINED: selection only (38 collections examined)

NEW SOUTH WALES:- McKee 7564-7565, Michelago, 6.xi.1960. m.fl./f.fl. (CANB90854, NSW131459).

VICTORIA:- Beaglehole 38017, 4m ENE of Dergholm P.O., 7.xii.1971. fr., f.fl. (MEL).- Beaglehole 30469-30470 & Orchard, Grampians, nr. Victoria Valley Hall, 11.ii.1969. f.fl., fr. (AD97728395, AD97728397, MEL).- R. Hill 1091, Doradong area, 20km E of Penola, 7.x.1962 (AD).- Ingwersen s.n., Billwing Swamp, 40m N of Hamilton, 18.ii.1965. fr. (CBG10257).- Muir 4473-4474, S side of Lake Fyans, 10m SW of Stawell, 29.x.1966. f.fl., fr./m.fl. (MEL).- Phillips s.n., Horsham-Hamilton rd., W of Grampians, 31.x.1960. m.fl. (NSW131460).- West 3534-3540, 8.2km E of Victoria/S. Aust. border, 23.3km E of Penola, 28.xii.1978. fr./m.fl.

(AD).- West 3556-3560, Grampians, at Victoria Valley Hall, 29.xii.1978.
fr./mature m.fl. (AD).- West 3566-3570, W of Grampians, at Red Rock
Creek crossing of Henty Hwy., 30.xii.1978. fr./mature m.fl. (AD).

9. *Dodonaea hirsuta* (Maiden et Betche) Maiden et Betche, Proc. Linn. Soc.

N.S.Wales 38:245 (1913); Radlkofer, Pflanzenreich IV.165:1376-1377 (1933); Mueller, Fragm. 9:87 (1875) in obs. sub *D. peduncularis*: "Varietatem hispidulo-pubescentum, foliis antice profundius fissis, ad flumen Clarence-River reperit Wilcox".

D. peduncularis Lindl. var. *hirsuta* Maiden et Betche, Proc. Linn. Soc.

N.S.Wales 27:57 (1902), basionym; [Radlkofer, Pflanzenreich IV.165:1376 (1933) pro syn.]

TYPE: "Jennings (J.L. Boorman; October, 1901)." Holotype: J.L. Boorman s.n., Jennings, x.1901. fr. (NSW108357). Isotype: W6941.

DESCRIPTION (Fig.7.10):

Dioecious shrub, 0.5-1.5m high, erect, usually single-stemmed. Branches dense, spreading; branchlets terete, densely hirsute. Leaves simple; petiole 0.5-0.8mm long, hirsute; lamina obtriangular or angular-obovate, rarely narrow-angular-obovate & conduplicate, (0.5-)0.4-0.5(-0.6) x (0.25-)0.35-0.45(-0.5)cm, dark green above, paler below, coriaceous, scabrous, rarely with sparse verruculose glands, hirsute, base cuneate, rarely attenuate, margin revolute, entire, apex truncate & 3(-5)-toothed, usually to approx. 1/3 length of the leaf, midvein prominent below, impressed above, lateral venation obscure. Flowers unisexual, (male flowers not available), monadic, axillary; pedicels (4.5-)5-6.5(-7)mm long, hirsute. Sepals (female only) 4, lanceolate, (1.5-)1.8-2.2(-2.6) x 0.7-1mm, acute, outer surface pubescent, inner surface glabrous or with sparse villous hairs at apex only, persistent; at anthesis the sepals in female flowers are free, erect & surrounding the ovary. Stamens in male flowers not seen. Ovary in female flowers 3(-4)-carpellate, +globose, angled, 1-1.3 x 1-1.2mm, densely pubescent; styles 3(-4), connate, twisted in upper half, 8-10mm long, red, glabrous, separating unequally

at the apex, each free arm to 0.2mm long, recurved. Capsule 3(-4)-winged, in lateral view transversely broad-elliptic to orbicular, (11-) 12.5-14(-15.5) x (12-)13.5-15.5(-17)mm, coriaceous, hirsute, orange-brown to deep red at maturity, base cordate, apex obcordate, with wings sometimes overlapping; carpel excluding wing navicular, rarely also lunate, (7-)8.5-10(-12) x (2.5-)4-4.5mm; wing (2.5-)3-4.5mm broad, extending from apex to base of carpel, broadest at the capsule apex, usually narrower than the valve, sometimes equal, coriaceous; dehiscence septifragal. Seeds 2-3, lenticular, usually compressed towards the margin, 2.6-3 x (2.2-)2.4-2.6mm, black, +dull; aril absent. Seedling not seen.

Chromosome number: not known

DISTRIBUTION (Fig.7.10):

D. hirsuta is confined to a small area of south-eastern Queensland and north-eastern New South Wales. The main centre of distribution is on the Great Dividing Range in the Stanthorpe-Wallangarra-Torrington area with an extension further east in N.S.W. to the Copmanhurst region. One collection (Whaite 3511) has been made further south near Nundle (south of Tamworth).

ECOLOGY:

In the Wallangarra-Stanthorpe area *D. hirsuta* grows on granite slopes and hillsides or in granitically derived soils. It is usually a shrub of dry sclerophyll forest or heathlands. Associated species include *Acacia lanigera*, *Leptospermum* sp. and *Callitris* sp.

On the eastern side of the ranges near Copmanhurst *D. hirsuta* is found in heath among sandstone or in sandy soils with *Acacia ruppii*, *A. bauerlinii*, *Daviesia* sp. and *Bossiaea* sp.

D. hirsuta flowers from June to September and mature fruit is usually present in October through to early January.

NOTES:

1. The collections from the Copmanhurst populations have a slightly different leaf shape from those in the Wallangarra area. The former plants have longer leaves, with attenuate bases which are usually almost sessile. They are often conduplicate and sometimes bear sparse verruculose or sessile glands, which are absent from the Wallangarra individuals. Apart from this leaf variation the two forms are very similar and at this stage do not warrant subspecific recognition. Field work in north-eastern N.S.W may help reveal the relationship between these forms and the isolated record further south.

2. Its restricted distribution to a specific habitat type has resulted in *D. hirsuta* being included by Hartley & Leigh (1979) as a rare species which occurs only in small populations, but which is not currently endangered.

AFFINITIES:

D. hirsuta most closely resembles *D. peduncularis* in flower, seed and some capsule characters, but the two species are readily distinguished on leaf shape. The solitary flowers and pubescent indumentum of *D. hirsuta* are distinct.

SPECIMENS EXAMINED: selection only (29 collections examined).

NEW SOUTH WALES:- Blakely & Shiress s.n., Mt. Mullengen, 4ml E of Ramornie, vii.1922. fr. (NSW108361).- Boorman s.n., Wallangarra, vii.1904. mature f.fl. (MEL84129, NSW108358).- Clarke, Pickard & Coveny 1891, 5ml S of Coaldale, 31.vii.1969. f.fl., fr. (BRI, MEL, NSW).- White

3511, foot of Cawney Pass, 4ml SW of Nundle, 25.iv.1973. f.fl. (NSW).-
Wilcox s.n., Clarence R., s.dat. fr. (MEL).- Williams s.n., 5ml N of
Torrington, 17.xii.1966. fr. (NSW108356).

QUEENSLAND:- Bowen 563 nr. Jolly's Falls, parish of Stanthorpe,
30.x.1956. fr. (BRI).- Clemens s.n., base of Mt. Norman via Wallangarra,
8.xi.1944. fr. (BRI230242).- Goebels s.n., Eukey via Stanthorpe, xi.1944.
fr. (BRI239105).- Telford 3113, Mt. Norman, 7km NE of Wallangarra,
25.x.1973. fr. (CBG50082, NSW).

10. *Dodonaea peduncularis* Lindl. in Mitchell, Journ. Exped. Trop. Aust. 361 (1848); Bentham, Fl. Aust. 1:478 (1863); Mueller, Fragm. 9:87 (1875), p.p. (excl. "Varietatem hispidulo-pubescentem, foliis antice profundius fissis, ad flumen Clarence-River reperit Wilcox", see *D. hirsuta*, and "Moreton's Bay (Eaves)"); Moore, Fl. N.S.Wales 94 (1893); Bailey, Fl. Qld. 1:315 (1899), p.p. (excl. "Moreton Bay, S.H. Eaves"); Turner in Proc. Linn. Soc. N.S.Wales 30:57 (1905); Radlkofer, Pflanzenreich IV.165:1376 (1933).

TYPE: leg. Mitchell, at the Depot Camp near Mt. Sowerby, 19.x.1846. Lectotype (here designated): Lieut.-Col. Sir T.L. Mitchell 319, Sub-tropical New Holland, 1846. fr. (CGE). Isolectotype: L908.270-215. Syntypes: Lieut.-Col. Sir T.L. Mitchell 508, Sub-tropical New Holland, Camp 29, viii.1846. immat.fr. (CGE); Lieut.-Col. Sir T.L. Mitchell 509, Sub-tropical New Holland, Camp 29, 27.viii.1846. f.fl. (CGE). Isosyn- type: Mitchell 508, (NSW). Probable isosyn- type: Mitchell s.n., from range bearing SW from Camp 29, 27.viii.1846. f.fl. (BM).

D. pubescens Lindl. in Mitchell, Journ. Exped. Trop. Aust. 342 (1848); [Bentham, Fl. Aust. 1:478 (1863) pro syn.; Bailey, Fl. Qld. 1:315 (1899) pro syn.; Radlkofer, Pflanzenreich IV.165:1376 (1933) pro syn.]

TYPE: Leg. Mitchell, Mt. Pluto area, 6.x.1846. Lectotype (here designated): Lieut.-Col. Sir T.L. Mitchell 357, Sub-tropical New Holland, 20.ix.1846. immat.fr. (CGE). Isolectotypes: CGE, NSW.

DESCRIPTION (Fig. 7.11):

Dioecious shrub, 0.5-1.5(-2)m high, spreading. Branches dense; branchlets biconvex or angular, puberulent. Leaves simple, sessile, erect, rigid, narrow-angular-obovate to oblanceolate, sometimes broad-angular-obovate, usually conduplicate or with concave upper surface,

(0.5-)0.7-1.5(-1.8) x (0.2-)0.25-0.4(-0.45)cm, olive-green, coriaceous, viscous, with sessile glands, glabrous, base attenuate, margin entire, apex usually 3(-4)-toothed, the teeth acute, the central tooth longest & usually recurved, sometimes entire & acute, midvein impressed above, prominent below, lateral venation obscure. Flowers unisexual, in compound inflorescences composed of monads to boryoids, terminating branchlets; pedicels 2.5-7.5(-10)mm long, viscous, glabrous. Sepals 4, lanceolate to ovate, (1.3-)1.5-2(-2.4) x (0.7-1)1-1.2(-1.4)mm, acute or acuminate, viscous, outer surface with sessile glands & glabrous, inner surface villous, persistent; at anthesis the sepals in male flowers are spreading, in female flowers they surround the ovary & are free at the apex only, valvate below. Stamens in male flowers 8, approx. equal in length to the sepals, erect; filaments 0.2(-0.3)mm long, glabrous; anther lobes oblong, 1.8-2 x 0.7-0.8mm, glabrous; apical appendage broad-triangular, thick, 0.2mm long, glabrous; stamens in female flowers absent. Ovary in female flowers 4-carpellate, ovoid, angled, 0.9-1.3 x 0.8-1mm, viscous, glabrous, or rarely pubescent, with resin layer; styles 4, connate, usually straight, sometimes twisted above the middle, excluding free arms (2-)4-7mm long, glabrous, rarely pubescent at base, separating unequally above the middle, each free arm 0.5-2mm long, divergent, usually recurved; in male flowers rudimentary ovary usually present. Capsule 4-winged, in lateral view broad-oblong, (7-)9-11.5(-12.5) x (8-)9.5-12.5 (-18)mm, membranous, glabrous, dark red to brown at maturity, base cordate, apex obcordate, wings often overlapping; carpel excluding wing lunate and navicular, 4.5-6.5 x 2-3mm; wing 2-3.5mm broad, extending from apex to base of carpel, broadest near the capsule apex, usually broader than the valve; dehiscence septifragal. Seeds 1-2, lenticular, compressed towards the margin, wrinkled, 1.8-2.3 x 1.6-1.9mm, dark brown to black, dull; aril absent. Seedling not seen.

Chromosome number: not known.

TYPIIFICATION:

It was necessary to designate a lectotype for *D. peduncularis* as several syntypes have been seen and Lindley did not nominate any one of them as the type. None of the 6 sheets of Mitchell specimens examined contain information on locality or date which exactly corresponds to that in Mitchell's Journal. The 3 specimens held at CGE were in the Lindley herbarium and bear labels with his handwriting. He would certainly have used these specimens when originally describing this species. Mitchell 319, contains mature capsules and leaves which correspond best with the protologue and it is here selected as the lectotype. The BM specimen is regarded as a probable isosyntype as, although it was collected on the same date as Mitchell 509 and also bears female flowers, it does not contain a number.

The CGE Mitchell 357 sheet, which was in the Lindley herbarium has been chosen as the lectotype of *D. pubescens* although the date does not correspond with those in Mitchell's Journal. This sheet bears Lindley's handwriting and closely agrees with the protologue.

DISTRIBUTION (Fig. 7.11):

D. peduncularis is widespread on the western slopes of the Great Dividing Range in New South Wales and southern Queensland. It extends from the Griffith area in southern N.S.W to Coonabarabran and Warialda in the north, then through the Darling Downs and Leichhardt districts of Queensland as far as Jericho in the north and Charleville to the west.

ECOLOGY:

D. peduncularis is a shrub of semi-arid, undulating or flat country and is usually on sandy soils or sandstone hills. In N.S.W. it is found in mallee broombush associations (e.g., near Griffith) and commonly in open forests dominated by *Eucalyptus fibrosa*, *E. beyeri*, *E. crebra*, *E. dwyeri* and *E. trachyphloia*. Associated shrub species include *Acacia gladiiformis*, *Grevillea floribunda* and *Casuarina* sp. In Queensland *D. peduncularis* occurs in *Eucalyptus populnea*-*Callitris* woodlands, in *Eucalyptus terminalis*-*Acacia shirleyi* woodlands and in open *Eucalyptus peltata* forest. In the western parts of its distribution it grows in *Triodia* sp. hummock grasslands with mixed shrubs such as *Grevillea juncea*, *Acacia leptostachya* and *Calytrix longiflora*.

D. peduncularis flowers in winter and spring (June to September) and capsules are mature in early summer (i.e. October to December).

NOTES:

Two Queensland collections (Carroll 875-876 (CBG) and Althofer NSW141109) differ from most other specimens in having emarginate leaves with visible lateral venation and very flattened capsules lacking a definite wing. They have thick, shorter pedicels and seeds which are not wrinkled or compressed towards the margin. However, the pubescent branchlets, glabrous leaves and inflorescence structure place them in this species.

AFFINITIES:

D. peduncularis resembles *D. viscosa* ssp. *cuneata* in fruit and some leaf characters, but the two taxa are readily distinguished on the glabrous branchlets, more complex inflorescence and broader, flat leaves of *D. viscosa* ssp. *cuneata*.

D. triangularis has been confused with *D. peduncularis*, especially in sterile condition. However, the leaves of the latter species are narrower and conduplicate or concave, rigid and always glabrous. The two species differ greatly in flower and fruit characters.

SPECIMENS EXAMINED: selection only (176 collections examined)

NEW SOUTH WALES:- Boorman s.n., Dubbo, viii.1908. m.fl. (NSW141103).- G. Cunningham & Milthorpe 439, Shepherd's Hill, 16.ix.1972. f.fl. (NSW).- Johnson & Constable s.n., Etoo Ck., NE of Kenebri, 5.xi.1954. fr. (NSW 30375).- Phillips s.n., 26ml from Lake Cargellico towards Mt. Hope, 13.ix.1966. m.fl. (CBG23424,AD97011176).- Sikkes 433 & Telford, 22km S of Mt. Hope, 30.x.1972. fr. (CBG).

QUEENSLAND:- Boorman s.n., Beta, vi.1913. fr. (NSW141110).- Lazarides & Story 31, Leichhardt distr., 17ml WSW of Rolleston township, 1.ix.1961. fr. (AD,BRI,CANB,PERTH).- Olsen & Byrnes 3557-3558, Leichhardt distr., Gap Creek, 25.v.1977. f.fl./m.fl. (BRI).- K.A. Williams 75065, Darling Downs, 19km S of Gurulmundi, 1.x.1975. fr. (BRI).- K.A. Williams 77097, Leichhardt distr., Injune-Rolleston rd., 4.8km N of third crossing of Dawson R., 5.viii.1977. m.fl. (BRI).

11. *Dodonaea camfieldii* Maiden et Betche, Proc. Linn. Soc. N.S.Wales 22(1):150 (1897); Maiden, Illustr. of N.S.Wales Pl. 2:35-36, t.12 (1908); Radlkofer, Pflanzenreich IV.165:1374 (1933); Beadle et al., Fl. Syd. Reg. 387 (1972).
 TYPE: "Waterfall Creek, Nowra, N.S.W., W. Bäuerlen, November, 1888); about midway between Como and Sutherland, near Sydney, (J.H. Camfield, May, 1897)." Lectotype (here designated): W. Bauerlen s.n., Waterfall Creek, Nowra, xi.1888. fr. (NSW140461). Syntype: J.H. Camfield s.n., between Como and Sutherland, v.1897. mature f.fl. (NSW140462).

FIGURES: Maiden, Illustr. of N.S.Wales Pl. t.12 (1908); Martin, Aust. J. Bot. Suppl. 6:18, fig.76 (1973) - pollen only.

DESCRIPTION (Fig. 7.12):

Dioecious or rarely polygamo-dioecious shrub, 0.2-0.5(-1)m high, spreading. Branches winged, spreading, often prostrate & rooting at the nodes; branchlets ascending, winged, sometimes ribbed, pubescent. Leaves simple, sessile, linear to oblong, (1-)1.5-2.6(-3.5) x (0.2-)0.25-0.5(-0.8)cm, coriaceous, viscous, with sessile glands, glabrous or sparsely pubescent on midrib only, base decurrent, the margin & midrib extending into wings on the stem, margin revolute, undulate, entire or sometimes irregularly dentate with teeth up to 5mm long, apex acute, midvein prominent, lateral venation obscure. Flowers unisexual or rarely bisexual, in compound inflorescences composed of monads & diads, terminating branchlets; pedicels 2-4mm long, viscous, pubescent or sometimes glabrous above the middle. Sepals 4(-5), (2-)2.5-3 x 1-2mm, viscous, glabrous, or outer surface sparsely pubescent, inner surface villous near the apex, caducous, in male & bisexual flowers oblong, acute, in female flowers ovate, acuminate; at anthesis the sepals in male flowers are strongly recurved, in female & bisexual flowers they are free, erect, recurved at the apex,

imbricate near the base, surrounding the ovary. Stamens in male & bisexual flowers 8(-10), approx. equal in length to sepals, divergent; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 1.6-2 x 0.6-0.8mm, glabrous; apical appendage broad-triangular, 0.2-0.3mm long, pubescent; stamens in female flowers absent. Ovary in female & bisexual flowers 4-carpellate, oblong, 1-1.3 x 0.8-1mm, viscous, pubescent; styles 4, connate, twisted in upper half, 7.5-15mm long (including free apical arms), pubescent near the base, separating very unequally above the middle, each free arm 1.5-3(-5)mm long, divergent; in male flowers rudimentary ovary present. Capsule 4-winged, in lateral view broad-oblong, 10-14(-15.5) x 9-12(-16)mm, coriaceous, with sessile glands, glabrous or sparsely pubescent, brown or purplish at maturity, base cordate or rounded, apex cleft to obcordate; carpel excluding wing navicular, transverse-oblong, 8-11 x 3-4.5(-5)mm; wing 1-2.5(-3)mm broad, extending from apex to base of carpel, usually broadest at the capsule apex, narrower than the valve; dehiscence septifragal. Seeds 0-2, lenticular, compressed towards the margin, 2.5-2.7 x 2.4-2.6mm, dark brown or black, dull; aril absent. Seedling not seen.

Chromosome number: not known.

TYPIFICATION:

It was necessary to choose a lectotype for the name *D. camfieldii* Maiden et Betche as two collections were cited with the protologue. NSW holds a specimen collected by Bäuerlen and another by Camfield, both of which contain labels bearing the information as in the type citation. The Bäuerlen specimen (NSW140461) is here chosen as the lectotype as it contains capsules and agrees more closely with the protologue than the old female flowers of the NSW140462 Camfield specimen.

DISTRIBUTION (Fig. 7.12):

D. camfieldii is confined to the central coast region of New South Wales. Its range extends from the Hawkesbury River region in the north to the Jervis Bay/Nowra area in the south.

ECOLOGY:

This low, spreading or prostrate shrub grows on the Hawkesbury sandstones usually in dry sclerophyll forest or woodland. It is often found on exposed rocky sites growing in small pockets of soil in both heath and forest communities.

D. camfieldii has been observed colonising disturbed roadsides and forming dense soil-binding, multistemmed mats.

Flowering usually occurs in the summer months of November to February. Mature fruit are present in October and November.

AFFINITIES:

D. camfieldii is a very distinct species. It is the only member of the genus with decurrent leaf bases and the undulate, revolute, linear leaves are also characteristic. The capsules of this species resemble those of *D. procumbens*, from which it can be distinguished on leaf shape and texture, and the lenticular, laterally compressed seeds of *D. camfieldii*.

SPECIMENS EXAMINED: selection only (38 collections examined).

NEW SOUTH WALES:- Blakely & Shiress s.n., Wondabyne, Hawkesbury R., 15.x.1922. fr. (NSW140472).- Boorman s.n., Gosford, i.1903. f.fl. (NSW 140466).- Boorman s.n., Gosford, x.1907. fr. (NSW140465).- Camfield s.n., near Como, x.1897. fr. (NSW140475).- Cleland s.n., Hawkesbury R., 3.xi. 1916. m.fl./f.fl. (AD96232219).- Constable s.n., Point Perpendicular,

Jervis Bay, 6.x.1960. fr. (NSW52719).- Maiden s.n., Cataract Dam,
xi.1906. m.fl. (NSW140459).- Rodway 1465, between Currajong and Drum
and Drumsticks, Jervis Bay, xii.1924. m.fl. (NSW140460).- West 2571-
2578, 30km SW of Nowra on Nowra-Braidwood rd., 30.iv.1978. fr. (AD).

12. *Dodonaea intricata* West, sp. nov.

Species nova Sect. *Dodonaeae*, *D. viscosae* Jacq. ssp. *cuneatae* (Sm.)
West foliis truncatis, capsulisque similaribus affinis, sed differt
floribus in axillis solitariis vel raro duobus, glandibus verruculosis,
indumentio puberulo, foliis angustioribus oblongis crassis apicibus
truncato-emarginatis.

TYPE: Holotype: J.G. West 2155, South Australia, Eyre Peninsula, Gawler Ranges, Barber Hill, 7km SE of Hiltaba H.S., 32°12'S 135°07'E, 30.vii. 1977. fr. (AD98008410). Isotypes: to be distributed.

The specific epithet refers to the habit of the plant.

DESCRIPTION (Fig. 7.13, 7.14 & 7.70):

Dioecious shrub, 0.2-1m high, spreading. Branches intricate, spreading; branchlets angular, viscous, with verruculose glands, puberulent. Leaves simple; petiole 1-2.5(-3.5)mm long, with brown verruculose glands, glabrous or puberulent; lamina oblong, rarely oblanceolate or narrow-elliptic, (0.7-)0.9-1.2(-1.7) x (0.25-)0.3-0.5(-0.55)cm, olive-green, coriaceous, thick, viscous, with brown verruculose glands, glabrous to puberulent, base attenuate to cuneate, tapering to the petiole, margin thickened, entire, unevenly sinuate or with very small regular teeth or lobes, apex usually truncate-emarginate, sometimes obtuse or irregularly (2-)3-toothed, midvein prominent, lateral venation obscure. Flowers unisexual, monadic or rarely diadic, axillary; pedicels 2.5-5mm long, viscous, with verruculose glands, usually sparsely puberulent. Sepals 4, ovate to broad-oblong, 1.5-2.5 x 1-1.5mm, shorter in female flowers, acute, viscous, outer surface with verruculose glands, glabrous or sparsely pubescent, inner surface villous, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are free, erect & surrounding the ovary. Stamens in male flowers 8, approx. same length as the sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes

oblong, 2.1-2.3 x 0.7-0.8mm, glabrous; apical appendage triangular-acuminate, to 0.3mm long, pubescent; stamens in female flowers absent. Ovary in female flowers 4-carpellate, obovoid, angled, 1.1-1.4 x 1mm, viscous, with resin layer; styles 4, connate, twisted in upper part, 5.7-6.5mm long, glabrous, separating at the apex, each free arm to 0.2mm long; in male flowers rudimentary ovary present. Capsule 4-winged, in lateral view broad- to transverse-elliptic, (10-)10.5-13 x (9-)11-14mm, membranous, viscous, with sparse verruculose glands on carpel, usually glabrous, sometimes sparsely pubescent, purple-red at maturity, base cordate, usually with wings overlapping, apex obcordate, with wings overlapping; carpel excluding wing depressed-ovate, navicular, 5-6.5 x (2-)2.5-3.5mm; wing 2-4mm broad, extending from apex to base of carpel, usually broadest at the apex, sometimes the same width for entire length; dehiscence septifragal. Seeds not seen. Seedling not seen.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.13):

D. intricata is restricted to the Gawler Ranges of Upper Eyre Peninsula in South Australia.

ECOLOGY:

This species grows on the granite hilltops and slopes and rocky outcrops in the Gawler Ranges. It is a low spreading, intricate shrub and grows in association with *Melaleuca uncinata*, *M. raphiophylla* and *M. lanceolata*, and smaller shrubs such as *Grevillea aspera*, *Halgania cyanea*, *Spyridium parvifolium* and *Triodia irritans*.

D. intricata flowers at the end of summer (February to March) and mature capsules are present in spring.

AFFINITIES:

D. intricata is most closely related to *D. viscosa* ssp. *cuneata* from which it differs by having solitary flowers (or rarely two together), narrower, oblong, thicker leaves usually with a truncate-emarginate apex. *D. intricata* has verruculose glands and a puberulent indumentum, while *D. viscosa* ssp. *cuneata* has sessile glands and is glabrous.

In leaf shape *D. baueri* shows some similarity to *D. intricata*. Besides the clearly distinguishable fruits these two species can be differentiated on the sessile glands, and the obovate, broader, truncate or rounded leaves of *D. baueri*.

SPECIMENS EXAMINED: selection only (47 collections examined).

SOUTH AUSTRALIA:- Barker 3582, 10.5km by rd. NNE of Peterby Tank on Minnipa-Yardea rd., 24.ix.1978. fr. (AD).- Donner 3256, Mount Ive, 2i.ix.1969 fr. (AD).- Lang 1234a & b, 0.7km along turnoff to Corrobinnie Hill from Stock Route, 16.ii.1978. m.fl./f.fl. (AD).- Orchard 1791, 40km N of Minnipa on rd. to Yardea, 27.x.1968. fr. (AD).- Rohrlach 253, Buckleboo Stn., 50km NW of Kimba, 14.iii.1959. f.fl. (AD,BM,G,K).- West 2151-2161, Barber Hill, 7km SE of Hitaba H.S., 30.viii.1977. mature m.fl./fr. (AD).- West 2178-2184, Scrubby Peak, 40km NNE of Minnipa, 30.viii.1977. mature m.fl./immat.fr./fr. (AD).- West 2201-2205, 11.3km E of Nonning H.S. and 3km SW of Miccollo Hill on Nonning-Iron Knob rd., 30.viii.1977. mature f.fl./st. (AD).- Wilson 510-512, Yandinga Falls, 1km W of Minnipa-Yardea rd., 16.x.1958. fr. (AD,IA,K).

13. *Dodonaea serratifolia* D. McGillivray, *Telopea* 1:66 (1975).

TYPE: "NEW SOUTH WALES: Grassy Creek, Gibraltar Range National Park, R. Paine NSW121560, 13.xii.1966." Holotype: R. Paine s.n., Grassy Creek, Gibraltar Range N.P., 13.xii.1966. fr. (NSW121560).

DESCRIPTION (Fig. 7.15):

Polygamo-dioecious shrub, to 1.5m high, erect. Branches erect; branchlets angular to flattened, glabrous. Leaves simple; petiole (1-) 1.5-2(-2.5)mm long, thick, glabrous; lamina narrow-elliptic, (3.5-)4.5-6(-7.2) x (0.65-)0.8-1.05(-1.2)cm, dark green above, paler below, thick, dull, coriaceous, glabrous, base attenuate, margin irregularly serrulate, apex acute or obtuse, midvein prominent, lateral venation obscure. Flowers unisexual & bisexual, (female flowers at anthesis not available), in 3-6-flowered botryoids, terminating branchlets; pedicels 2-2.5mm long, viscous. Sepals 4, ovate, 2-2.3 x 1.2-1.5mm, acute, viscous, outer surface glabrous, inner margin pubescent, inner surface glabrous, caducous; at anthesis the sepals in male & bisexual flowers are spreading. Stamens in male & bisexual flowers 6-8, just exceeding the sepals, spreading; filaments 0.5-1mm long, glabrous; anther lobes oblong, 1.8-2.2 x 0.7-0.8mm, glabrous; apical appendage acuminate, incurved, 0.3-0.4mm long, glabrous. Ovary in bisexual flowers 3(-4)-carpellate, oblong to narrow-elliptic, angled, 0.6-0.7 x 0.6-0.8mm, with sessile glands, glabrous; styles 3(-4), connate, straight, 1.5-2.5(-3.4)mm long, glabrous, separating at the apex, each free arm 0.1(-0.2)mm long. Capsule 3(-4)-winged, in lateral view broad-elliptic or broad-obovate, 14-15.5(-17) x 13-15mm, membranous, with sparse sessile glands, glabrous, base cordate, apex obcordate; carpel excluding wing transverse-oblong, navicular, slightly depressed in centre of dorsal face, 10-12 x 3.5-4mm; wing 4-5mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve,

membranous, dehiscence septifragal. Seeds 2-4, lenticular-globose, 2.3-2.4 x 2-2.1mm, dark brown to black, shiny, with hyaline membrane lifting at the margin; aril absent. Seedling not seen.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.15):

D. serratifolia is confined to a small number of populations in a restricted area of the northern tablelands of New South Wales east of Glen Innes.

ECOLOGY:

D. serratifolia grows on granite or granitic soils in dry sclerophyll forest. It has been found associated with *Eucalyptus andrewsii*, *Acacia falciformis*, *A. floribunda* and *Leucopogon lanceolatus*.

Flowering occurs in October and fruit develop slowly to reach maturity at the time of the following year's flowering.

NOTES:

This species appears to be strongly polygamo-dioecious. All specimens examined during this study which contain male flowers also contain a large number of bisexual flowers. Some of these flowers may be female sterile, but it seems that the majority are true bisexual flowers. No female flowers at anthesis have been seen, but the type specimen (Paine NSW121560) contains a number of fruit with mature seed and old female flowers with no evidence of anthers. The fruit have probably developed from the previous season's female flowers and not bisexual ones. (See Chapter 4 for further discussion.) Field work is needed before any definite conclusions can be made on the breeding system of this species.

AFFINITIES:

D. serratifolia most closely resembles *D. viscosa* in flower and fruit characters, but the serrulate leaves of *D. serratifolia* are very distinctive. The dull appearance and lack of obvious sessile glands on the leaves and the hyaline membrane lifting at the margin of the seeds resemble *D. amblyophylla* and *D. bursariifolia*.

SPECIMENS EXAMINED:

NEW SOUTH WALES:- Coveny 5702 & Lander, Gibraltar Ra. N.P., 3.x.1974. m.fl.,bisex.fl. (BRI,CANB,NSW).- J.B. Williams 646, Gibraltar State Forest, 38ml E of Glen Innes, 5.x.1958. m.fl.,bisex.fl. (NSW).- J.B. William s.n., Henry R., nr. Mt. Slow (SE of Glen Innes), 21.x.1966. m.fl.,bisex.fl. (NSW121586).

14. *Dodonaea triquetra* Wendl., Bot. Beobacht. 44 (1798); Andrews, Bot. Reposit. 4, t.230 (1802), p.p. (excl. ref. to specimens from New Zealand, America and Asia - see *D. viscosa*); Smith in Rees, Cyclop. 12 n.4. (1809); Link, Enum. Hort. Berol. 1:381 (1821); DC., Prodr. 1:617 (1824); Loudon, Hort. Brit. 154 (1830); G. Don, Gen. hist. 1:674 (1831); A. Gray, U.S. Expl. Exped., Phan. 262 (1854), p.p. (excl. ref. to plants from Fiji); Mueller, Fragm. 1:73-74 (1859); Mueller, Pl. indig. Col. Vic. 1:86,87 in obs., Addit. 226 (1862); Bentham, Fl. Aust. 1:474-475 (1863); Mueller, Fragm. 9:88 (1875), Native Pl. Vic. 1:121 (1879); Woolls, Contrib. Fl. Aust. 133 (1867), Pl. indig. & natur. Neighbour. Syd. 16 (1891); Moore, Fl. N.S.Wales 94 (1893); Bailey, Fl. Qld. 1:313 (1899); Hamilton, J. R. Soc. N.S.Wales 51:348-349 (1917); Domin, Biblioth. Bot. 22(89⁴):910 (1927); Ewart, Fl. Vic. 737 (1931); Radlkofer, Pflanzenreich IV.165:1358-1360 (1933); Beadle et al., Fl. Syd. Reg. 386 (1972); Willis, Hdbk. Pl. Vic. 2:357 (1972).
 TYPE: "Australien". Lectotype (here designated): Wendland s.n., in Herb. Willdenow, habitat in Nova Hollandia, s.dat. m.fl. (B), photograph only seen.

D. laurina Sieb. ex Spreng. in Linnaeus, Syst. Veg. edn 16. 4(2) Cuvae posteriores 152 (1827); G. Don, Gen. hist. 1:674 (1831); Stuedel, Nom. bot. 522 (1840); Schldl., Linnaea 17:640 (1843); [Bentham, Fl. Aust. 1:475 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1358 (1933) pro syn.]
 TYPE: "Nov. Holl." Syntypes: Sieber 272, Fl. Novae Holl., 1825. mature f.fl./immat.fr. (BM,G,L,MEL,P,W (2 sheets)).

D. laurifolia Sieb. ex Loudon, Hort. Brit. 154 (1830); [Radlkofer, Pflanzenreich IV.165:1359 (1933) pro syn.]
 TYPE: "N. Holl." (cult.), n.v.

D. longipes G. Don, Gen. hist. 1:674 (1831); [Bentham, Fl. Aust. 1:475 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1359 (1933) pro syn.]
 TYPE: "Native of New Holland ... v.s. herb. Lamb.", n.v.

D. dioica DC. in Mém. Soc. Phys. Hist. Nat. Genève 1:445-9 (1822), Prodr. 1:617 (1824); G. Don, Gen. hist. 1:674 (1831).

TYPE: Syntype: Lambert s.n., s.loc., 1861. m.fl. (G-DC).

D. heterophylla Hort., Dum. Cours., Bot. Cult. edn 2. 6:233 (1811), nom. nud.; [DC., Prodr. 1:617 (1824) pro syn. sub *D. dioica*]; Colla, Hortus ripul. App 2. 347 (1826); G. Don, Gen. hist. 1:674 (1831); Bentham, Fl. Aust. 1:474 (1863), sp. ign.; [Radlkofer, Pflanzenreich IV.165:1358 (1933) pro syn.]

D. cestroides Sieb. ex Schldl., Linnaea 17:640 (1843), nom. nud.; [Radlkofer, Pflanzenreich IV.165:1358 (1933) pro syn.] - based on Sieber 271 (BM,G,L,MEL,W (3 sheets)).

FIGURE: Andrews, Bot. Reposit. 4, t.230 (1802).

DESCRIPTION (Fig. 7.16):

Dioecious or rarely polygamo-dioecious shrub, 1-3m high, erect. Branches erect, often slender, spreading; branchlets angular to flattened, glabrous. Leaves simple; petiole (2-)3-4.5(-7)mm long, glabrous; lamina narrow- to broad-elliptic, sometimes lanceolate or ovate, (4.5-)6.5-9.5 (-12) x (1-)2-4(-4.7)cm, bright green above, paler below, coriaceous, thin, glabrous, base narrow-cuneate to attenuate, margin entire or sinuate, apex long-acuminate to acute, midvein prominent, lateral venation conspicuous. Flowers unisexual or rarely bisexual, in panicles composed of monads to metabotryoids, terminating branchlets; pedicels (4.3-)6-8.5(-15)mm long, glabrous. Sepals 4(5), broad-triangular, 0.6-1.1 x 0.4-0.7(-1)mm, acute, viscous, glabrous, caducous early; at anthesis the sepals in male & bisexual flowers are recurved, in female flowers they are free & erect at base of ovary, shorter than the ovary. Stamens in male & bisexual flowers 8(10), much exceeding the sepals, divergent; filaments 1-1.5mm long, glabrous; anther lobes linear, twisted at anthesis, 3.5-4 x 0.6-0.8mm, glabrous;

apical appendage triangular-acuminate, to 0.2mm long, glabrous; stamens in female flowers absent. Ovary in female & bisexual flowers 3-carpellate, ovoid, angled, 0.9-1.5 x 0.8-1.2mm, viscous, glabrous; styles 3, connate, twisted in upper part, (4.5-)6-13mm long, glabrous, separating unequally at the apex, each free arm 0.5-2mm long, divergent; in male flowers rudimentary ovary usually present. Capsule 3-winged, in lateral view broad-obovate or broad-oblong, (9.5-)11-14(-16) x (10-)11-14.5(-15)mm, glabrous, carpels brown or purple and wings yellow to light brown at maturity, base cordate, apex obcordate; carpel excluding wing transverse-ovate & navicular, (7.5-)9-11 x (2.5-)3-4mm, coriaceous; wing (2-)2.5-5mm broad, extending from apex to base of carpel, broadest at the capsule apex, usually broader than the valve, membranous; dehiscence septifragal. Seeds 2-3, lenticular, 2.5-2.7 x 2.1-2.3mm, black, shiny, usually with hyaline membrane lifting at the margin; aril absent. Seedling sparsely pubescent on stem, leaves glabrous; cotyledons not seen; first 8-10 leaves simple, alternate, petiolate, broad-elliptic or obovate, the lower leaves usually with 2 elliptic, obtuse, deeply divided lobes near the base, upper leaves irregularly obtusely lobed, apex obtuse.

Chromosome number: n = 14 (West 822)

TYPIFICATION:

J.C. Wendland, the author of *D. triquetra*, was a German horticulturalist (Stafleu, 1967) who worked in the Royal Gardens at Herrenhausen near Hannover. *D. triquetra* was widely cultivated in Europe by the time it was first described and it is likely that Wendland used horticultural material when drawing up the protologue for this taxon. Radlkofer (1933) implied that Wendland based this species on cultivated material from Hort. Herrenhausen, and that the specimen (n. 7318) in Herb. Willdenow, which he saw,

originated from the same source - "cult. in Ht. Herrenhausen; vidi specim. in Hb. Willd. n. 7318". A photograph of this male-flowering specimen in the Willdenow herbarium (held at B), which was examined by Radlkofer, has been made available to me. The sheet bears Wendland's signature and almost certainly was available to him when he described *D. triquetra*. Wagenitz (1972) stated that many types of J.C. Wendland are contained in the herbarium of the former Royal Gardens at Herrenhausen, which was given to GOET in 1969. It has not been possible to this time to determine whether GOET holds a Wendland specimen of *D. triquetra*. Given that Radlkofer saw only the specimen in Willdenow's herbarium and that types of other Wendland species have not been found at GOET (Tölken, 1977 p. 503) the specimen in Willdenow's herbarium, which agrees with the protologue is here selected as the lectotype. Further attempts will be made to ascertain the location of any other Wendland specimens from that period.

A lectotype has not been selected from among the syntypes of the synonymous name *D. laurina* because Sieber's collections were distributed widely among herbaria (Burdet, 1978) and duplicates of Sieber no. 272 from PR, in which Sieber's main collection is housed (Holmgren and Keuken, 1974), have not been examined.

G. Don described *D. longipes* from material in the Lambert herbarium. No specimens of *D. triquetra* belonging to this herbarium have been located during this study (see *D. filiformis* typification for details).

DISTRIBUTION (Fig. 7.16):

D. triquetra grows on the east coast of Australia extending from Bundaberg in south-east Queensland down the New South Wales coast and into eastern Victoria as far as Orbost. It is mainly confined to the coastal plain, but it is found on the eastern side of the Great Dividing Range in the Blue Mountains and Barrington areas in N.S.W. and in the Macpherson Ranges and Tenterfield area on the Queensland/N.S.W. border.

ECOLOGY:

This species is a shrub of dry and wet sclerophyll forests on sand or sandstone or sometimes on shale. Associated species vary over the distributional range of *D. triquetra*. On the south coast of N.S.W. it grows in forest dominated by *Eucalyptus maculata* or with *E. globoidea* and *Angophora costata*, while in the central coastal region it is common with *Eucalyptus gummifera* and *E. eugenioides*, *E. fibrosa*, *E. pilularis*, *E. intermedia* and *Melaleuca nodosa*. In Queensland *D. triquetra* more often grows in open eucalypt forests in sandy soils, with such trees as *Eucalyptus signata* and *Tristania conferta*.

Flowers of *D. triquetra* are at anthesis in summer (January to early April) and capsules reach maturity by the following spring or early summer (September to January).

Floyd (1976) included *D. triquetra* in studies on the effect of burning on regeneration from seeds in wet sclerophyll forest. He classified this species as a fire weed due to its high germination following a hot fire. In laboratory studies maximum germination (100%) occurred following pre-treatment at the optimum temperature of 90°C for 10-50 minutes. In field observations Floyd (1966) found that *D. triquetra* seeds can emerge from a maximum depth of approx. 5cm. Thus, a hot fire with increased soil temperatures penetrating to greater depths in the soil profile, could result in germination of a large proportion of the soil reservoir of stored seed which may be the product of several years successful fruiting. Following a hot burn and consequent high germination percentage *D. triquetra* is likely to become a dominant species of the regenerating wet sclerophyll forest understorey.

PUTATIVE HYBRIDS:

D. triquetra x ?*D. boroniaefolia*

One collection from Port Stephens (Constable NSW45245) appears to be an intermediate between *D. triquetra* and a pinnate-leaved species, probably *D. boroniaefolia*. The capsule and inflorescence structure are typical of *D. triquetra*, but the leaves vary from being simple and oblanceolate to imparipinnate with 2-3 pairs of opposite, lanceolate, sinuate lateral leaflets and a much larger, elliptic terminal leaflet. Some branchlets are glabrous, while others have arched hairs characteristic of *D. boroniaefolia*. The seeds are small, lenticular and compressed towards the margin.

Specimens:

NEW SOUTH WALES:- Constable s.n., Tahlee, Port Stephens, 24.x.1956. fr. (NSW45245, AD97236253).

AFFINITIES:

D. triquetra is most closely related to *D. lanceolata* var. *sessilifolia*, with which it shares a similar capsule shape, seeds with the hyaline membrane lifting at the margin and similar leaf shape and texture. The two taxa can be distinguished by the terminal inflorescences of bisexual flowers, the larger sepals and smaller anthers of *D. lanceolata* var. *sessilifolia*. *D. triquetra* leaves have a definite petiole usually greater than 2mm long and the capsule wings are membranous and not coriaceous.

SPECIMENS EXAMINED: selection only (324 collections examined).

NEW SOUTH WALES:- Canning 763A, Yadboro S.F., 24.i.1968. m.fl. (CBG).- Constable s.n., Bodalla S.F., NW of Narooma, x.1957. fr. (NSW43104).- Jacobs 704, Berowra Ck., nr. Crosslands junction of Calma Ck. and Berowra Ck., 11.iii.1974. f.fl. (NSW).- Salasoo 2166, Buxton, 21.x.1961. fr.

(NSW).- Webb & Tracey s.n., Whian Whian S.F., 20ml N of Lismore, vii.1956.
fr. (BRI85156A).- West 821-825, 0.4km E of turnoff to Bermagui from
Princes Hwy. (S of Tilba Tilba), 8.ii.1975. m.fl./f.fl./fr. (AD).- West
828-835, 1.6km S of Merimbula on Princes Hwy., 8.ii.1975. m.fl./f.fl./fr.
(AD).

QUEENSLAND:- Blake 4933, Moreton distr., Geebung, Brisbane, 17.ix.1933.
fr. (BRI,CANB).- Sharpe 1974, 2km N of Coolum Beach, 130km N of Brisbane,
31.i.1976. m.fl. (BRI).- D.A. Smith 119, Wide Bay distr., Fraser Is.,
Ungowa, 20.viii.1971. fr. (BRI).- Specht 1426A, Fraser Is., nr. Maryborough,
22.ii.1949. m.fl./f.fl. (AD).

VICTORIA:- West 842-843, 1.6km E of Cabbage Tree P.O. between Orbost and
Cann River on Princes Hwy., 11.ii.1975. m.fl./f.fl.,fr. (AD).

15. *Dodonaea lanceolata* F. Muell., *Fragm.* 1:73 (1859); Bentham, *Fl. Aust.* 1:475 (1863), p.p. (excl. "Clarence River, Beckler" - see *D. viscosa*); Mueller, *Fragm.* 9:88-89 (1875), *Vic. Nat.* 8:93 (1891); Bailey, *Fl. Qld.* 1:313 (1899); Ewart & Davies, *Fl. N. Terr.* 175 (1917); Domin, *Biblioth. Bot.* 22(89⁴):911 (1927), p.p. (excl. reference to South Australia and New South Wales); Radlkofer, *Pflanzenreich* IV.165:1360-1361 (1933); Beard, *W. Aust. Pl.* edn 1. 60 (1965), edn 2. 81 (1970); Chippendale, *Proc. Linn. Soc. N.S. Wales* 96:246 (1972).

TYPE: "In collibus petraeis terrae Arnhemicae." Lectotype (here designated): F. Mueller s.n., Victoria River, xii.1855. fr. (MEL84104).

Syntype: Mueller s.n., Victoria R., s.dat. bisex.fl. (MEL84103).

DESCRIPTION (Fig. 7.17 & 7.71):

Polygamo-dioecious or polygamous shrub, 1-3m high, erect. Branches slender, spreading; branchlets angular or flattened, glabrous. Leaves simple, sessile or petiolate; petiole (when present) (4.5-)8-15(-28.5)mm long, glabrous; lamina narrow- to broad-elliptic, sometimes lanceolate, or oblong to oblanceolate, (3-)5.5-8(-10.5) x (0.85-)1-2.2(-3)cm, bright or dull olive-green, coriaceous, glabrous, base attenuate & tapering into petiole or cuneate & sessile, margin thickened, entire or obscurely sinuate, sometimes revolute, apex long-acute to acuminate, acute, obtuse or mucronate, midvein prominent, lateral venation usually conspicuous, sometimes obscure. Flowers predominantly bisexual, sometimes unisexual, in terminal panicles composed of monads to botryoids; pedicels (5.5-)6.3-8.5(-12)mm long, glabrous. Sepals 4, lanceolate to ovate, (1.4-)1.8-2.5 x 0.8-1.1 mm, acute or obtuse, viscid, glabrous, usually persistent; at anthesis the sepals in male & bisexual flowers are spreading, in female flowers they are erect & free. Stamens in male & bisexual flowers (7-)8 (-10), approx. twice as long as the sepals, divergent; filaments 0.2-0.3mm

long, glabrous; anther lobes narrow-oblong, twisted at anthesis, 3-3.4 x 0.7-1mm, glabrous; apical appendage triangular-acuminate, 0.2-0.4mm long, glabrous; stamens in female flowers absent. Ovary in female & bisexual flowers 3-carpellate, ovoid or obovoid, angled, 1-1.6 x 1-1.5mm, glabrous, sometimes viscous; styles 3, connate, (5-)8-15.5(-20)mm long, glabrous, separating unequally at the apex, each free arm 0.1-0.4(-1)mm long, recurved; in male flowers rudimentary ovary usually present. Capsule 3-winged, in lateral view broad-oblong or obovate, (13-)16.5-19 x 14-19mm, coriaceous, glabrous, purple-brown to brown at maturity, base cordate to truncate, apex obcordate, with wings sometimes overlapping; carpel excluding wing navicular, 12.5-15 x 3-4mm; wing 4.5-5.5mm broad, extending from apex to base of carpel, broadest near the capsule apex, broader than the valve; dehiscence septifragal. Seeds 2-4, lenticular, 2.8-3.2 x 2.3-2.5mm, black, shiny, with hyaline membrane lifting at the margin; aril absent. Seedling not seen.

Chromosome number: not known.

KEY TO VARIETIES OF *D. lanceolata*

Leaves with petiole 4.5-28.5mm long, lamina narrow- to broad-elliptic, base attenuate, apex long-acute to acuminate

var. *lanceolata*

Leaves sessile or rarely with petiole of 1-2mm long, lamina oblong to oblanceolate, base cuneate, apex acute, obtuse or mucronate

var. *sessilifolia*

var. *lanceolata*

Leaves petiolate, narrow- to broad-elliptic, tapering to apex & base, base attenuate & tapering into petiole, apex long-acute to acuminate, lateral venation conspicuous.

DISTRIBUTION (Fig. 7.17):

D. lanceolata var. *lanceolata* is widely distributed in northern and Central Australia. In Western Australia it occurs in the Hamersley Ranges and the Kimberleys, it is widespread in the Northern Territory and extends into western Queensland.

ECOLOGY:

Over its distributional range var. *lanceolata* occurs in a variety of habitats. In W.A. it is often on stony ridges or hills or in gravelly stream channels. It has been found associated with *Acacia maitlandii* and spinifex, with *Adansonia gregorii*, *Gyrocarpus* sp. and annual sorghum, as well as in *Eucalyptus brevifolia* and *E. dichromophloia* low open woodland and hummock grassland. In Central Australia var. *lanceolata* occurs on high ridge tops, in steep rocky gullies and in stony watercourses and associated margins. In north-eastern N.T. and western Queensland it often grows on lateritic soils in *Trioda basedowii* open hummock grassland with *Eucalyptus leucophloia*.

Given the geographical range of this species it is not surprising that it does not have any definite flowering period. Many specimens bear flowers at anthesis and mature fruit simultaneously.

SPECIMENS EXAMINED: selection only (104 collections examined)

NORTHERN TERRITORY:- Beaglehole 20474, George Gill Ra. Reolly Rock Hole, 10.x.1966. fr. (BEAUGL, AD).- Burbridge & Gray 4359, base of Mt. Gillen,

Alice Springs, 27.ix.1955. fr. (CANB).- Gittins 1296, Calvert Hills, vii.1967. bisex.fl.,m.fl.,?f.fl.,fr. (BRI,NSW).- Orchard 877, Barkly Tableland, Gibsons Creek, 56km N of Tennant Creek, 19.vii.1968. bisex.fl., fr. (AD,NT).

QUEENSLAND:- Carolin 8939, 8ml NE of Werandangi, 29.iv.1974. m.fl., bisex.fl. (AD,SYD).- Ollerenshaw 1203 & Kratzing, 13km NE of Mt. Isa on rd. to Lake Moondarra, 4.vii.1974. m.fl.,bisex.fl.,fr. (BRI,CBG).- Purdie 1059, Gregory North Distr., 30km NNW of 'Alderley', 11.ix.1977. m.fl.,bisex.fl. (BRI).

WESTERN AUSTRALIA:- Carr 3362 & Beauglehole 47140, Kimberleys, 6.5km W of King R., 10.vii.1974. m.fl.,immat.fr. (BEAUGL,AD).- Kenneally 7079, Kimberley, Camp Creek, Mitchell Plateau, 7.ii.1979. m.fl.,bisex.fl.,fr. (PERTH).- Trudgen 1093, Hamersley Ra., Marandoo Mine Site, first ridge S of Mt. Bruce, 24.ix.1974. m.fl.,bisex.fl.,fr. (PERTH).

var. *subsessilifolia* West, var. nov.

Folia plerumque subsessilia, raro petiolum 1-2mm longum tenentia; lamina oblonga usque oblanceolata, basi cuneata, apice acuto usque obtuso, interdum mucronato.

HOLOTYPE: K.A.W. Williams 2, Queensland, Port Curtis district, Rockhampton-Marlborough Road, Glen Geddes, 23°04'S 150°17'E, 10.x.1974. fr. (BRI241254).

The variety name refers to the subsessile nature of the leaves.

Leaves subsessile, rarely with petiole of 1-2mm long, lamina oblong to oblanceolate, rarely broad-elliptic, base cuneate, apex acute, obtuse or mucronate, lateral venation often obscure, especially on narrow leaves.

DISTRIBUTION (Fig. 7.17):

D. lanceolata var. *subsessilifolia* occurs in eastern Queensland from

the Warrego district in the south to Cape York Peninsula. It is found on many off-shore islands as well as along the Dividing Range.

ECOLOGY:

var. *subsessilifolia* grows on stony hills or ranges of sandstone, granite or laterite base. It is most commonly found in open *Eucalyptus* forests.

SPECIMENS EXAMINED: selection only (83 collections examined)

QUEENSLAND:- Althofer 304, Nth Kennedy distr., Herberton, 23.x.1972. fr. (BRI).- Dockrill 347, Herberton to Watsonville rd., 30.i.1972. m.fl., bisex.fl. (BRI).- Donohue 6, Burra Ra., 9.6km W of Warrigal Creek, 2.v.1972. bisex.fl., fr. (BRI).- Everist 3862, Mitchell distr., Corinda, 85ml N of Aramac, 4.vi.1949. bisex.fl., m.fl., ?f.fl. (BRI).- Everist 8004, Port Curtis distr., Glen Geddes, 25ml NW of Rockhampton, 25.ix.1968. fr. (BRI).- Everist 8092, Leichhardt distr., Isla Gorge, 29km SW of Theodore, 28.ix.1968. bisex.fl., fr. (BRI).- Gittins 535, Cook distr., Stannary Hills, vi.1962. m.fl., bisex.fl., fr. (BRI).- Pedley 1005, Port Curtis distr., 4ml W of Calliope, 9.v.1962. fr. (BRI).- Specht & Specht 334 & 441, Cook distr., Lizard Is., 24.xii.1974. fr. (BRI).

TYPIIFICATION:

No specimens of *D. lanceolata* have been found during this study which bear locality data exactly as Mueller cited in the protologue. Two specimens of this species at MEL (MEL84103, MEL84104) were collected by Mueller at 'Victoria River', which flows through the southern part of Arnhem Land. On his north-west expedition in 1855-1857 Mueller travelled along the Roper and Victoria Rivers, but the party did not venture further north into Arnhem Land (Willis, 1949). One of the MEL specimens mentioned

above (MEL84104) contains fruit and the other has bisexual flowers, both of which are described in the protologue. The two sheets bear labels in Mueller's handwriting. MEL84104 is here selected as the lectotype of *D. lanceolata* F. Muell. because it is dated 'Dec. 1855', and the undated MEL84103 is regarded as a syntype.

NOTES:

1. *D. lanceolata* is morphologically consistent in flowering and fruiting characters. The variation in leaf shape, here recognised by describing a new taxon at the varietal level, is consistent within more than 80 percent of the material examined. This morphological variation corresponds to a geographical disjunction, although this is regarded as being of secondary significance. The consistency in leaf shape within any one population is not known and field work is required to establish the importance of environmental influences.

2. References to the occurrence of *D. lanceolata* in New South Wales on Lord Howe and Norfolk Island (e.g. Hemsley, 1896 and Maiden, 1904) are actually misidentifications of *D. viscosa*. *D. lanceolata* is not known from New South Wales.

3. Tate (1882) appears to be the source of the erroneous records of *D. lanceolata* in South Australia (e.g. Tate, 1890 and Mueller & Tate, 1896). Tate refers to Kempe's collections on the Finke River, which flows from S.A. into the Northern Territory. Kempe (1880) includes *D. lanceolata* among the indigenous plants in the neighbourhood of Hermannsburg on the Finke River in Central Australia, but there appear to be no records of Kempe having collected this species in S.A. No material of *D. lanceolata* from S.A. has been seen during this study and I believe the species does not occur in that state.

AFFINITIES:

D. lanceolata is most closely related to *D. triquetra*, with which it shares similar capsules, seeds, leaf texture and the lack of sessile glands or indumentum. The two species can be distinguished on the axillary inflorescences of usually unisexual flowers, the small sepals and large, linear anthers, membranous capsule wings and petiolate leaves of *D. triquetra*. Sterile material of *D. lanceolata* can be confused with leaves of *D. platyptera*. However, the latter species has pubescent branchlets, and leaves with sessile glands and which are often pubescent at least on the margin and midrib.

16. *Dodonaea bursariifolia* F. Muell., Definitions of rare or hitherto undescribed Aust. pl. in Trans. Phil. Soc. Vic. 1:8 (1855), published again in Hooker's J. Bot. Kew Gard. Misc. 8:33 (1856), Pl. indig. Col. Vic. 1:87-88, t.v. (1862); Bentham, Fl. Aust. 1:482 (1863); Mueller, Fragm. 9:87 (1875), Native Pl. Vic. 1:122, fig.26 (1879); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:346 (1904); Turner, Bot. S. Western N.S.Wales in Proc. Linn. Soc. N.S.Wales 29:152 (1904); Black, Fl. S. Aust. edn.1. 363, fig.160L-M (1926); Ewart, Fl. Vic. 739 (1931); Radlkofer, Pflanzenreich IV.165:1362-1363 (1933); Black, Fl. S. Aust. edn 2. 541-2, fig.693L-M, 696 (1952); Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965); Eichler, Suppl. Black's Fl. S. Aust. 215 (1965); Beard, W. Aust. Pl. edn 2. 81 (1970); Willis, Hdbk. Pl. Vic. 2:357 (1972).

TYPE: "In the barren scrub-country on the Murray and St. Vincent Gulf."
Lectotype (here designated): Mueller s.n., Murray scrub versus Wellington, iv.1849. fr. (MEL84079). Syntypes: Behr s.n., pine forest ultra Salt Creek, ix.1848. m.fl./f.fl./fr. (MEL84080, MEL84081). Probable syntypes: Anon., in the Mallee scrub on the Murray, s.dat. mature f.fl. (MEL84084); Anon., Murray desert, s.dat. fr. (MEL84082).

? *D. bursariifolia* F. Muell. var. (?) *major* Benth., Fl. Aust. 1:482 (1863);
[Radlkofer, Pflanzenreich IV.165:1361 (1933) pro syn.]

TYPE: "Sharks Bay and Dirk Hartog's Island, Milne". Holotype: Milne s.n., s.dat. m.buds (K). Isotype: K.

FIGURES: Mueller, Pl. indig. Col. Vic. 1, t.v. (1862), Native Pl. Vic. 1:122, fig.26 (1879); Black, Fl. S. Aust. edn 1. 361, fig.106L-M (1926), Fl. S. Aust. edn 2. 539, fig.693L-M, 542, fig.696 (1952); Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956).

DESCRIPTION (Fig. 7.18):

Dioecious or rarely polygamo-dioecious shrub, 0.5-1.5m high, spreading. Branches dense, spreading; branchlets terete or weakly angular, usually purberulent, sometimes glabrous; shoot apices viscous. Leaves simple, sessile, obovate, sometimes oblanceolate or oblong, rarely broad-obovate, (-0.8)1-2(-3.5) x (0.3-)0.45-0.7(-1.5)cm, bright green, thick, dull, coriaceous, glabrous, base cuneate, margin entire, apex obtuse or rounded, midvein prominent, lateral venation obscure. Flowers unisexual & rarely bisexual, usually diadic or triadic, rarely few-flowered botryoids, terminating branchlets; pedicels (1.5-)2-2.6mm long, glabrous. Sepals (4-)5, linear or linear-lanceolate, (1.4-)1.8-2.5(-3) x 0.3-0.5(-0.7)mm, usually smaller in female flowers, acute, viscous, outer surface glabrous, inner surface sparsely pubescent near the apex or glabrous, caducous; at anthesis the sepals in male & bisexual flowers are spreading, in female flowers they are free, erect & surround the ovary. Stamens in male & bisexual flowers (5-)8, exceeding the sepals, divergent; filaments (0.6-)0.8-1mm long, glabrous; anther lobes oblong, twisted at anthesis, 2-3 x 0.6-0.9mm, glabrous; apical appendage acuminate, incurved, to 0.5mm long, glabrous; stamens in female flowers absent. Ovary in female & bisexual flowers 3(-4)-carpellate, oblong, 0.8-1.2 x 0.8-1mm, viscous, with layer of resin, glabrous; styles 3(-4), connate, usually twisted spirally in upper half, 5-8(-11.5)mm long, glabrous, separating unequally near the apex, each free arm up to 1.5mm long, recurved; in male flowers rudimentary ovary present. Capsule 3(-4)-angled, in lateral view oblong or obovate, 6.5-8.5 x (5-)7-8.5mm, glabrous, with sessile glands, brown to yellow at maturity, base broad-cuneate or truncate, apex truncate, rarely rounded, style base persistent; carpel navicular, excluding appendage 6.5-8.5 x 2.5-3(-3.5)mm, crustaceous; appendage usually present, a

narrow wing, rarely above middle of capsule only, 0.5-1mm broad, much narrower than the valve, coriaceous; dehiscence septicidal. Seeds 0-1(-2), lenticular, 2-2.2 x 1.8-2, black, shiny, with hyaline membrane lifting at the margin; aril absent. Seedling not seen.

Chromosome number: $n = 14$ (West 1124, 1963, 1983, 2070)

TYPIFICATION:

Five sheets of *D. bursariifolia*, which Mueller probably used when he described this species, are held at MEL. That selected as the lectotype (MEL84079) is the only dated specimen which also bears Mueller's handwriting and which contains capsules and mature seeds. The two sheets of specimens collected by Dr Behr in 1848 were probably available to Mueller and MEL84080 has a label in his handwriting. They contain male flowers, of which Mueller gives details in the protologue, as well as fruit and female flowers, however, the locality data does not exactly correspond with that of the type citation. Two other sheets (MEL84082 & MEL84084) bear labels with locality data in agreement with the protologue, but they have no collector or date of collection and are regarded as probable syntypes.

DISTRIBUTION (Fig. 7.18):

D. bursariifolia is widespread in southern Australia. It occurs from the Sharks Bay area of Western Australia, into the south-west of W.A. and, with some disjunction on the Nullarbor Plain, extends into South Australia, north-western Victoria and to the south-west of New South Wales. In South Australia this species is common on Eyre and Yorke Peninsulas, the Murraylands and in the upper south-east of the state.

ECOLOGY:

D. bursariifolia is a shrub of semi-arid mallee scrub communities. It usually occurs on sandy loam soils and associates with a variety of species over its distributional range. In north-western Victoria it is found in red sand in open mallee scrub with *Codonocarpus continifolius* and *Triodia irritans*. In S.A. the dominant tree species with which *D. bursariifolia* grows include *Eucalyptus foecunda*, *E. aff. cyanophylla*, *E. calycogona*, *E. pileata*, *E. dumosa*, *E. socialis*, *E. incrassata* and *E. anceps*. Understorey species frequently include *Triodia irritans*, *Acacia rigens*, *Correa* spp., *Maireana* spp., *Melaleuca uncinata* and the larger shrub *Melaleuca lanceolata*. In W.A. *D. bursariifolia* grows in similar mallee scrub, although the dominant tree species vary. For instance, *Eucalyptus flocktoniana*, *E. celubris*, *E. sheathiana*, *E. redunca*, *E. wandoo* and *E. salmonophloia* are often components of the upper canopy.

D. bursariifolia flowers in spring to early summer and the fruit may take almost one year to reach maturity. Capsules are most commonly found in September and October, but they fall from the bush very soon after ripening.

NOTES:

1. The original spelling of the specific epithet for this species (i.e. 'bursarifolia') has been corrected in accordance with Stafleu et al., 1978 (Rec.73G 1.(a)).

2. The variety questionably described by Bentham, *D. bursariifolia* F. Muell. var. (?) *major* Benth., is not recognised as a separate taxon. (See *D. amblyophylla* Notes.)

AFFINITIES:

D. bursariifolia most closely resembles *D. amblyophylla*, with which it shares a similar leaf texture lacking sessile glands, and seeds with

the hyaline membrane lifting at the margin. The capsules of these two species are quite different, with those of *D. amblyophylla* having distinct wings usually greater than 1mm broad and septifragal dehiscence.

SPECIMENS EXAMINED: selection only (292 collections examined).

NEW SOUTH WALES:- Moore 6111, "Bidura", 40m N of Balrandald, 14.x.1971. m.fl. (CANB).

SOUTH AUSTRALIA:- Alcock 2464, Eyre Pen., Hincks N.P., 13.x.1968. m.fl., fr. (AD).- Blaylock 701, Yorke Pen., Curramulka, 2.x.1967. m.fl. (AD).- Carrick 3404, Upper South East, Scorpion Springs N.P., 21.x.1973. bisex.fl. (AD).- Copley 4534, Yorke Pen., Innes N.P., 6.x.1974. f.fl., fr. (AD).- Eichler 15083-15084, Murray Mallee, Monarto South, 4.x.1958. f.fl., fr./m.fl. (AD).- Kraehenbuehl 1241, South East, 16km N of Wolseley, 6.xi.1964. m.fl./f.fl. (AD).- Rohrlach 558, Eyre Pen., 32km SW of Kimba, 19.ix.1959. fr. (AD).- West 1852-1856, Murray Mallee, 3km N of Yumali, 16.v.1977. f.fl., fr./fr. (AD).- West 2082-2086, Eyre Pen., Bascombe Well C.P., 26.viii.1977. m.fl./f.fl. (AD).- West 2114-2116, Eyre Pen., 1km SE of Wudinna, 27.viii.1977. f.fl./f.fl., fr./m.fl./fr. (AD).- West 2280-2283, Upper South East, 30km SE of Lameroo, 3.x.1977. f.fl./m.fl. (AD).- West 2373-2382, Upper South East, 37km S of Lameroo, 8.x.1977. f.fl./m.fl./fr. (AD).

VICTORIA:- West 1711-1713, 20km SE of Ouyen, 29.x.1976. m.fl./f.fl. (AD).

WESTERN AUSTRALIA:- Haegi 1204-1205, Coolgardie Distr., 21km NW of Holt Rock P.O., 5.x.1976. m.fl./f.fl., fr. (AD).- Keighery 176, 16km S of Cunderdin, 8.xi.1974. bisex.fl., m.fl./fr. (PERTH).- Kuchel 1713, 80km N of Esperance, 12.ix.1964. fr. (AD).- West 1120-1124, Jilbadgie Rock, 36.8km S of Southern Cross, 17.viii.1975. m.fl., bisex.fl./fr. (AD).- West 3202-3203, Wyalkatchem, 1.xii.1978. m.fl./fr. (AD).

17. *Dodonaea amblyophylla* Diels in L. Diels et E. Pritzel, *Fragm. Phytogr. Aust. occid.* in Engler's *Bot. Jahrb.* 35:345-346, fig.42C-E (1904); Radlkofer, *Pflanzenreich* IV.165:1361-1362, fig.43C-E (1933); Blackall & Grieve, *W. Aust. Wildfls.* 2:324 (1956); Beard, *W. Aust. Pl.* edn 1. 60 (1965), edn 2. 81 (1970).

TYPE: "in distr. Austin pr. Menzies in fruticetis lutosus fruct. m. Oct. (D. 5186)". Lectotype (here designated): L. Diels s.n., Goldfields, Menzies, s.dat. fr. (PERTH).

? *D. bursariifolia* F. Muell. var. (?) *major* Benth., *Fl. Aust.* 1:482 (1863); [Radlkofer, *Pflanzenreich* IV.165:1361 (1933) pro syn.]

TYPE: "Sharks Bay and Dirk Hartog's Island, Milne". Holotype: Milne s.n. Shark Bay and Dirk Hartog's Is., s.dat. m.buds (K). Isotype: K.

FIGURES: Diels in Diels et Pritzel, *Fragm. Phytogr. Aust. occid.* in Engler's *Bot. Jahrb.* 35:346, fig.42C-E (1904); republished in Radlkofer, *Pflanzenreich* IV.165:1362, fig.43C-E (1933); Blackall & Grieve, *W. Aust. Wildfls.* 2:324 (1956).

DESCRIPTION (Fig. 7.19):

Dioecious or rarely polygamo-dioecious shrub, 0.5-1.5(-2)m high, erect, multistemmed. Branches erect; branchlets terete, biconvex or weakly angular, puberulent. Leaves simple, sessile, linear to oblong or oblanceolate, (2.2-)2.5-4(-4.5) x (0.4-)0.5-0.7(-1)cm, bright green, often drying dark blue to black, thick, dull, coriaceous, glabrous, base attenuate, margin entire, often dark blue to black, apex acute, or obtuse, rarely mucronate, midvein prominent, lateral venation obscure. Flowers unisexual and rarely bisexual, in 4-6-flowered botryoids, terminating branchlets; pedicels (4-)5-7(-7.5)mm long, glabrous. Sepals 4, linear to lanceolate, 1.6-2 x 0.4-0.8mm, acute, viscous, glabrous, caducous;

at anthesis the sepals in male flowers are spreading, in bisexual flowers they form an open cup-shaped structure, in female flowers they are free, erect & surround the ovary. Stamens in male & bisexual flowers (6-)8, usually shorter than the sepals, spreading; filaments 0.2mm long, glabrous; anther lobes broad-oblong, 1.4-1.8 x 0.7-0.8mm, glabrous; apical appendage absent; stamens in female flowers absent. Ovary in female & bisexual flowers 3(-4)-carpellate, oblong, 0.8-1 x 0.7-1mm, viscous, with layer of resin, glabrous; styles 3(-4), connate, usually straight, sometimes twisted in upper half, 5-7.5mm long, glabrous, usually 4-lobed at the apex, rarely separating into free arms up to 0.2mm long; in male flowers rudimentary ovary present. Capsule 3(-4)-winged, in lateral view oblong or obovate, (7.5-)9-11(-12) x (8-)10-14(-17)mm, glabrous, with sessile glands, dark brown to purple-black at maturity, base cordate, rarely truncate, apex emarginate to obcordate; carpel excluding wing transverse-oblong, (6-)7.5-8.5(-10) x (2-)3-4(-4.5)mm, coriaceous; wing (1-)3-4mm broad, extending from apex to base of carpel, usually broadest near the capsule apex, sometimes same width over carpel length, much narrower than the valve, membranous; dehiscence septifragal. Seeds 2-3, lenticular, 2.3-2.5 x 1.8-2mm, black, shiny, with hyaline membrane lifting at the margin; aril absent. Seedling glabrous, cotyledons not seen; first 2-10 leaves simple, alternate, sessile, oblanceolate to obovate, base cuneate, margin entire, sometimes irregularly toothed, apex lobed or toothed.

Chromosome number: not known.

TYPIIFICATION:

Diels cited one of his own collections (D.5186) with the protologue of *D. amblyophylla*. Diels' herbarium was held at B (Stafleu & Cowan, 1976)

and Radlkofer (1934) indicated that he saw a fruiting specimen of Diels No. 5186 at B. As no Diels collections of *Dodonaea* species can be located at B now it is likely that this specimen was destroyed during world war II. PERTH holds a specimen (with one fruit) collected by Diels from Menzies, which has no collection number of date. This material is probably part of the collection which Gardner brought back to PERTH from Berlin (with permission) as duplicate specimens. This specimen, which was most likely available to Diels at the time of describing *D. amblyophylla* and which agrees with the protologue is here designated the lectotype.

DISTRIBUTION (Fig. 7.19):

D. amblyophylla occurs in the south-west of Western Australia. It is mainly confined to the goldfields areas from Menzies in the north to the Lake King and Newdegate area in the south-west of its range. It is also found in the western end of the Great Australian Bight at Twilight Cove and south of Madura.

ECOLOGY:

D. amblyophylla is a species of the semi-arid to arid mallee scrub communities found in the goldfields areas of W.A. This species usually grows in sand in sandplain country or in sandy loam in mixed mallee shrubland. On the western edge of the Nullarbor Plain (e.g. at Madura) *D. amblyophylla* occurs on the white sand dunes seaward from the limestone plain. In these habitats it associates with *Eucalyptus gracilis*, *E. uncinata*, *E. brachycalyx*, *E. aff. dumosa*, *Callitris* sp., *Rhagodia* sp. on the dunes, but it is absent from the swales between the dunes. In the sandplain vegetation *Eucalyptus redunca*, *E. incrassata* and *E. eremophila*

often dominate, with *Melaleuca uncinata* and *Callitris* sp. contributing to the dense heath understorey.

D. amblyophylla appears to regenerate readily from seed following fire. Considerable variation in age structure in a post-fire population near Boorabbin in 1978 indicated the staggered nature of germination, which has been found in other species in germination trials in the glass-house.

D. amblyophylla usually flowers in autumn, but in unusual seasonal conditions it can flower early in summer. Fruit is present in spring, i.e. September, October.

NOTES:

The Milne collections from Sharks Bay and Dirk Hartog's Island, on which Bentham tentatively based *D. bursariifolia* var. *major* contain buds of male flowers only. It is not possible to positively identify the several specimens (on 2 sheets) held at K, as belonging to *D. amblyophylla* or *D. bursariifolia*. The material has characteristics of the former species in its larger, lanceolate and glabrous sepals, which are longer than the stamens and the flowers are arranged in 3-4-flowered botryoids. On the other hand, these specimens have certain features which are more characteristic of *D. bursariifolia*, e.g. the obovate leaves and the presence of an apical appendage on the anthers. The location of the collection is within *D. bursariifolia* distribution, but is a great distance outside the distributional range of *D. amblyophylla* (see fig.7.19).

AFFINITIES:

D. amblyophylla shows most resemblance to *D. bursariifolia*. These species both lack sessile glands, have similar leaf shapes and seeds with the membrane lifting at the margin. They can be readily distinguished

with the capsules. *D. bursariifolia* capsules often lack wings or the wing is less than 1mm broad and usually at the apex only, and the capsules dehisce septicidally.

SPECIMENS EXAMINED: selection only (36 collections examined)

WESTERN AUSTRALIA:- Chinnock 3277, 6.9km E of Rabbit Proof Fence on Hyden-Lake Cronin rd, 7.x.1976. fr. (AD).- Chinnock 4149, 3.2km beyond W edge of Lake King, 26.ix.1977. immat.fr. (AD).- Kenneally 1263, Lake Magenta Fauna Reserve, 14.iv.1974. m.fl. (PERTH).- Royce 5512, 8ml N of Cundeelee, N of Zanthus, 1.x.1956. fr. (PERTH).- Royce 10203, Frank Hann N.P., 10.xii.1971. fr. (PERTH).- West 2687-2691, 19.8km S of Madura, 21.xi.1978. f.fl./m.fl. (AD).- West 3529-3533, loc. cit., 16.xii.1978. f.fl./m.fl. (AD).- West 2928-2933, 6.8km E of Scaddan, 23.xi.1978. fr. (AD).- West 3126-3131, 13.5km W of Lake King township, 28.xi.1978. fr. (AD).- West 3378-3383, 2.7km E of Boorabbin, 11.xii.1978. fr. (AD).- West 3437a, Comet Vale, 12.xii.1978. fr. (AD).

18. *Dodonaea falcata* West, sp. nov.

[*D. filifolia* auct. non Hook.: Bentham, Fl. Aust. 1:478-479 (1863), p.p.; Maiden et Betche, Proc. Linn. Soc. N.S.Wales 22:147-148 (1897), p.p.; Bailey, Fl. Qld. 1:315 (1899), p.p.; Maiden et Betche, Proc. Linn. Soc. N.S.Wales 29:738 (1905); Domin, Biblioth. Bot. 22(89⁴):911 (1927), p.p.; Radlkofer, Pflanzenreich IV.165:1382-1383 (1933), p.p.]

Species nova Sect. *Dodonaeae*, *D. filifoliae* Hook. *foliis canaliculatis linearibus glabris, glandes sessiles ferentibus, inflorescentiis capsulisque similaribus, et seminibus lenticularibus, versus marginem lateratiter compressis affinis, sed differt ramulis puberulis, foliis brevioribus falcatis, pedicellis puberulis reflexis, sepalisque maioribus ovatis.*

TYPE: Holotype: I.R. Telford 1326, Queensland, Darling Downs distr., Bald Rock Creek, Girraween N.P., NE of Wallangarra, 31.viii.1969. m.fl. (CBG29801). Isotype: BRI94562.

The specific epithet refers to the leaves.

DESCRIPTION (Fig. 7.20, 7.21 & 7.72):

Dioecious shrub, 1.5-2m high, erect. Branches slender; branchlets terete or weakly angular, puberulent. Leaves simple, sessile, linear, or subfiliform, concave or channelled above, convex below, falcate, (2.5-) 3-4(-5) x 0.1cm, olive-green, coriaceous, viscous, with sessile glands, glabrous, base terete, margin entire, apex obtuse, often recurved, mid-vein visible below, lateral venation obscure. Flowers unisexual, in (2-)3-4-flowered botryoids, terminating branchlets; pedicels (2.5-)3-4.5 (-5.5)mm long, reflexed, viscous, puberulent. Sepals 4, ovate, (1.5-) 1.8-2.2(-2.5) x 0.8-1mm, acute to acuminate, viscous, outer surface glabrous, with sessile glands, inner surface villous, persistent; at anthesis the sepals in male flowers are spreading or sometimes recurved,

in female flowers they are free, erect, often recurved in upper half, surrounding the ovary. Stamens in male flowers 8, shorter than or equal in length to the sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 1.2-1.8 x 0.8mm, glabrous; apical appendage broad-triangular, to 0.2mm long, glabrous; in female flowers rudimentary stamens usually present. Ovary in female flowers 4-carpellate, obovoid, angled, 1-1.2 x 0.8-1mm, viscous, with resin layer, sparsely pubescent; styles 4, connate, straight, (1.5-)3.5-6(-7)mm long, glabrous, separating unequally at the apex, each free arm to 1mm long, divergent; in male flowers rudimentary ovary present. Capsule 4-winged, in lateral view transverse-elliptic, 9.5-11(-12) x 11-12.5(-14)mm, membranous, with sessile glands, sparsely puberulent, reddish brown at maturity, base cordate, apex obcordate, with wings sometimes overlapping; carpel excluding wing lunate & navicular, 5.5-6.5 x 2.5-3.5mm; wing 2.5-4mm broad, extending from apex to base of carpel, broadest at the capsule apex, approx. same width as the valve, membranous; dehiscence septifragal. Seeds 2-3, lenticular, compressed towards the margin, 2.4-2.5 x 2-2.1mm, black, dull; aril absent. Seedling not seen.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.20):

D. falcata is found in south-eastern Queensland, in the Stanthorpe-Wallangarra area of the Darling Downs, and extends south into New South Wales along the Great Dividing Range as far as Sydney.

ECOLOGY:

This species is associated with granite or sandstone hills usually in dry sclerophyll forest.

Flowering occurs in early spring, capsules develop over summer and usually mature by February or March.

NOTES:

1. This species was previously included in *D. filifolia* Hook. (see AFFINITIES for distinguishing features).

2. Betche collected *D. falcata* in 1894 in the Double Bay-Rose Bay area of Port Jackson. Both of these localities are now residential suburbs of Sydney. Maiden and Betche (1897) discussed the distribution of this species and its relationship with the Queensland species *D. filifolia* s.str. and *D. ericaefolia* (= *D. filiformis*) from Tasmania. They indicated a considerable loss of plants in the Port Jackson district by 1896 and it appears as though this species does not occur in the Sydney area now. Recent collections have been made in the Howe's Valley area south of Singleton (Burgess CBG19519).

AFFINITIES:

D. falcata is most closely related to *D. filifolia*, with which it was previously combined. The two species differ in *D. filifolia* having glabrous branchlets, longer, straight leaves, narrower, lanceolate sepals and glabrous, erect pedicels.

D. filiformis from Tasmania also shows affinities with *D. falcata*, but several features readily distinguish the two species. *D. filiformis* has shorter (less than 2cm long) leaves, which are very dense and which obscure the branches, smaller sepals, 5-6 anthers, very short pedicels, 3-winged capsules, and small, lenticular seeds which are not compressed at the margin.

SPECIMENS EXAMINED: selection only (27 collections examined).

NEW SOUTH WALES:- Boorman s.n., Wallangarra, vii.1904. f.fl. (AD,BRI, MEL,NSW).- Burgess s.n., Putty rd., 25ml S of Singleton, 31.xii.1961.fr. (CBG19519).- Constable s.n., Castlereagh S.F., Windsor, 25.vii.1947. m.fl. (NSW,U).- Kleinschmidt 130, Pilliga Scrub, 58km S of Narrabri, 23.vi.1970. m.fl. (BRI).-

QUEENSLAND:- Carroll 710 & Telford, Bald Rock Creek, Girraween N.P., 16.v.1967. fr. (BRI,CBG).- Copley 5084, Fletcher, 30km SSW of Warwick, 18.x.1977. fr. (AD).- Gittins 2818, 3.3km SE of Glen Aplin, 23.ix.1974. m.fl./f.fl. (BRI,NSW).- Gordon 50, Stanthorpe, 24.xi.1947. fr. (BRI).- Hocking s.n., Wyberba, 1961. fr. (BRI31580).- Telford 3184, Bald Rock Creek, 10km N of Wallangarra, 26.ix.1973. f.fl. (CBG).

19. *Dodonaea filiformis* Link, Enum. Hort. Berol. 1:381 (1821); Desfontaines, Tabl. de l'école d'hist. nat. edn 3. 231 (1829), n.v.; Loudon, Hort. Brit. 154 (1830); G. Don, Gen. hist. 1:674 (1831); Bentham, Fl. Aust. 1:478 (1863) in obs. sub *D. ericifolia*; Radlkofer, Pflanzenreich IV.165:1381-1382 (1933).

TYPE: "Hort. angl." Neotype (here designated): Hort. Paris., '*D. filiformis* Hort. Berol', s.dat. m.fl. (Hb. Webb ex Hb. Desf.), n.v.

D. ericaefolia G. Don, Gen. hist. 1:674 (1831); Bentham, Fl. Aust. 1:478 (1863); Mueller, Fragm. 9:87 (1875); Rodway, Fl. Tasm. 30 (1903); [Radlkofer, Pflanzenreich IV.165:1381 (1933) pro syn.]; Curtis, Fl. Tasm. 118 (1956); Curtis & Stones, Endemic Fl. Tasm. 2:126-127, 133, Pl.46 (1969).

TYPE: "v.s. herb. Lamb.", n.v.

D. salsolifolia A. Cunn. ex Hook., London J. Bot. 1:251 (1834); Hook., London J. Bot. 2:415 (1840); Schlechtendal, Linnaea 17:640 (1843); Hook.f., Fl. Tasm. 1:55 (1856); [Bentham, Fl. Aust. 1:478 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1381 (1933) pro syn.]

TYPE: "Mr. Cunningham. Mr Fraser, Mr Lawrence, (1831, n. 231.) Mr Gunn." Lectotype (here designated): R.C. Gunn s.n., Van D's. Land, s.dat. m.fl. (K). Syntypes: A. Cunningham s.n., Hort. Kew, 1833. m.buds (K); Anon. s.n., fr. (K).

? *D. cunninghami* Hort. Petrop., Regel, Indice semin. Hort. Petrop. 36 (1856), nom. nud.; Verlot, Catal. Jard. Grenoble 17 (1856), n.v.

[*D. angustissima* auct. non DC.: Schlechtendal, Linnaea 17:640 (1843); Regel, Indice semin. Hort. Petrop. 36 (1856).]

FIGURES: Curtis & Stones, Endemic Fl. Tasm. 2, Pl.46 (1969).

DESCRIPTION (Fig. 7.22):

Dioecious shrub, 1-2m high, erect, multistemmed. Branches dense; branchlets terete or weakly angular, puberulent. Leaves simple, very dense, obscuring the branches, sessile, linear, concave or channelled above, convex or ridged below with prominent midrib, (1.2-)1.5-2(-2.2) x 0.05-0.1cm, bright green, thick, coriaceous, viscous, with sessile glands, glabrous, base narrow-cuneate, margin entire, apex obtuse, midvein prominent below, lateral venation obscure. Flowers unisexual, monadic in compound inflorescences or in 3-4-flowered botryoids, terminating branchlets; pedicels 1-1.5(-3)mm long, shorter in male flowers, viscous, puberulent or glabrous. Sepals 4-5, caducous, in male flowers oblong, flat, 0.6-0.8(-1) x 0.4-0.6mm, obtuse, viscous, outer surface glabrous, inner surface usually pubescent at apex, in female flowers linear to linear-lanceolate, concave, 1.2-1.5 x 0.3-0.5mm, acute, viscous, usually glabrous, inner surface sometimes pubescent; at anthesis the sepals in male flowers are spreading, in female flowers they are free, erect, surrounding the ovary. Stamens in male flowers 5(-6), more than twice as long as the sepals, divergent; filaments 0.2-0.3mm long, glabrous; anther lobes broad-oblong, 1.2-1.6(-1.8) x 0.7-0.9mm, glabrous; apical appendage absent, or rarely a very small lobe less than 0.1mm long; stamens in female flowers absent. Ovary in female flowers 3-carpellate, oblong or obovoid, angled, 0.8-1 x 0.4-0.6mm, viscous, with resin layer, glabrous; styles 3, connate & twisted in lower part, (2.5-)3-4mm long (including free apical arms), glabrous, separating unequally at or above the middle, each free arm up to 1.4mm long, straight or divergent; in male flowers very small rudimentary ovary sometimes present. Capsule 3-winged, in lateral view transverse-elliptic, 9.5-11 x 12-15(-16.5)mm, membranous, with sparse sessile glands, glabrous, dark red at maturity, base cordate, apex emarginate to obcordate, wings sometimes overlapping; carpel exclud-

ing wing lunate & navicular, (4-)4.5-5.5 x 3-3.5mm; wing 3-5mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve, translucent; dehiscence septifragal. Seeds 2-3, lenticular, 2-2.1 x 2mm, black, dull; aril absent. Seedling with puberulent stem, leaves glabrescent; hypocotyl 6.5mm long; cotyledons linear, 13 x 1-1.5mm, acute, glabrous; epicotyl 2.5-3mm long; first 12 leaves alternate, sessile, pinnatifid with 2 linear segments 2-3mm long, glabrescent, base narrow-cuneate, margin entire, apex obtuse, minutely 3-toothed.

Chromosome number: not known.

TYPIFICATION:

It appears that the specimen(s) on which Link based *D. filiformis* has been destroyed. de Candolle (1824) indicated the specimen had been destroyed and it has not been located at B, the herbarium in which Link's types were housed. As Link described the species from cultivated material, it is possible that no herbarium specimen was kept. Radlkofer (1933) saw a specimen 'ex Hort. Paris', in Desfontaines' herbarium (now in Webb's herbarium) with the annotation "*Dod. filiformis* Hort. Berol." in Desfontaines' handwriting. Presumably this specimen originated from the stock growing in Berlin, which was described by Link. It appears therefore, to be the material closest to that used by Link and is here selected as a neotype. A request has been made to borrow the specimen from FI, the holder of the Webb herbarium, in order to confirm this designation.

G. Don described *D. ericaefolia* from material in the Lambert herbarium. This herbarium was sold in 317 lots in 1842 following Lambert's death (Miller, 1970). The collections are now housed in a number of institutions in Europe and the United States. Miller (1970) detailed the acquisition

and dispersal data and gave the present location of most of the collections represented in the herbarium. Enquiries have been made and/or material has been borrowed from the majority of European herbaria known to hold Australian material from the Lambert herbarium. No specimens of *D. filiformis* which may have belonged to the Lambert herbarium have been found during this study. Given that this search has not been exhaustive no decision has been made at this stage with respect to the type of the name *D. ericaefolia* G. Don.

Hooker named the collections of Gunn, Fraser, Cunningham and Lawrence in the type citation of *D. salsolifolia*. The only sheet seen with specimens collected by any one of these people before 1834 is one at K which bears Hooker's handwriting. There are three specimens on this sheet:-

- (1) collected by Gunn in van Diemen's land contains male flowers,
- (2) Cunningham specimen cultivated at Kew, 1833, with male buds, and
- (3) a fruiting specimen, with no information.

The Gunn specimen has been chosen as the lectotype as it originated in Tasmania and agrees closely with the protologue. The cultivated Cunningham specimen and the fruiting specimen which lacks data are regarded as syntypes.

DISTRIBUTION (Fig. 7.22):

D. filiformis is an endemic Tasmanian species, which is widespread on the eastern half of the island.

ECOLOGY:

Little information is available on the habitat in which *D. filiformis* grows. Many collections have been made from river banks, often in gravelly or rocky soils. Jackson (1965) classified the vegetation in the areas in which *D. filiformis* is found as sclerophyll forest.

NOTES:

As the types of *D. filiformis* Link and *D. ericaefolia* G. Don have not been seen (see Typification), I have followed Radlkofer (1933) in believing that these two species are conspecific. Radlkofer saw the only available specimen, which most probably originated from the material on which Link based *D. filiformis*. Several specimens annotated by Radlkofer as *D. filiformis* Link have been examined and found to agree with the protologue of *D. ericaefolia*. The species known as *D. ericaefolia* in Australia today is a very distinct taxon and is the same as that which Radlkofer named *D. filiformis*. There seems to be little doubt therefore that these two species are conspecific.

AFFINITIES:

D. filiformis is most closely related to *D. falcata* West of north-eastern New South Wales and south-eastern Queensland. The leaves of these two species are very similar, but they differ markedly in the male flowers, pedicels and seeds. *D. falcata* has larger, ovate sepals, which are villous on the inner surface, 8 stamens, longer, reflexed pedicels, 4-winged capsules and lenticular seeds.

SPECIMENS EXAMINED: selection only (49 collections examined)

TASMANIA:- Brown 5432, Cataract R., Port Dalrymple, 10.i.1804. f.fl./fr.

(BM).- Giblin H162, Russell R. Upper Huon, 23.xi.1928 (BRI).- Gunn s.n.,

Glen Leith, 24.x.1840. fr. (NSW141143).- Gunn s.n., New Norfolk, 11.xii. 1840. fr. (NSW14137).- Gunn s.n., New Norfolk, 24.x.1840. m.fl. (BM).- Hannaford s.n., the Cataract, 1863. fr. (NSW141136).- King s.n., Launceston, Distillery Ck., 9.xii.1961. fr. (MEL).- Lucas s.n., Bicheno, xi.1924. f.fl.,fr./m.fl. (NSW141140).- Story s.n., Tasmania, 1876. m.fl. (G).

20. *Dodonaea filifolia* Hook. in Mitchell, Journ. Exped. Trop. Aust. 241 (1848); [Mueller, Fragm. 1:71 (1859) pro syn. sub *D. acerosa*]; Bentham, Fl. Aust. 1:478-479 (1863), p.p. (excl. material pertaining to *D. falcata* West); Maiden et Betche, Proc. Linn. Soc. N.S.Wales 22:147-148 (1897), p.p. (as in preceding); Bailey, Fl. Qld. 1:315 (1899), p.p. (as in preceding); Domin, Mém. Soc. Sci. Bohême 1921-22, 2:62 (1923), p.p. (excl. material pertaining to *D. falcata* West and *D. rigida* West); Domin, Biblioth. Bot. 22(89^h):911 (1927), p.p. (as in preceding); Radlkofer, Pflanzenreich IV.165:1382-1383 (1933), p.p. (as in preceding).

TYPE: leg. Mitchell, Mt. Mudge area, 19.vii.1846. Lectotype (here designated): Lieut.-Col. Sir T.L. Mitchell 212, Sub-tropical New Holland, 19.vii.1846. f.fl. (K). Syntype: Lieut-Col. Sir T.L. Mitchell 202, Interior of New South Wales & Queensland, near Mt. Mudge, 19.vii.1846. f.fl. (BM).

D. acerosa, Lindl. in Mitchell, Journ. Exped. Trop. Aust. 273 (1848); Mueller, North-Aust. Exped. in Hooker's J. Bot. Kew Gard. Misc. 9:197 (1857); Mueller, Fragm. 1:71 (1859); [Bentham, Fl. Aust. 1:479 (1863) pro syn.]; Mueller, Fragm. 9:87 (1875); [Bailey, Fl. Qld. 1:315 (1899) pro syn.; Domin, Biblioth. Bot.22(89^h):911 (1927) pro syn.; Radlkofer, Pflanzenreich IV.165:1382 (1933) pro syn.]

TYPE: leg. Mitchell, ?Mt. Faraday area, 11.viii.1846. Holotype: Lieut.-Col. Sir T.L. Mitchell 352, Sub-tropical New Holland, 14.ix.1846. fr. (CGE). Isotype: P.

[*D. filifolia* auct. non Hook.: Mueller et Tate, Trans. R. Soc. S. Aust. 16:343 (1896); Spencer-Moore, J. Linn. Soc. 34:184 (1899); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:345, fig.42B (1904); Maiden et Betche, Proc. Linn. Soc. N.S.Wales 29:738 (1905); Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956).]

DESCRIPTION (Fig. 7.23):

Dioecious shrub or small tree, 1-3(-5)m high, erect. Branches slender, erect, often arching; branchlets angular, or terete, glabrous. Leaves simple, sessile, linear-filiform, grooved or channelled or rarely flat above, convex below, (3.2-)5.5-8(-10.5) x 0.1cm, dark green, coriaceous, viscous, with sessile glands, glabrous, base terete, margin entire, apex obtuse, midvein visible, lateral venation obscure. Flowers unisexual, in 5-6-flowered botryoids, terminating branchlets; pedicels (3.3-)5-6.5(-7.5)mm long, viscous, glabrous. Sepals 4, lanceolate, 1.2-1.5 x 0.4-0.6mm, acute, viscous, outer surface glabrous, inner surface villous, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are free, erect & surrounding the ovary. Stamens in male flowers 8, exceeding the sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 1.7-1.9 x 0.8mm, glabrous; apical appendage broad-triangular, 0.2mm long, glabrous or pubescent; in female flowers rudimentary stamens, or filaments only, sometimes present. Ovary in female flowers (3-)4-carpellate, obovoid, angled, 1-1.2 x 0.8-1mm, viscous, with resin layer, usually glabrous, sometimes sparsely pubescent; styles (3-)4, connate, 4.5-6.5mm long, glabrous, separating at the apex, each free arm up to 0.4mm long, recurved; in male flowers rudimentary ovary sometimes present. Capsule (3-)4-winged, in lateral view broad- to transverse-elliptic, (9.5-)11-12.5 x 11.5-13mm, membranous or coriaceous, with sessile glands, glabrous, bright red or purple-brown at maturity, base cordate, sometimes with wings overlapping, apex deeply obcordate, with wings often overlapping; carpel excluding wing navicular, 4.5-6 x 2-3mm; wing 2.5-4mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve, membranous, sometime coriaceous; dehiscence septifragal. Seeds 2-3, lenticular, compressed towards the margin, 2.6-2.7 x 2.3-2.5mm, black,

dull; aril absent. Seedling sparsely pubescent; hypocotyl 10-10.5mm long, red; cotyledons oblong, (10-)13-16 x 1.5-3mm, acute, glabrous; epicotyl 1.5-2mm long; first 2-5 leaves irregularly pinnate, alternate, petiolate; leaflets 4-5, obovate, base cuneate, margin entire or toothed, apex usually 3-lobed or -toothed.

Chromosome number: not known.

TYPIIFICATION:

Two specimens, which were collected by Mitchell and which bear labels containing information corresponding to that of the type collection of *D. filifolia* have been seen. One specimen held at K bears a label in Hooker's handwriting and the other, at BM, contains label data agreeing precisely with Mitchell's locality and the date of collection. Both specimens have mature female flowers and could be from the same plant. The K specimen is here designated the lectotype as it is quite certain that Hooker used this material in drawing up the protologue for *D. filifolia*.

The Mitchell specimen here given as the holotype of *D. acerosa* Lindl. is the only one in the Lindley herbarium at CGE. The date on this specimen does not correspond exactly with that on which the diagnosis is included in the account of the expedition, but since the sheet contains a label with Lindley's handwriting it is the only specimen known to have been available to him at the time he described this species. Apart from the P specimen, which has the same number as the holotype, several other Mitchell collections (BM, CGE, L,W,NSW (2 sheets)) have been examined. None of these sheets includes information indicating Lindley used them, and so they are not regarded as part of the type collection.

DISTRIBUTION (Fig. 7.23):

D. filifolia is widespread in eastern Queensland, extending from west of Ingham in the north to the northern part of the Darling Downs in the south. In a westerly direction it ranges as far as the Cunnamulla and Charleville areas.

ECOLOGY:

D. filifolia is a common shrub of the sandstone plateaus and hillsides in the Great Dividing Range. It is also found in sandy soils amongst sandstone and most often in low open eucalypt forest. The dominant trees in these associations include *Eucalyptus howittiana*, *E. trachyphloia*, *E. peltata* and *Callitris* sp.

Flowering occurs early winter and fruit are usually mature by late spring.

NOTES:

D. filifolia Hook. previously included two other species here recognised for the first time. Examination of a range of material has indicated that this taxon was extremely variable morphologically, as well as showing significant geographic disjunctions. It has been found to encompass two distinct species, *D. falcata* n.sp. from north-eastern New South Wales and *D. rigida* n.sp. from Western Australia.

AFFINITIES:

D. filifolia is closely related to, and up to this time included, both *D. falcata* and *D. rigida*. *D. falcata* differs from *D. filifolia* in having puberulent branches and pedicels, shorter, falcate leaves, broader, ovate sepals and reflexed pedicels. From *D. rigida* *D. filifolia* can be distinguished on leaf characters alone. The former species has rigid

foliage, which is four-angled or terete in cross section, acute, with brown, verruculose glands, and linear juvenile leaves. The axillary inflorescences and lenticular seed lacking a compressed margin of *D. rigida* also serve to distinguish the two taxa.

SPECIMENS EXAMINED: selection only (48 collections examined).

QUEENSLAND: Blaxell 509, 10km NE of Valley of Lagoons H.S., Upper Burdekin R., 20.v.1971. fr. (BRI,NSW).- Chapman 1327, North Kennedy distr., 25km W of Pentland, 23.vii.1975. fr. (AD,CANB,BRI).- Gittins 1139, Leichhardt distr., 6ml W of "Mt. Playfair", 90ml SW of Springsure, vii.1966. f.fl. (BRI,NSW).- Henderson 729, Andrews & Sharpe, Blackdown Tableland, 32km SE of Blackwater, 20.iv.1971. fr. (BRI,CANB,MEL).- Olsen 349, Port Curtis distr., Many Peaks Ra., 22.v.1967. immat.fr. (BRI,NSW).- Olsen & Byrnes 3553, Leichhardt distr., Isla Gorge, 24.v.1977. f.fl. (BRI).- Speck 1927, Leichhardt distr., Natham Gorge, 12ml SSW of Cracow, 28.x.1963. fr. (AD,BRI,CANB,MEL,PERTH).- Story & Yapp 326, Leichhardt distr., Rockland Spring, 26ml SSE of Blackwater Township, 15.ix.1962. fr. (BRI, CANB,MEL).- C.T. White 9439, Leichhardt distr., Carnarvon Ra., between Roma & Springsure, 26.x.1933. fr (BRI).- C.T. White 12394, Mitchell distr., Enniskillen, 14.xi.1943. fr. (BRI).

21. *Dodonaea rigida* West, sp. nov.

[*D. filifolia* auct. non Hook.: Mueller et Tate, Trans. R. Soc. S. Aust. 16:343 (1896); Spencer-Moore, J. Linn. Soc. 34:184 (1899); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:345, fig.42B (1904), p.p.; Domin, Mém. Soc. Sci. Bohême 1921-22, 2:62 (1923), p.p.; Domin, Biblioth. Bot. 22(89^h):911 (1927), p.p.; Radlkofer, Pflanzenreich IV.165:1382-1383, fig.43B (1933), p.p.; Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).]

FIGURES: Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:345, fig.42B (1904); republished in Radlkofer, Pflanzenreich IV.165:1362, fig.43B (1933); Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956).

Species nova Sect. *Dodonaeae*, *D. filifoliae* Hook. ramulis glabris, foliis subfiliformibus, capsulisque similaribus affinis, sed differt foliis teretibus 4-costatisve rigidis acutis, sepalis latioribus ovatis, inflorescentiis axillaribus, seminibus lenticularibus, versus marginem lateraliter non compressis, et foliis juvenalibus linearibus oblongis.

TYPE: Holotype: J.G. West 3459, Western Australia, 18.4km N of Broad Arrow, 42.5km S of Comet Vale, 30°17'S 121°15'E, 13.xii.1978. fr. (AD98008409). Isotypes: to be distributed.

The specific epithet refers to the leaves.

DESCRIPTION (Fig. 7.24, 7.25 & 7.73):

Dioecious shrub, 1-2m high, open, erect. Branches ascending, rigid; branchlets terete to weakly angular, glabrous. Leaves simple, falling off early so that usually only at ends of branchlets, sessile, rigid, erect, subfiliform, terete or 4-ribbed, (3.4-)4-7.5(-10.2) x 0.1cm, coriaceous, viscous, with brown verruculose glands, glabrous, base terete,

margin entire, apex acute, sometimes pungent, midvein prominent giving the leaf its 4-ribbed form, lateral venation obscure. Flowers unisexual, (male flowers not available), in axillary 3-4-flowered botryoids; pedicels (4.5-)5.5-6.5(-7.5)mm long, viscous, glabrous. Sepals 3-4, broad-ovate, 1.4-1.7 x 0.8-1.2mm, acute, viscous, outer surface glabrous, with verruculose glands, inner surface villous, caducous; at anthesis the sepals in female flowers are free, erect & surrounding the ovary. Stamens not seen. Ovary in female flowers 3-4-carpellate, obovoid, angled 1-1.2 x 0.9-1mm, viscous, with resin layer, glabrous; styles 3-4 connate, twisted, 4-5.5(-6.5)mm long, glabrous, separating at the apex, each free arm up to 0.5mm long, recurved. Capsule 3-4-winged, in lateral view broad-elliptic, (10-)11.5-13.5(-15) x 14-17mm, membranous, usually with sparse verruculose glands on carpel, glabrous, red or red-brown at maturity, base cordate, sometimes with wings overlapping, apex deeply obcordate, with wings often overlapping; carpel excluding wing navicular, 4-4.5 x 2.5-4mm; wing 4-6.5mm broad, often undulate, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve, membranous; dehiscence septifragal. Seeds 3-4, lenticular, 2.3-2.5 x 1.8-2.2mm, black, dull; aril absent. Seedling glabrous, with verruculose glands; hypocotyl 21-31 mm long; cotyledons linear to narrow-lanceolate, 17-22 x 2.2-3.1mm, acute, glabrous; epicotyl 2-4.5mm long; first 2-6 leaves simple, alternate, sessile, linear, base attenuate, margin entire, apex acute.

DISTRIBUTION (Fig. 7.24):

D. rigida is confined to southern, eremean Western Australia. It extends from the Payne's Find and Merriden areas in the west to the Gibson and Great Victoria Deserts in the east. It is common in the Menzies and Laverton areas.

ECOLOGY:

D. rigida is a species of arid shrublands. It occurs on sand dunes, stony ironstone rises, in sandy creeks or gullies and in red sandy loam. It is found in association with spinifex, in *Acacia-Casuarina* shrublands, and in the Menzies area it grows with *Eucalyptus oleosa* in a tall mallee community.

The flowering time of *D. filifolia* appears to be seasonally dependent. Mature capsules are usually present in September to November.

NOTES:

This species was previously included in *D. filifolia* Hook. (see AFFINITIES for distinguishing features).

AFFINITIES:

D. rigida is most closely related to *D. filifolia* of eastern Queensland. These two species share such characters as glabrous branchlets, subfiliform leaves and similar capsules. They differ in *D. rigida* having rigid, terete or 4-ribbed, often pungent leaves. *D. filifolia* has narrower, lanceolate sepals, terminal inflorescences and lenticular seeds which are compressed towards the margin. The juvenile foliage of the two species is very distinct. The first 2-6 leaves of *D. filifolia* are pinnate while those of *D. rigida* are simple and linear.

Some plants of *D. viscosa* ssp. *linearis* show resemblance to *D. rigida*, but the former species can be distinguished on its terminal inflorescences, its flat or channelled leaves and the sessile, rather than verruculose glands.

SPECIMENS EXAMINED: selection only (69 collections examined).

WESTERN AUSTRALIA:- Ashby 2611, Irwin distr., Anketell, 13.ix.1968. fr.

(AD,PERTH).- Beaglehole 60076 & Erroy 3776, Great Victoria Desert, 372km by rd. NE of Laverton, 17.ix.1978. fr. (AD,BEAUGL).- Carolin 5810, Poison Ck., 50ml N of Leonora, 23.vii.1967. fr.,f.fl. (NSW).- Donner 4529, 70km S of Leonora, 3.ix.1973. fr. (AD).- George 4076, Miss Gibson Hill, SW of Warburton, 26.viii.1962. fr. (PERTH).- Maiden s.n., Laverton, ix.1909. fr. (NSW141152).- Speck 1299, 7ml S of Wongawol Ck., 24.iii.1959. fr. (BRI,CANB,MEL,PERTH).- Tindale 20 & Bennett, 5.8ml S of Menzies, iii.1970. f.buds. (NSW).- West 3446-3451, 8.6km S of Menzies, 13.xii.1978. fr. (AD).- West 3452-3455, 18.7km S of Menzies, 13.xii.1978. fr. (AD).- West 3459-3462, 18.4km N of Broad Arrow, 42.5km S of Comet Vale, 13.xii.1978. fr. (AD).

II. Sect. *Platypterae* (Benth.) West, stat. nov.

Ser. *Platypterae* Benth., Fl. Aust. 1:479 (1863), basionym.

Ser. *Platypterae* subser. *Euplatypterae* Radlk., Pflanzenreich IV.165:1355 (1933).

TYPE SPECIES: Holotype: *D. platyptera* F. Muell.

DIAGNOSIS:

Leaves simple, and rarely pinnate (*D. heteromorpha*), sessile or petiolate, margin entire; capsule in lateral view transverse-oblong, -elliptic or-obovate, apex usually emarginate, rarely truncate, carpel crustaceous or coriaceous, wing membranous, rounded or pointed, oblique, longer than broad, rarely extending to central axis at apex & base of capsule; seed exarillate.

TYPIFICATION:

Although Bentham (1863) did not designate a type for his series *Platypterae*, *D. platyptera* must be considered the holotype since Bentham's series name was based on the specific epithet (Stafleu et al., 1978, Art. 22.4).

DISTRIBUTION:

Members of this section are widespread in eastern and northern Australia. *D. platyptera* extends across northern Australia above 18°S, *D. pachyneura* is confined to the Hamersley Ranges of Western Australia, while the remaining four species occur in the east extending from Victoria to Queensland on the western slopes and tablelands.

D. heteromorpha West

D. rhombifolia N.A. Wakefield

D. pachyneura F. Muell.

D. stenophylla F. Muell.

D. platyptera F. Muell.

D. truncatiales F. Muell.

KEY TO SPECIES OF SECTION *PLATYPTERAE*

- 1a. Leaves usually \geq 1cm broad, with length:width \leq 5:1, usually elliptic, rarely narrow- or broad-elliptic 2
- 1b. Leaves usually $<$ 1cm broad, with length:width $>$ 5:1, usually linear, lanceolate or oblanceolate, rarely narrow-elliptic 3
- 2a. Capsules septicidal, wing not extending right to central axis at apex & base of capsule; branchlets usually pubescent, not viscous; lateral venation conspicuous 22. *D. platyptera*
- 2b. Capsules septifragal, wing extending right to central axis at apex & base of capsule; branchlets glabrous, usually white-viscous; lateral venation usually obscure below 23. *D. rhombifolia*
- 3a. Leaves linear, rigid, \leq 0.25cm broad; sepals $<$ 1mm broad 24. *D. stenophylla*
- 3b. Leaves oblanceolate, rarely linear or narrow-elliptic, $>$ 0.2cm broad (rarely 0.2cm broad); sepals of ♀ flowers $>$ 1mm broad, rarely $<$ 1mm broad in ♂ flowers . . 4
- 4a. Capsule septicidal, wing \leq 5.5mm long; leaves sessile or with petiole 3-12mm long, lateral venation striate below; stamen filaments \leq 0.3mm long 25. *D. pachyneura*
- 4b. Capsule septifragal, wing usually $>$ 5.5mm long; leaves sessile, lateral venation obscure; stamen filaments \geq 0.4mm long 5
- 5a. Leaves always simple, $>$ 0.5cm broad (rarely 0.5cm broad); capsule with inflated, globose carpels, septa thickened & crustaceous; inflorescence axillary panicle 26. *D. truncatiales*
- 5b. Leaves simple & rarely irregularly pinnate, \leq 0.5cm broad; capsule with flattened carpels, septa membranous; inflorescence axillary botryoid 27. *D. heteromorpha*

22. *Dodonaea platyptera* F. Muell., North-Aust. Exped. in Hooker's J. Bot. Kew Gard. Misc. 9:197 (1857); Mueller, Fragm. 1:73 (1859); Bentham, Fl. Aust. 1:480 (1863); Mueller, Fragm. 9:87 (1875), Pl. coll. in Capric. W. Aust. by H.S. King 2 (1886), published again in Trans. & Proc. R. Soc. Vic. 23:51 (1887); Ewart & Davies, Fl. N. Terr. 175 (1917); Radlkofer, Pflanzenreich IV.165:1393 (1933); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970); Chippendale, Proc. Linn. Soc. N.S.Wales 96:246 (1972).

TYPE: "In collibus scopulosis flumen Fitzmaurice versus". Lectotype (here designated): F. Mueller s.n., dry stony places toward the Fitzmaurice, x.1855. fr. (MEL84127).

D. hansenii F. Muell., Vic. Nat. 8:93 (1891); Bailey, Fl. Qld. 1:316 (1899); Domin, Biblioth. Bot. 22(89^h):912 (1927); Radlkofer, Pflanzenreich IV.165:1393 (1933) -syn. nov.

TYPE: "On Stuart's River; Stephen Johnson". Lectotype (here designated): S. Johnson s.n., Stuart's River, 1891. fr. (MEL84096). Isolectotypes: MEL84097, BRI.

DESCRIPTION (Fig. 7.26):

Dioecious shrub or small tree, 2-6(-10)m high, erect. Branches erect; branchlets terete or angular, usually pubescent. Leaves simple; petiole (6-)8-10(-12)mm long, triquetrous, usually pubescent, sometimes sparsely so; lamina narrow- to broad-elliptic, (3.5-)5-7.5(-8.8) x (1-)1.2-2(-3.3)cm, coriaceous, with sessile glands, viscous, glabrous or sparsely pubescent on margin & midrib, base attenuate, margin entire, apex acute, rarely retuse or obtuse, midvein & lateral venation conspicuous. Flowers unisexual, (female flowers at anthesis not available, see Note 2), in axillary botryoids & axillary & terminal panicles composed of monads to botryoids; pedicels pubescent at base or glabrescent, in male flowers

7.5-10mm long, in fruit 10-20mm long. Sepals 4, oblong, 2.3-2.7 x 1.2-1.5mm, acute, membranous, with conspicuous venation, viscous, outer surface glabrous, with sessile glands, inner surface villous, caducous; at anthesis the sepals in male flowers are spreading. Stamens in male flowers 8, just exceeding the sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, (2.3-)2.5-2.8 x 1.3-1.5mm, glabrous; apical appendage triangular, 0.4-0.5mm long, pubescent. Ovary in female flowers (buds only), pubescent, with sessile glands; in male flowers rudimentary ovary sometimes present. Capsule 3-4-winged, (7-)9.5-12.5(-15) x 20-30mm, coriaceous, viscous when young, with sessile glands, glabrous, light brown at maturity, base broad-cuneate or truncate, apex broad-emarginate; carpel excluding wing suborbicular to broad-ovate, with septa enclosing ventral surface, 3.5-5.5(-6) x 3.5-4.5(-6)mm; wing 8-11.5mm long, oblique, acute or rounded, not extending to apex or base of carpel, longest near the capsule apex & much larger than the valve, coriaceous or sometimes membranous; dehiscence septicidal. Seeds 1-3, globose with a small ridge above the hilum, 2.7-2.8 x 2.6-2.8mm, black, shiny; aril absent. Seedling glabrous; hypocotyl 18-25mm long; cotyledons oblong, 17-18 x (2.5-)3-4mm, acute or acuminate, glabrous; epicotyl 0.5mm long; first 2-3 leaves simple, alternate, shortly petiolate, obovate or spatulate, base attenuate, margin entire, apex obtuse; later leaves elliptic & as in mature foliage.

Chromosome number: not known.

TYPIIFICATION:

Although Mueller first cited the Fitzmaurice River collection of *D. platyptera* in the more detailed description of 1859, it almost certainly was the only collection available to him in 1857 at the time of writing

to Hooker and including the diagnosis for this species. Thus, the sheet, MEL84127, consisting of a few leaves, (most of which are broken) and one carpel with the wing attached, is here designated the lectotype.

It is necessary to choose a lectotype for the name *D. hansenii* as duplicate material of the Johnson collection is contained in BRI and MEL (2 sheets). The two MEL sheets contain fruiting specimens in good condition and MEL84096 is here designated the lectotype.

DISTRIBUTION (Fig. 7.26):

D. platyptera is a northern Australian species being confined to Western Australia, Northern Territory and Queensland north of latitude 18°S.

ECOLOGY:

This species grows as a shrub or small tree usually in close proximity to water, especially on rivers and in estuarine situations. It is found on coastal beach sites in beach sand (and shell) dunes associated with coastal dune vegetation, often on the edge of rainforest or in monsoon scrub. Further inland and south of the Gulf of Carpentaria *D. platyptera* grows in low open forest of *Melaleuca acacioides*, *Bauhinia carronii* and *Terminalia* spp. with mixed understorey. In parts of north-western W.A. this species is a component of tall shrublands or semi-deciduous vine thickets in sandy soils.

D. platyptera usually flowers in summer in February or March and fruits are present through winter, sometimes until October.

NOTES:

1. Mueller distinguished *D. platyptera* & *D. hansenii* as separate species, as he regarded *D. hansenii* as a taxon with larger leaves, of

thinner texture and lacking conspicuous "glandular punctation", and with fruits having larger wings. At the time of publication, Mueller had available to him only one collection of each taxon. Detailed examination of a greater range of available material and of the type collections indicates that *D. hansenii* F. Muell. is conspecific with *D. platyptera* F. Muell. *D. hansenii* is regarded as a synonym of the earlier published *D. platyptera* (Stafleu et al., 1978, Art. 11).

2. Despite the larger number of collections made in the last 10-15 years no female-flowering material is available at this time. One specimen (George 12677) contains female buds and flowers at post anthesis stage. Inflorescence structure can be determined from the fruit arrangement (besides male inflorescences) and the sepal details are taken from male flowers.

AFFINITIES:

D. platyptera is a distinct species which shows affinities with *D. pachyneura* in fruit shape, but the latter species has linear to oblanceolate leaves. The leaves of *D. platyptera* are of similar shape to those of *D. triquetra* & *D. lanceolata*, from which it is distinguished on leaf texture, indumentum and apex shape as well as the very different fruit and wing shape.

SPECIMENS EXAMINED: selection only (41 collections examined).

NORTHERN TERRITORY:- Beauglehole 54600, Victoria R. district, Shoeing Tree Creek Outstn., 11.vii.1976. fr. (AD, BEAUGL).- Craven 4007, M^CArthur R. area, between Barraloola & Batten Point, 1.vi.1976. fr. (CANB,BRI,NT).- Holtze s.n., Port Darwin, 1886. m.fl. (BM).- Schomburgk s.n., north-coast, s.dat. m.fl. (W).- Specht 14, Nightcliff, Darwin, 19.iii.1948. m.fl./fr. (AD,BRI,NSW,MEL).

QUEENSLAND:- Brass 188, Massacre Inlet, viii.1922. fr. (BRI,CANB). -
Bycroft & Memmolt 54, Mornington Is., s.dat. fr. (BRI).- Specht & Salt
W492, 8.5km NW of Weipa Mission, 24.vii.1974. fr. (BRI).

WESTERN AUSTRALIA:- Beaglehole 52467, Kimberleys, Barnett Gorge, i.vi.
1976. fr. (AD,BEAUGL).- George 12677, Mt. Trafalgar, Prince Regent R.
Res., 26.viii.1974. f.buds. (PERTH).- Wilson 11139, Sir Graham Moore
Is., 29.vi.1973. fr. (PERTH).

23. *Dodonaea rhombifolia* N.A. Wakefield, Vic. Nat. 72:22-23, fig.1 (1955);
Willis, Hdbk. Pl. Vic. 2:357 (1972).

TYPE: "Granitic gullies on the lower Hume River ... Jan. 1874 ... F.v.M."

Holotype: F. Mueller s.n., granitic gullies on the lower Hume River, i.1874.
fr., mature f.fl. (MEL84136). Isotype: NSW140691. Probable isotype: F.
Mueller s.n., Hume's River and Mitta Mitta, i.1874. mature f.fl. (MEL84135).

FIGURES: Wakefield, Vic. Nat. 72:23, fig.1 (1955).

DESCRIPTION (Fig. 7.27):

Dioecious shrub, 0.5-1.5(-2)m high. Branches erect; branchlets angular, ribbed or flattened, usually white-viscous. Leaves simple; petiole (4-)5-9(-10.5)mm long, triquetrous, white, with sessile glands; lamina narrow-to broad-elliptic, rarely obovate, (4.5-)6.2-7.5(-8.2) x (1.4-)1.6-2.2(-2.7)cm, dark green above, paler & usually white-spotted below, sometimes both surfaces white-spotted when dry, coriaceous, thick, with white sessile glands, glabrous, base attenuate, tapering to the petiole, margin entire, revolute, apex acute, midvein prominent, lateral venation conspicuous above, usually obscure below. Flowers unisexual, in axillary botryoids & metabotryoids; pedicels 3.5-8.5mm long, shorter in male flowers, white-viscous. Sepals 4, lanceolate to ovate, (2-)3-3.4 x (1-)1.5-2mm, acute, viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrescent, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are erect, free & surround the ovary. Stamens in male flowers 8, just exceeding the sepals, erect; filaments 0.4-0.5mm long, glabrous; anther lobes oblong, 2.5-3(-3.5) x 0.9-1mm, glabrous; apical appendage broad-triangular, 0.2-0.3mm long, puberulent; stamens in female flowers absent. Ovary in female flowers 4-carpellate, angled, 1.2 x 1-1.2mm, viscous, glabrous;

styles 4, connate, 5-7 mm long, separating at the apex into free arms to 0.5mm long, strongly recurved; in male flowers rudimentary ovary present. Capsule 4-winged, including wings depressed-obovate or transversely elliptic in lateral view, 10-12(-13) x (15-)18-21(-24)mm, glabrous, light brown at maturity, base cordate, apex obcordate, sometimes the wings overlapping above the apex; carpel excluding wing deeply navicular, 4-5 x 3.5-4.5mm, crustaceous and thickened; wing 6-8(-8.5)mm long, usually oblique, rounded, extending from apex to base of carpel, usually longest near the capsule apex, larger than the valve, membranous; dehiscence septifragal. Seeds 1-2, lenticular, 2.8-3 x 2.5-2.6mm, black, dull; aril absent. Seedling not seen.

Chromosome number: not known

DISTRIBUTION (Fig. 7.27):

D. rhombifolia exhibits a disjunct distribution pattern between the upper reaches of the Murray River in north-eastern Victoria and south-eastern New South Wales and the mountains of north-eastern New South Wales. In this northern area of N.S.W. it grows in the Warrumbungle Mountains on the western slopes of the Great Dividing Range and further east in the Dividing Ra. at Gloucester, Walcha and at Wollombi.

ECOLOGY:

D. rhombifolia grows in rocky situations. It is found in creek beds and in stony gullies as well as on cliff tops and slopes. Usually this species grows in crevices of granitic or basaltic outcrops and has been found associated with *Casuarina cunninghamiana* & *Beyeria lasiocarpa*.

Flowering takes place in spring & early summer with fruit developing over winter and being mature in September to November of the following spring.

NOTES:

Given the disjunction in the distribution of this species some morphological variation might be expected. However, *D. rhombifolia* is extremely constant morphologically and apart from leaf size there is little difference between populations.

AFFINITIES:

D. rhombifolia is most closely related to *D. truncatiales* with which it shares capsule characters such as the thickened and crustaceous carpels and broad membranous wings. The two species can be easily distinguished by the narrower leaves and shorter fruits of *D. truncatiales*.

SPECIMENS EXAMINED: selection only (26 collections examined).

NEW SOUTH WALES:- Betche s.n., Apsley Falls, Walcha distr., xii.1898. m.fl./f.fl. (NSW31006).- Constable 36, "Guneemooroo", Warrumbungle Mts., 12.xii.1961. m.fl. (NSW).- Coveny s.n., Gloucester Bucketts, 1.5ml W of Gloucester, 26.ix.1965. f.fl.,fr. (NSW130512).- Coveny s.n., loc. cit., 8.ix.1967. fr./m.fl. (NSW140481).- Olsen s.n., Upper Tuross R. area, "The Scout", 11.iv.1971. f.fl. (NSW140484).- Streimann 765, Mt. Naman, 34km NW of Coonababran, 13.xii.1973. m.fl. (CBG,AD,NSW).- J.B. Williams G55, Wollombombi Falls, xi.1961. fr. (NSW).

VICTORIA:- Rowe s.n., Pine Mt., 12.xi.1959. fr.,f.fl. (MEL).- Wakefield 4688, Snowly R. gorge tract, E of Butcher's Ridge, 31.viii.1952. f.fl. (MEL).- Willis s.n., Pine Mt., 8.xii.1974. fr. (MEL).

24. *Dodonaea stenophylla* F. Muell., *Fragm.* 1:72 (1859); Bentham, *Fl. Aust.* 1:480 (1863); Mueller, *Fragm.* 9:87 (1875); Bailey, *Fl. Qld.* 1:316 (1899); Domin, *Biblioth. Bot.* 22(89⁴):912 (1927); Radlkofer, *Pflanzenreich* IV.165:1394 (1933).

TYPE: "In virgultis Brigalow Scrub a montibus Newcastle Range usque ad flumen Burnett." Lectotype (here designated): F. Mueller s.n., Upper Burdekin R., xi.1856. m.fl. (MEL). Possible syntypes: Nuth s.n., Springsure, s.dat. fr. (MEL); Brown s.n., East Coast, s.dat. (MEL 2 sheets, NSW).

DESCRIPTION (Fig. 7.28):

Dioecious shrub, 1-2.5(-4)m high, slender, erect. Branches dense, erect; branchlets angular, sometimes almost flat, with sessile glands, viscous, glabrous. Leaves simple, erect, rigid, sessile or tapering to a petiole 5-7mm long; lamina linear, (3-)6.5-9.5(-10.5) x (0.1-)0.15-0.2(-0.25)cm, coriaceous, thick, with sessile glands, viscous, glabrous, base attenuate, tapering to petiole, margin entire, thickened, revolute, apex acute, mid-vein prominent, lateral venation not visible. Flowers unisexual, in axillary botryoids & metabotryoids, or rarely terminal panicles composed of monads to botryoids; pedicels in male flowers 2-5.5mm long, in female flowers 10-15mm long. Sepals 4, lanceolate or ovate, (1.2-)1.5-1.8 x 0.8-1mm, acute, viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrous, caducous; at anthesis the sepals in male flowers form a cup-shaped structure, in female flowers they are free, erect & surround the ovary. Stamens in male flowers 8, approx. equal in length to the sepals; filaments 0.2-0.3mm long, glabrous; anther lobes broad-oblong, 1.2-1.5 x 0.6-0.8mm, glabrous; apical appendage broad-triangular, 0.1-0.2mm long, pubescent; stamens in female flowers absent. Ovary in female flowers (3-)4-carpellate, angled, 1 x 0.8mm, viscous, glabrous,

rarely pubescent near the apex; styles (3-)4, connate, 3.5-5mm long, glabrous, separating near the apex, each free arm up to 0.7mm long, recurved; in male flowers rudimentary ovary usually present. Capsule (3-)4-winged, (5-)7-10(-11) x (11-)13-15mm, glabrous, reddish-brown or light brown at maturity, base truncate, apex emarginate; carpel excluding wing broad-ovate, with septa enclosing ventral surface, (2-)3.5-4 x 2-3mm, coriaceous; wing (3.5-)5-7(-8)mm long, oblique, rounded or acute, sometimes flattened on upper surface, not extending to apex or base of carpel, longest at the capsule apex and much larger than the valve, membranous; dehiscence septicidal. Seeds 1-2, lenticular-globose, 1.5-1.7 x 1.4-1.6mm, black, shiny; aril absent. Seedling not seen.

Chromosome number: not known.

TYPIFICATION:

Given the type citation it is likely that Mueller based *D. stenophylla* on more than one collection. This is also evident from the protologue, which includes details of the male flowers, but not female flowers specifically, and fruits. The Melbourne herbarium, in which Mueller worked, contains only one specimen which fulfills the various criteria to qualify for lectotypification. This sheet has two specimens, one sterile and the other with male flowers, and bears a label in Mueller's handwriting "Upper Burdekin R. Nov 1856 FvMueller". The Burdekin River is within the broad type locality as stated by Mueller, the specimen agrees with the protologue, the collection was made prior to 1859, and as it was collected by Mueller the specimen was definitely available to him at the time of describing this species. For these reasons this MEL sheet is here designated the lectotype of *D. stenophylla* F. Muell.

Two other collections are possible syntypes. MEL holds an undated sheet of fruiting material collected by Dr. Nuth at Springsure and Robert Brown collections are held at NSW and MEL (East Coast, undated). These specimens may have been available to Mueller at the time he described this species, so they are regarded as possible syntypes.

DISTRIBUTION (Fig. 7.28):

D. stenophylla is primarily a Queensland species, but it also occurs in the New England area of New South Wales and from one locality east of Daly Waters in Northern Territory. Within Queensland this species is mainly confined to the Great Dividing Range from north of Charters Towers to the N.S.W. border. Collections have also been made from further west at Mt Isa and Prairie.

ECOLOGY:

D. stenophylla is usually found in rocky sandstone, or red sandy soils as well as in limestone and basalt outcrops. It grows in mixed shrubland, in *Eucalyptus* species open woodland with *Melaleuca tamariscina*, or in dry forests. In the western areas *D. stenophylla* is found in flat sandplain *Triodia mitchellii* hummock grassland with *Eucalyptus melanophloia* and to the south with clumps of *Dodonaea boroniaefolia*.

From the data on herbarium sheets there does not appear to be any definite flowering season in this species, and fruits are present in summer and winter. This may reflect the variation in climatic conditions over the distributional range of this species and further field work may reveal a geographical difference in flowering times.

AFFINITIES:

D. stenophylla most closely resembles *D. viscosa* ssp. *angustissima*. The two species can be distinguished on the broader, less rigid leaves, the large, circular wings of the fruit, and the larger, lenticular seeds of the latter species.

SPECIMENS EXAMINED: selection only (38 collections examined)

NEW SOUTH WALES:- Boorman s.n., Bingara, ix.1907. fr. (NSW).

NORTHERN TERRITORY:- Byrnes 2553, 60ml E of Daly Waters, 20.iii.1972. fr. (NSW,NT,CANB).

QUEENSLAND:- Blake 10396, 18ml W of Jericho, 7.xii.1935. fr (BRI, CANB).- Gittins 310, Bauhinia Downs, vii.1960. fr. (BRI).- Lavery 51, Mt. Isa, 13.i.1958. fr. (BRI).- Lazarides 3721, 7ml N of Craigie Stn., 2.vii.1953. fr. (BRI,CANB).- Olsen & Byrnes 3568, Glenhaughton-Mapala rd., 26.v.1977. m.fl. (BRI).- White 12393, Enniskillen, 14.xi.1943. m.fl. (BRI).- Wyatt s.n., Lotus Creek, N of Marlborough, ii.1965. fr. (BRI60914).

25. *Dodonaea pachyneura* F. Muell., Pl. coll. in Capric. W. Aust. by H.S. King 2 (1886), published again in Trans. & Proc. R. Soc. Vic. 23:51 (1887); Radlkofer, Pflanzenreich IV.165:1393 (1933); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).

TYPE: Holotype: H.S. King s.n., between the Gascoyne & Fortescue River, 1885. fr. (MEL84118).

DESCRIPTION (Fig. 7.29):

Dioecious shrub, 1-4m high, erect. Branches erect; branchlets terete, biconvex or weakly angular, with sessile glands, glabrous to puberulent. Leaves simple, sessile or tapering to a petiole (3-)6-9(12)mm long, glabrous or sparsely pubescent, sometimes triquetrous; lamina linear or oblanceolate, (2-)2.8-4.5(-6) x (0.2-)0.35-0.5(-0.7)cm, coriaceous, thick, with brown sessile glands, viscous when young, glabrous or rarely sparsely puberulent on midrib & margin, base attenuate, tapering to petiole, margin entire, sometimes irregularly denticulate, apex acute, obtuse or mucronate, midvein prominent, lateral venation conspicuous below giving the leaf a striate appearance. Flowers unisexual, in axillary botryoids; pedicels (1.5-)2-4mm long, viscous. Sepals 3(-4), broad-lanceolate to ovate, (1.2-)1.5-1.7 x 1.2-1.5(-1.7)mm, acute, viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrous, caducous, sometimes persistent; at anthesis the sepals in male flowers form a broad cup-shaped structure, in female flowers they are free, erect & surround the ovary. Stamens in male flowers 6(-8), approx. equal in length to sepals, erect; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 1.4-1.5 x 0.7-0.8mm, glabrous; apical appendage triangular, 0.1-0.2mm long, glabrous; stamens in female flowers absent. Ovary in female flowers 3(-4)-carpellate, lobed, 1 x 1mm,

viscous, glabrous; styles 3(-4), connate and twisted spirally in upper half, 4-6mm long, glabrous, separating unequally near the apex, each free arm up to 1mm long, usually straight, sometimes recurved; in male flowers rudimentary ovary present. Capsule 3(-4)-winged, including wings depressed-obovate in lateral view, 6-9 x 11-13(-16)mm, with sessile glands, viscous, glabrous, red to purple-brown at maturity, base cordate, apex emarginate; carpel excluding wing broad-elliptic or globose, with septa enclosing ventral surface, 2-3.5(-4) x 3-4mm, crustaceous; wing 2.5-4 (-5.5)mm long, oblique, rounded, usually extending from apex to base of carpel, longest near the capsule apex and usually larger than the valve, membranous; dehiscence septicidal. Seeds 1-2, lenticular, 2-2.2 x 1.8-2mm, black, dull; aril absent. Seedling not seen.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.29):

D. pachyneura is confined to the Hamersley and Robinson Ranges of Western Australia, extending as far south as Meekatharra.

ECOLOGY:

This species is found on rocky hillsides, ironstone ridges or red sandy and stony soils.

From the small number of flowering specimens available it appears that *D. pachyneura* flowers in autumn and early winter and fruits are mature in August and September.

AFFINITIES:

D. platyptera shows the closest affinity to *D. pachyneura*. The two species can be readily distinguished as *D. platyptera* has broader

leaves, lacking the prominent lateral vein striations, and larger fruits with more oblique wings that do not extend right to the apex or base of the carpel. *D. pachyneura* fruits are characterised by rounded carpels with very small septa.

In leaf morphology *D. pachyneura* most closely resembles *D. viscosa* ssp. *angustissima*, but the latter subspecies has a circular wing on the fruit and sinuate to sinuolate leaves lacking the lateral vein striations.

SPECIMENS EXAMINED: selection only (32 collections examined).

WESTERN AUSTRALIA:- Barker 1980, Dale's Gorge, Hamersley Ra. N.P., 18.viii.1977. m.fl. (AD).- Barker 1981, loc. cit., 18.viii.1977. f.fl. (AD).- Beauglehole 48565, Yampire Gorge, Hamersley Ra. NP., 7.viii.1974. fr. (AD, BEAUGL).- Chinnock 3911, Beasley R., 68km N of Ashburton Downs, 8.ix.1977. m.fl. (AD).- Gardner 2314, Meekatharra, 16.vii.1931. immat.fr. (PERTH).- Royce 6554, Henry R., Barlee Ra., 18.viii.1961. fr. (AD, PERTH).- Royce 8421, Dale's Gorge, Hamersley Ra., 14.vi.1968. fr. (PERTH).- Speck 1009, 8m W of Mileura-Nookawarra rd, 18.iv.1959. fr. (CANB, BRI, PERTH, AD).- Trudgen 507, Weeli Wollie Ck., Hamersley Ra., 13.viii.1973. fr. (PERTH).- Wittwer 1262, Weld Ra., 31.vii.1974. fr. (PERTH).

26. *Dodonaea truncatiales* F. Muell., *Fragm.* 2:143 (1861); Mueller, *Pl. indig. Col. Vic.* 1:226 (1862); Bentham, *Fl. Aust.* 1:479-480 (1863); Mueller, *Fragm.* 9:89 (1875), *Native Pl. Vic.* 1:121 (1879); [Domin, *Biblioth. Bot.* 22(89^h):911 (1927) pro syn. sub *D. calycina*; Ewart, *Fl. Vic.* 737 (1931) pro syn. sub *D. calycina*]; Radlkofer, *Pflanzenreich* IV.165:1392-1393 (1933), p.p. (excl. reference to Woolls Parramatta collections - see *D. megazyga*); Beadle et al., *Fl. Syd. Reg.* 386 (1972); Willis, *Hdbk. Pl. Vic.* 2:357 (1972).

TYPE: "In vallibus silvaticis ad ripas glareosas fluminum Towamba, Yowaka et Genoa River." Lectotype (here designated): F. Mueller s.n., gravelly banks of the Towamba River, ix.1860. m.buds. (MEL84144). Syntypes: F. Mueller s.n., on the Yowaka River, ix.1860. fr./immat.fr./f.buds,fr. (MEL84145); F. Mueller s.n., ad. fl: Yowaka australiae, s.dat. m.fl. (BM).

D. calycina A. Cunn. ex A. Gray, *U.S. Expl. Exped.*, *Phan.* 15 Bot 1:262 (1854), nom. nud.; [Bentham, *Fl. Aust.* 1:480 (1863) pro syn.]; Domin, *Biblioth. Bot.* 22(89^h):911 (1927); Ewart, *Fl. Vic.* 737 (1931); [Radlkofer, *Pflanzenreich* IV.165:1392 (1933) pro syn.]

D. calycina A. Cunn ex A. Gray var *genuina* Domin, *Biblioth. Bot.* 22(89^h):912 (1927), nom. illeg. (Stafleu et al., 1978, Arts. 24.3, 43).

D. calycina A. Cunn. ex A. Gray var *truncatiales* (F. Muell.) Domin, *Biblioth. Bot.* 22(89^h):912 (1927), nom. illeg. (Stafleu et al., 1978, Art. 43).

DESCRIPTION (Fig. 7.30):

Dioecious, rarely polygamo-dioecious shrub, 1-2.5(-3)m high, erect, usually multistemmed. Branches erect; branchlets angular, ribbed, with sessile glands, glabrescent. Leaves simple, sessile, erect, narrow-elliptic, rarely oblanceolate or linear, (5.5-)7.5-10(-13.5) x (0.5-)0.7-

1(-1.3)cm, dark green above, usually paler below, coriaceous, with white sessile glands, viscous, glabrous, base attenuate, almost decurrent, extending as a rib or small wing down the stem, margin entire or denticulate, sometimes dentate, thickened, revolute, apex acute, rarely mucronate, midvein prominent, lateral venation usually obscure, sometimes conspicuous below. Flowers unisexual & rarely bisexual, in axillary panicles composed of monads to botryoids; pedicels (3-)6.5-8.5(-14)mm long, with sessile glands, usually white, glabrous or sparse puberulent. Sepals 4, viscous, outer surface glabrous, with sessile glands, inner surface villous, caducous, in male & bisexual flowers ovate, 2-3(-3.5) x 1.4-1.8(-2)mm, acute, at anthesis recurved or spreading, in female flowers lanceolate, 1.5-2(-2.3) x (0.6)0.8-1mm, acute, at anthesis erect, free, surrounding the ovary, recurved at the apex. Stamens in male & bisexual flowers 8, approx. equal in length to sepals, divergent; filaments 0.4-0.7mm long, glabrous; anther lobes oblong, 1.5-1.8(-2) x 0.6-0.9mm, pubescent on dorsal surface near the apex; apical appendage broad-triangular, 0.2mm long, pubescent; stamens in female flowers absent. Ovary in female & bisexual flowers 3-4-carpellate, oblong or obovate, angled, 0.8-1.2 x 0.8-1.2mm, with white sessile glands, viscous, pubescent; styles 3-4, connate, usually straight, rarely twisted in upper part, 3.5-6(-10)mm long, glabrous, separating near the apex, each free arm up to 0.4mm long, recurved; in male flowers rudimentary ovary present. Capsule 3-4-winged, 5.5-8 x (17-) 21-25mm, with sessile glands, glabrous or sparsely puberulent, red to purple-brown or light brown at maturity, base truncate, apex emarginate, rarely truncate; carpel excluding wing transverse-broad-elliptic, globose, or broad-ovate, (3-)4-5 x (3.5-)4-4.5mm, thickened, crustaceous; wing (4.5-)7-10mm long, usually oblique, broad-acute, sometimes rounded, not extending to base or apex of carpel, longest near the capsule apex &

larger than the valve, membranous; dehiscence septifragal. Seeds 1-2, lenticular, 2.6-2.8 x 2.4-2.7mm, black, + shiny; aril absent. Seedling not seen.

Chromosome number: n = 14 (West 2568)

TYPIFICATION:

Lectotypification is necessary for *D. truncatiales* as Mueller cited three type localities, from which three sheets of specimens have been examined. MEL84145 contains three specimens which are obviously from different plants. The BM sheet contains a label and no. 8700 which appear to have been added while the specimen was in the possession of H.F. Hance. MEL84144 is a single specimen agreeing with the protologue, and is here designated the lectotype.

DISTRIBUTION (Fig. 7.30):

D. truncatiales is confined to the central and south coast and central tablelands regions of New South Wales and eastern Victoria. The species is commonly found in the Hunter Valley area and in the mountains west of Sydney. It extends down the south coast and into the far eastern part of Victoria in the vicinity of Mallacoota and the Genoa River.

ECOLOGY:

This species usually grows in sandstone formations and in dry sclerophyll forests. It is often near fresh water and river systems. Associated species include *Eucalyptus crebra*, *E. siderophloia*, *E. gummifera*, *E. eximia* & *E. cypellocarpa* in the upper canopy, with such shrub species as *Leptospermum flavescens*, *Acacia elata*, *Grevillea longistyla* & *Bursaria spinosa*.

AFFINITIES:

D. truncatiales is most closely related to *D. heteromorpha* which was previously recognised as an infraspecific taxon of this species. The two can be distinguished on their leaves, which are narrower, linear to linear-lanceolate, sometimes compound and entire in *D. heteromorpha*. The carpels of the capsule are almost flat in *D. heteromorpha*, while they are globose in *D. truncatiales*, giving the carpels of the fruit a lobed appearance in vertical view.

SPECIMENS EXAMINED: selection only (71 collections examined)

NEW SOUTH WALES:- Boorman s.n., Bermagui, xi.1911. m.fl./f.fl., fr. (NSW140499).- Burgess s.n., gorge of the Bulga Mts., 25ml S of Singleton, 29.ix.1963. f.fl., fr. (CBG20575).- Burgess s.n., Bulga Gorge, 30.ix.1963. m.fl. (CBG6173).- Constable s.n., Newnes Railway line, 13.xii.1948. fr. (NSW17637).- Constable 6225, Nepean R., Douglas Park, 13.x.1965. f.fl., fr. (NSW).- Constable 7159, Mt. Yengo, 10ml S of Howes Valley. 22.ix.1966. m.fl. (AD, MEL, NSW).- Constable 7178, loc. cit., 23.ix.1966. f.fl., fr. (NSW).- Crisp 1306, Mt. Towinhingy, 20km E of Rylstone, 5.x.1975. fr. (AD, CBG).- Crisp 2214 & Telford, Green Gully, 2km S of Glen Davis P.O., 26.x.1976. m.fl. (AD, BRI, CBG). Pickard 220-221, "Valley Apiary" on Capertee Nile Ck, 9km NNW of Glen Alice, 1.ix.1969. m.fl./m.fl., fr/f.fl., fr. (NSW).- West 2567, Nowra showgrounds, 30.iv.1975. f.fl. (AD).
VICTORIA:- West 840-841, 5 km SE of Genoa, 11.ii.1975. m.fl./f.fl. (AD).

27. *Dodonaea heteromorpha* West, nom. et stat. nov.

- based on *D. truncatiales* F. Muell. var. *heterophylla* Maiden et Betche, Proc. Linn. Soc. N.S.Wales 29:738 (1905); [Radlkofer Pflanzenreich IV.165:1392 (1933) pro syn.]; Wakefield, Vic.Nat.72:23-25, fig.2 (1955) (as *D. truncatiales*); Willis, Hdbk. Pl. Vic. 2:357 (1972) (as *D. truncatiales*).

TYPE: "Herb. Rev. Dr. Woolls, without locality or date; Bidden Road, Gilgandra, and Mudgee Road, 4 miles from Dubbo (R.H. Cabbage; October, 1904)." Lectotype (here designated): R.H. Cabbage 1062, Mudgee Road, 4 miles from Dubbo, 13.x.1904. fr. (NSW). Syntype: R.H. Cabbage 1109, Gilgandra, x.1904. immat.fr. (NSW).

FIGURES: Wakefield, Vic. Nat. 72:23, fig.2 (1955) (as *D. truncatiales*).

DESCRIPTION (Fig. 7.31):

Dioecious shrub, 1-2.5(-3)m high, erect. Branches dense, erect, spreading; branchlets angular, ribbed to flattened, with sessile glands, glabrous. Leaves sessile, usually simple, or sometimes irregularly pinnate with 1-8(-10) opposite or alternate leaflets (see Note 4); simple leaves (3.5-)4.5-7.5(-8.3) x (0.2-)0.3-0.5cm; leaflets (0.6-)1-2 (-3) x (0.15-)0.2-0.3cm; rhachis winged; lamina of simple leaves & leaflets linear to linear-lanceolate, coriaceous, dull green, with sessile glands, glabrous, base attenuate, margin entire, thickened & revolute, apex acute, midvein prominent, lateral venation usually obscure. Flowers unisexual, in axillary botryoids; pedicels (3.5-)5.5-10(-12.5)mm long, with sessile, sometimes white glands. Sepals 4, ovate, 1.5-2.3 x 1.2-1.6mm, acute, viscous, outer surface glabrous, with sessile glands, inner surface villous, caducous; at anthesis the sepals in male flowers are usually recurved, sometimes spreading, in female flowers they surround

the ovary, are free & recurved at the apex, valvate below the middle. Stamens in male flowers 8, approx. equal in length to sepals, divergent; filaments 0.5-0.7mm long, glabrous; anther lobes oblong, 1.5-1.8 x 0.5-0.8mm, glabrous; apical appendage broad-triangular, 0.1-0.2mm long, usually pubescent, sometimes glabrous; stamens in female flowers absent. Ovary in female flowers 4-carpellate, obovate, angled, 1.1-1.2 x 1-1.4mm, with sessile glands, viscous; styles 4, connate, straight, 2.6-3mm long, glabrous, very shortly 4-lobed at the apex; in male flowers rudimentary ovary present. Capsule 4-winged, including wings transversely oblong, 5-6.5 x (15-)18-25mm, glabrous, brown at maturity, base truncate, apex truncate, rarely emarginate; carpel excluding wing navicular, 3-5 x 2-4mm, crustaceous; wing 6.5-10mm long, often oblique, acute or rounded, not extending to base or apex of carpel, longest near the capsule apex and larger than the valve, membranous, rarely coriaceous; dehiscence septi-fragal. Seeds 1-2, lenticular, (1.7-)2-2.4 x 1.7-2mm, black, dull; aril absent. Seedling glabrous; hypocotyl (10-)14-21mm long, brown; cotyledons linear, 12-15 x 1.6-2mm, acute, glabrous; epicotyl 2-2.5mm long, red; first 2-5 leaves simple, alternate, sessile or shortly petiolate, oblanceolate to obovate, base attenuate, margin entire, apex tri-lobed.

Chromosome number: not known.

TYPIIFICATION:

Maiden and Betche cited three specimens of *D. truncatiales* var. *heterophylla* and two of these, Cabbage 1062 & 1109, are held at NSW. Cabbage 1062 is here designated as the lectotype. However, the Woolls collection 'without locality or date' has not definitely been located. NSW140591 contains a fruiting specimen and bears a label with 'leaves

occasionally pinnate' and in pencil (almost certainly added recently) 'ex herb Woolls'. There is no direct evidence that this is a specimen of the Woolls syntype.

DISTRIBUTION (Fig. 7.31):

D. heteromorpha is found mainly on the western slopes of the Great Dividing Range in New South Wales and southern Queensland as far north as Springsure. There is a westerly extension into the western plains of N.S.W. and one record in western Victoria at Mt. Zero in the Grampians (see Note 5).

ECOLOGY:

D. heteromorpha is a species of semi-arid areas and grows in skeletal soils on stony ridges with mallee ironbark or in *Callitris* spp. associations in sandy loam. In certain parts of its N.S.W. distribution this species is found on the red soil plains with *Acacia pendula* & *Callitris* sp. or in undulating country in open forest dominated by *Eucalyptus pilligaensis*.

NOTES:

1. This taxon is raised to specific rank, as several features indicate that it is quite distinct from *D. truncatiales* F. Muell. The leaves of *D. heteromorpha* are both simple and compound, linear and entire compared with the simple, elliptic, often denticulate, viscous leaves of *D. truncatiales*. The capsules of the two taxa are consistently different in such characters as the rounded and globose carpels in the latter species compared with the flattened, navicular ones of *D. heteromorpha* (fig.7.31), and the capsule apex, which is truncate in *D. heteromorpha* and emarginate in

D. truncatiales. This last species exhibits sexual dimorphism in the sepal size and shape, and the anther lobes are usually pubescent near the apex while *D. heteromorpha* has glabrous anther lobes.

2. The specific epithet '*heterophylla*' is available for use in a new combination at the species level with the basionym *D. truncatiales* F. Muell. var. *heterophylla* Maiden et Betche. However, *D. heterophylla* Hort., Dum.Cours., Bot. Cult. edn 2. 6:233 (1811), is a nomen nudum which was used in several horticultural references in relation to *Dodonaea triquetra* Wendl. (e.g. Colla, Hortus ripul. App 2. 347 (1826); G. Don, Gen. hist. 1:674 (1831)). To avoid confusion a replacement name (Stafleu et al., 1978, Art. 72) is used which refers to the heteromorphous nature of the leaves.

3. When referring to *D. truncatiales* F. Muell. Wakefield (1955) and Willis (1972) were actually writing of the Mt. Zero *D. heteromorpha* West, except in reference to the records of *D. truncatiales* occurring in eastern Victoria.

4. *D. heteromorpha* is the only species of the genus which has both simple and compound 'mature' foliage. The rarer compound leaves are not regularly pinnate, but range from having one leaflet to 3, 4 or 5 alternate ones to 5 pairs of opposite leaflets. The leaves subtending branchlets are always simple, but no other developmental trends are visible even in cultivated specimens.

5. The single record of *D. heteromorpha* from Mt. Zero in Victoria is from specimens collected in 1894 by W.E. Matthews, who was employed at the Stawell Technical College. The herbarium sheet MEL84147 is accompanied by a letter from Matthews to Mueller indicating that Mueller had requested more material of a specimen sent to him previously by Matthews. This letter is dated March 20, 1894 and in part states "I shall be glad to revisit Mt. Zero during the Easter vacation with a view to

collecting more of the *Dodonaea* you wish if I can find it. There was but one small shrub of the kind that I came across on my last visit I send you the balance of the specimens I then collected." It appears Matthews did not collect any more of this species.

During this study extensive searches were made for *D. heteromorpha* in the rocky sandstone outcrops of Mt. Zero and the unlikely habitat of the surrounding sandy heath. A large *D. viscosa* ssp. *cuneata* population was located, but no individuals of *D. heteromorpha* were found. If this species still exists in the Grampians area it is obviously very rare.

The disjunction between the Mt. Zero collections and the next closest in southern N.S.W., a distance of c. 500km, is difficult to explain on grounds other than chance factors. Geologically the two areas are not isolated as various sandstone, quartz and conglomerate formations occur between them. Possibly clearance of native vegetation in southern N.S.W. and western Victoria for agricultural purposes may have influenced the distribution of *D. heteromorpha*, but it is unlikely to have been so thorough to cause the local extinction of species as early as the late 1800's. If there was only one plant at Mt. Zero, as indicated by Matthews, then it is quite possible that as a single female it was not able to reproduce and that it has since died out.

AFFINITIES:

D. heteromorpha is most closely related to *D. truncatiales* (see Note 1).

SPECIMENS EXAMINED: selection only (84 collections examined).

NEW SOUTH WALES:- Boorman s.n., Gungal, xii.1914. fr. (NSW140521).-

Crisp 4427-4428, Goonoo S.F., 17km SW of Mendooran, 12.x.1978. m.fl./

f.fl. (AD,CBG).- Johnson & Constable s.n., Cubbo Ck., 16ml NE of Kenebri,

Pilliga S.F., xi.1954. fr. (NSW30378).- Maiden s.n., Dubbo - Tomingley,
ix.1898. m.fl. (NSW140531).- Salasoo 5193, 6ml NNW of Tullamore,
19.xi.1973. fr. (NSW).- Tindale s.n., 32ml E of West Wyalong, x.1963.
fr. (NSW63771).

QUEENSLAND:- McDonald 268, 76km W of Westmar 20.ix.1966. fr. (BRI).-
Phillips s.n., between Dalby & Kogan, 22.viii.1961. m.fl./f.fl. (CGB22335,
CBG22336).- Sharpe & Lebler 2418, Little Mt. Edwards, 15km W of Boonah,
18.ix.1978. fr. (BRI).- K.A.W. Williams 75057, 6 ml S of Gurulmundi,
1.x.1975.fr. (BRI).

VICTORIA:- Matthews s.n., Mt. Zero, Grampians, 1894. fr. (MEL84147).

III. Sect. *Apterae* (Benth.) West, stat. nov.

Ser. *Apterae* Benth., Fl. Aust. 1:481 (1863), p.p. (excl. *D. bursariifolia*), basionym.

Ser. *Aphanopterae* subser. *Appendiculatae* Radlk., Pflanzenreich IV.165:1356 (1933), p.p.

[Ser. *Cornutae* auct.non. Benth.: Benth., Fl. Aust. 1:480 (1863), p.p. (as to *D. baueri*)].

[Ser. *Aphanopterae* subser. *Inappendiculatae* auct. non Radlk.: Radlk., Pflanzenreich IV.165:1357 (1933), p.p. (as to *D. triangularis* and *D. trifida*)].

TYPE SPECIES: Holotype: *D. aptera* Miq.

DIAGNOSIS:

Leaves simple, sessile or petiolate, margin entire, or with (1-)2(-4) irregular teeth below apex; capsule globose, obovoid to 3-angled, crustaceous, appendage above middle of capsule only, usually lobe-like & ≤ 1mm long, rarely a narrow wing ≤ 2.5mm broad, sometimes absent; seed arillate, or with enlarged funicle, or with hyaline membrane lifting at the margin.

TYPIFICATION:

Since Bentham based his series *Apterae* on *D. aptera*, that species is automatically the holotype of the group (Stafleu et al., 1978, Art. 22.4).

DISTRIBUTION:

Apart from *D. triangularis* which extends into south-east Queensland, the section is confined to southern Australia. Several species show restricted distributions in south-west Western Australia.

D. aptera Miq.

D. baueri Endl.

D. ericoides Miq.

D. hexandra F. Muell.

D. humifusa Miq.

D. tepperi F. Muell. ex Tepper

D. triangularis Lindl.

D. trifida F. Muell.

KEY TO SPECIES OF SECTION *APTERAE*

- 1a. Capsules globose, carpels rounded, usually 4; leaves usually glabrous, rarely puberulent, if pubescent then opposite, entire or with (1-)2(-4) irregular teeth below apex; sepals \geq 1mm broad; seed arillate or with enlarged funicle, hyaline membrane not lifting at the margin 2
- 1b. Capsules angled, carpels flattened, usually 3; leaves alternate, usually pubescent with adpressed hairs or pilose, tri-dentate or 3-lobed at apex; sepals $<$ 1mm broad (rarely 1.2mm broad); seed exarillate and lacking enlarged funicle, hyaline membrane lifting at the margin 7
- 2a. Leaves $>$ 1cm broad (rarely 1cm broad), elliptic, rarely obovate, petiole $>$ 2mm long; inflorescence botryoidal or paniculate . . . 28. *D. aptera*
- 2b. Leaves \leq 1cm broad, linear to obovate, never elliptic, sessile or with petiole $<$ 2mm long; flowers monadic or diadic 3
- 3a. Leaves usually $>$ 0.2cm broad, linear, oblong to obovate or orbicular, flat, sometimes revolute but not channelled below 4
- 3b. Leaves \leq 0.2cm broad, linear, convex above, strongly revolute & channelled below 6
- 4a. Sepals caducous; fruiting pedicel $>$ 4mm long; seed arillate; stamen filaments \geq 0.5mm long; leaves usually $>$ 1.5cm long, usually oblanceolate, rarely obovate or linear 29. *D. humifusa*
- 4b. Sepals persistent; fruiting pedicel $<$ 3.5mm long; seed exarillate; stamen filaments \leq 0.5mm long; leaves usually $<$ 1.5cm long, usually linear or obovate, rarely orbicular 5
- 5a. Leaves $>$ 0.3cm broad (rarely 0.3cm broad), obovate, rarely oblanceolate to orbicular, with sessile glands, with petiole 0.5-1.5mm long; capsule angled, transverse-oblong in lateral view, usually $>$ 5.5mm broad, not speckled, appendage 0.5-1mm broad 30. *D. baueri*
- 5b. Leaves \leq 0.3cm broad, linear to oblong, rarely narrow-elliptic, with brown verruculose glands, subsessile; capsule globose, broad-obovate in lateral view, $<$ 5.5mm broad, speckled, appendage $<$ 0.5mm broad 31. *D. tepperi*
- 6a. Leaves alternate, glabrous, entire; pedicels glabrous; capsule 3-angled, glabrous 32. *D. hexandra*
- 6b. Leaves opposite, pubescent, usually with 2(3-4) teeth above the middle, rarely entire; pedicels pubescent; capsule 4-angled, densely pubescent 33. *D. ericoides*
- 7a. Leaves \leq 1.2cm long, angular-obovate, apex tri-dentate or 3-lobed for distal $\frac{1}{3}$ of leaf, pilose; pedicels $<$ 2mm long 35. *D. trifida*
- 7b. Leaves $>$ 1.2cm long (rarely 1.2cm long), obovate to obtriangular, apex acute or if tri-dentate or 3-lobed then only for distal 1-2mm of leaf, pubescent with adpressed hairs; pedicels $>$ 3mm long . 34. *D. triangularis*

28. *Dodonaea aptera* Miq. in Lehm., Pl. Preiss. 1:225 (1845); Bentham, Fl. Aust. 1:481-482 (1863); Mueller, Fragm. 9:88 (1875); Radlkofer, Pflanzenreich IV.165:1396 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).
 TYPE: "Crescit in clivulo calcareo Arthur's-head (Perth) et in insulis Garden-island et Rotenest, 9 Nov. 1839. Herb. Preiss No. 2439." Lectotype (here designated): L. Preiss 2439, In Nova Hollandia ora occid. in clivulo calcareo Arthur's-head (Perth) et in insulis Garden island et Rottenest, 9.xi.1839. fr. (U91880). Isolectotypes: MEL84077, P.

D. sororia Miq. in Lehm., Pl. Preiss. 1:225-226 (1845). [Bentham, Fl. Aust. 1:482 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1396 (1933) pro syn.]
 TYPE: "Crescit in collibus arenosis insulae Rotenest 20 Aug. 1839. Herb. Preiss No. 2388." Lectotype (here designated): L. Preiss 2388, in Novae Hollandia ora occid. in collibus arenosis ins. Rottenest, 20.viii.1839. f.fl. (U91879). Isolectotypes: MEL84137, L,P,W.

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956).

DESCRIPTION (Fig. 7.32):

Dioecious shrub, 1-3.5m high, erect. Branches dense, spreading; branchlets angular, or furrowed, sometimes flattened. Leaves simple; petiole (2.5-)4-8(-10.5)mm long; lamina elliptic, sometimes broad- or narrow-elliptic, rarely obovate, (2.2-)3-4.5(-6) x (1-)1.5-2.5(-3.2)cm, olive-green above, paler below, coriaceous, with sessile glands, young leaves viscous, older leaves slightly scurfy, glabrous, base attenuate, tapering to petiole, margin entire, apex obtuse, sometimes retuse, mid-vein prominent, lateral secondary venation conspicuous on upper surface,

usually obscure below. Flowers unisexual, & rarely falsely bisexual (see Notes), arranged in terminal botryoids or panicles; pedicels (3-)4-6(-7)mm long, longer in female flowers than in male flowers. Sepals 4, lanceolate, 2.5-3 x 0.9-1.3mm, acute, viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrous, caducous; at anthesis the sepals in male & bisexual flowers are spreading or recurved, in female flowers they are erect, surrounding the ovary, free & sometimes imbricate; caducous. Stamens in male & bisexual flowers 8, exerted beyond sepals, widely divergent; filaments 0.5-0.7mm long, glabrous; anther lobes oblong, 1.3-2.3 x 0.7-1mm, glabrous; apical appendage triangular-acuminate, 0.2mm long, glabrous; stamens in female flowers absent. Ovary in female flowers 4-carpellate, obovoid, 4-angled, 0.9-1.2 x 0.8-1mm, glabrous, viscous, completely covered with a thick layer of resin; styles 4, connate, twisted spirally or straight, 9-10.5mm long, glabrous, viscous, separating unequally near the apex, each free arm 0.1-0.5(-1)mm long, recurved; ovary in bisexual flowers smaller than in female flowers, 0.7-0.9 x 0.5-0.7mm; styles 3-3.5mm long; in male flowers rudimentary ovary usually present. Capsule 4-angled, in lateral view transversely broad-obovate or broad-oblong, 5-6 x 6-7mm, crustaceous & thickened, glabrous, with sparse sessile glands, scurfy when dry, cinnamon to pinkish-brown at maturity, base & apex truncate; carpel deeply navicular, excluding appendage 4.5-5.5(-6) x 2.5-3mm; appendage usually present, narrow, lobe-like, at apex only, 0.5-1mm long, obtuse, much narrower than the valve, crustaceous; dehiscence septifragal. Seeds 2-3, lenticular-globose, 2.4-3 x 2.4-2.5mm, black, shiny; aril white, infundibular, 1.7-2mm long. Seedling very sparsely pubescent; hypocotyl 10-20mm long; cotyledons linear, 20-40 x 1mm, acute, glabrous; epicotyl 13-16mm long; first 2-6 leaves simple, alternate, petiolate, obtriangular to obovate, base attenuate, tapering to the petiole, margin entire, apex irregularly lobed or toothed, becoming obtuse in later leaves.

Chromosome number: not known

TYPIFICATION:

Lectotypification is necessary for *D. aptera* Miq. as the type collection consists of at least three specimens (U,MEL,P), none of which were designated by the author as the holotype. Miquel's herbarium and types are held at U, but Preiss collections were widely distributed among herbaria. There are similarities in the handwriting on the label of the U specimen with that of Miquel (Burdet, 1977), but the likeness is not clear enough to make a certain identification. The U specimen is the most complete, containing one whole fruit with valves and one seed, while the MEL specimen contains damaged valves and the P material has fruit dissepiments only. The specimen held at Utrecht (U91880) is therefore chosen as the lectotype.

DISTRIBUTION (Fig. 7.32):

D. aptera is restricted to part of the south-west coast of Western Australia. It occurs in a coastal strip from the Abrolhos Group of islands at Geraldton in the north to Yallingup/Canal Rocks area (west of Busselton) in the south.

ECOLOGY:

This species is usually found on coastal limestone cliffs or on shallow sand over limestone. In the southern range of its distribution it is often a large shrub in *Eucalyptus gomphocephala* open woodland.

Flowering occurs in the autumn to early winter months of April to June, and mature fruits are usually present from August to December.

NOTES:

Occasionally false bisexual flowers are present on predominantly male plants. No experimental work has been undertaken with this species, but it appears from field observations and herbarium material that the ovary of the bisexual flower is not fertile. The ovary and style are considerably smaller in the bisexual flower than in the female flower.

AFFINITIES:

D. aptera shows some affinities with *D. humifusa* & *D. ceratocarpa*, but it is a very distinct species, and can be readily distinguished from them. The fruits of this species and *D. humifusa* are similar, however *D. humifusa* is usually puberulent and has smaller, oblanceolate, sessile leaves, few-flowered, simple inflorescences, larger flowers with long pedicels, and dull, dark grey seeds. *D. aptera* sometimes resembles *D. ceratocarpa* in leaf morphology, but the horned fruit of the latter species enables the two to be distinguished.

SPECIMENS EXAMINED: selection only (29 collections examined)

WESTERN AUSTRALIA:- C. Andrews s.n., Blackwall Reach, Applecross (Perth), ix.1902. fr. (PERTH).- C. Andrews s.n., Claremont (Perth), vi.1903. f.fl. (PERTH).- George 14842, below Devil's Elbow, Bindaring Pde., Peppermint Grove (Perth), 21.viii.1977. immat.fr. (PERTH).- Meadly s.n., Garden Island, v.1946. m.fl. (PERTH).- Paust 1336, Yalgorup National Park, 20.x.1972. fr. (PERTH).- West 3246, 0.5km E of Canal Rocks, 32km W of Busselton, 3.xii.1978. st.(AD).- West 3248, loc. cit., 3.xii.1978. fr. (AD).- West 3257, Devil's Elbow, Peppermint Grove (suburb of Perth), W of Freshwater Bay, 5.xii.1978. m.fl. (AD).- West 3261, loc. cit., 5.xii.1978. fr. (AD).

29. *Dodonaea humifusa* Miq. in Lehm., Pl. Preiss. 1:226 (1845); Bentham, Fl. Aust. 1:482-483 (1863); Mueller, Fragm. 9:88 (1875); Radlkofer, Pflanzenreich IV.165:1397-1398 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).

TYPE: "Crescit in limoso-glareosis districtus Hay. Oct. 1840. Herb. Preiss. No. 2441." Lectotype (here designated): L. Preiss 2441, in Nova Hollandia ora occ. in limoso-glareosis districtus Hay, x.1840. fr. (U91924). Isolectotypes: Preiss 2441, in limoso-glareosis districtus Hay, X.1840. fr. (MEL84100); Preiss 2441, in Nova Hollandia, (Swan River Colonia, district Hay), 1843. fr. (MEL84099); Preiss 2441, in Col. Swan River, 1843. fr. (G); Preiss 2441, s.dat.st. (L908.269-892), fr. (W).

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956).

DESCRIPTION (Fig. 7.33):

Dioecious or rarely polygamo-dioecious shrub, prostrate, to 1m diam. Branches dense, prostrate, often rooting at the nodes; branchlets angular or biconvex. Leaves simple, sessile, oblanceolate to obovate, rarely linear, (1-)1.5-2.5(-4) x (0.2-)0.3-0.6(0.8)cm, coriaceous, with sessile glands, young leaves viscous, glabrous or sparsely puberulent on margin & midrib, base attenuate, with raised leaf scar, margin revolute, sometimes thickened, entire or with (1-)2(-4) irregular teeth or lobes up to 2mm long & usually near the apex, apex acute, sometimes mucronate, midvein prominent, lateral venation sometimes visible. Flowers unisexual & rarely bisexual, monadic, in 3-4-flowered compound inflorescences, terminating branchlets; pedicels erect, in male & bisexual flowers (11-)13-22(-28)mm long, in female flowers (4.5-)5-6mm long. Sepals 4(-5), ovate, (2.3-)3.5-4.5(-5) x (1.3-)2-3mm, smaller in female flowers, acuminate or acute,

viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrous, caducous; at anthesis the sepals in male flowers are recurved, in female flowers they are closed around the ovary & in bisexual flowers they are separated to form an open cup-shaped structure. Stamens in male & bisexual flowers 8(-9), approx. equal in length to sepals, divergent, or erect in bisexual flowers; filaments 0.5-1.2mm long, glabrous; anther lobes oblong, 2.3-3.5 x 0.6-0.7mm, glabrous; apical appendage triangular-acuminate, 0.3-0.4mm long, puberulent; stamens in female flowers absent. Ovary in female & bisexual flowers (3-)4(-5)-carpellate, oblong, (3-)4(-5) angled, 1-1.2 x 0.8-1mm, viscous, glabrous or sparsely puberulent; styles 4, connate, twisted spirally or straight, 10-22mm long, glabrous, usually separating unequally at the apex, each free arm being less than 0.1mm long, recurved; in male flowers rudimentary ovary present. Capsule (3-)4(-5)-angled, broad-obovoid, rarely oblong, (4-)4.5-8(-8.5) x 4.5-7.5(-8)mm, crustaceous, with sessile glands, glabrous or sparsely puberulent when young, light to pinkish-brown at maturity, base truncate, rounded or rarely broad-cuneate, apex truncate, rarely obtuse; carpel navicular, excluding appendage (4-)4.5-8(-8.5) x 1.5-3mm; appendage sometimes absent, narrow, lobe-like, at apex only, 0.5-1mm long, much narrower than the valve, crustaceous; dehiscence septifragal. Seeds 3-4, lenticular, 1.7-2 x 1.6-2mm, dark grey to black, dull; aril white, infundibular, 1-1.2mm long. Seedling not seen.

Chromosome number: not known.

TYPIIFICATION:

Six specimens of the type collection (Preiss 2441) have been examined, i.e. one from each of U,G,W, & L and two from MEL. Apart from the L specimen, which is sterile, they all contain fruit and most are in

reasonable condition. The W specimen is without locality or date and the material from G and one MEL specimen (MEL84099) give '1843' as the date of collection. The labels accompanying the U & MEL84100 specimens contain information exactly as in the type citation. The U specimen, which contains seed as well as fruit has been chosen as the lectotype primarily because it is kept in the same herbarium in which Miquel worked (and was therefore used by him in describing this species) and in which his types and herbarium are housed.

DISTRIBUTION (Fig. 7.33):

D. humifusa is restricted to a small area of the south-west of Western Australia. It occurs north of the Stirling Ranges as far as Narrogin and extends to Jerramungup in the east.

ECOLOGY:

This species is typically found as a prostrate, mat-like shrub in open *Eucalyptus wandoo* woodlands. It grows mainly in sandy loam which may be gravelly with a clayey subsoil, usually in flat or slightly undulating country and often associated with grass species. *Acacia acuminata* & *Casaurina* spp. are commonly found in these habitats, which mainly occupy the wheat belt area of Western Australia.

NOTES:

1. The long styles in the female flowers and the very long pedicels in the male and bisexual flowers probably indicate an attempt to raise the reproductive structures above the prostrate and dense foliage. This is especially necessary for wind pollination mechanisms.

2. Mueller in the "Fragmenta" (1875) cited a collection of *D. humifusa* from the granite hills of King George's Sound. MEL contains

a fruiting specimen from this locality with a label in Mueller's handwriting and dated Nov. 1867. This specimen belongs to *D. ceratocarpa* and was wrongly identified as *D. humifusa*, which is not found south of the Stirling Ranges.

AFFINITIES:

D. humifusa is most closely related to *D. procumbens* from the south-east of Australia. The leaves are very similar and the two species are of the same prostrate habit and occupy similar habitats. They can be distinguished easily on flower and fruit characters. *D. procumbens* has a winged fruit, the fruit itself is larger than that of *D. humifusa*, the sepals are smaller and the aril is absent from the black seed. The fruit of *D. humifusa* shows affinities to *D. aptera* fruits, but the two species can be differentiated by the larger, glabrous, elliptic, petiolate leaves, the smaller flowers arranged in more complex inflorescences and the shiny black seeds of *D. aptera*. The leaves of *D. ceratocarpa* & *D. humifusa* look similar in dried specimens, but are distinguished with fresh material, and the fruits of the former species are horned.

SPECIMENS EXAMINED: selection only (35 collections examined)

WESTERN AUSTRALIA:- Chinnock 4377, 13km SE of Jerramungup on Gairdner R., 12.xi.1978. fr. (AD).- George 14992, Fisher rd. turnoff, Kojonup-Frankland rd., 1.xi.1977. buds, m.fl., bisex.fl. (PERTH).- Morrison s.n., Broomehill, 16.iv.1904. m.fl./f.fl. (PERTH).- Morrison s.n., Narrogin, 21.iv.1904. f.fl. (BRI217665).- West 3057, Stirling Ra. N.P., 31.4km E of Borden, N of Stirling Ra., 26.xi.1978. fr. (AD).- West 3061, loc. cit., 26.xi.1978. fr. (AD).- West 3063, loc. cit., 26.xi.1978. fr. (AD).- West 3088, 21.2km NW of Katanning on rd. to Wagin, 27.xi.1978 fr. (AD).- West 3089, loc. cit., 27.xi.1978. f.fl. (AD).

30. *Dodonaea baueri* Endl. in Enum. Pl. Hügel 13 (1837); Bentham, Fl. Aust. 1:482 (1863); Mueller, Fragm. 9:87 (1875); Ewart, Fl. Vic. 739 (1931); Radlkofer, Pflanzenreich IV.165:1398 (1933); Black, Fl. S. Aust. edn 1. 363 (1926), edn 2. 541 (1952); Willis, Hdbk. Pl. Vic. 2:359 (1972).
 TYPE: "Salt Island, South Coast. (Ferd. Bauer.)". Neotype (here designated): West 1170, South Australia, Mt. Remarkable National Park, 50km SE of Port Augusta. 3km SW of Black Hill on northern scarp of Davey's Creek, 32°51'S 138°03'E, 11.x.1975. fr. (AD98008411). Isonotype: to be distributed.

D. deflexa F. Muell., Trans. Phil. Soc. Vic. 1:8 (1855), published again in Hooker's J. Bot. Kew Gard. Misc. 8:33 (1856); Mueller, Pl. indig. Col. Vic. 1:87 (1862); [Bentham, Fl. Aust. 1:482 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1398 (1933) pro syn.]

TYPE: "In the desert scrub along the Murray River and Spencer's Gulf."
 Lectotype (here designated): Behr s.n., Lovis saxosis ad fl. Murray iv.1849. f.fl. (MEL). Syntype: Mueller s.n., Spencer's Gulf, s.dat. m.fl. (MEL).

DESCRIPTION (Fig. 7.34 & 7.74):

Dioecious shrub, to 1m high, spreading, sometimes prostrate. Branches intricate, rigid; branchlets angular, with sessile glands, densely puberulent. Leaves simple; petiole 0.5-1.5mm long; lamina obovate, rarely broad-oblong or orbicular, (0.5-)0.6-1.2(-1.8) x (0.3-)0.4-0.7(-1)cm, when fresh dark green above & slightly paler green below, coriaceous, viscous, with sessile glands, glabrous to sparsely puberulent, becoming denser towards margin, base narrowly cuneate, margin slightly recurved, undulate, unevenly dentate or repand, apex truncate or rounded, irregularly 3(-6)-toothed, midvein impressed above, prominent on lower surface, lateral venation usually obscure. Flowers unisexual, monadic,

very rarely diadic, axillary; pedicels reflexed, 2-3.2mm long, sparsely puberulent to glabrous. Sepals 4(-5), ovate, (1.6-) 2-2.5(-2.8) x (1.2-) 1.5-2(-2.3)mm, acute, outer surface sparsely puberulent, inner margin villous, both surfaces sometimes almost glabrous; at anthesis the sepals in male flowers are spreading & revolute, in female flowers they are closed around the ovary & valvate, persisting in fruit, becoming revolute & strongly recurved. Stamens in male flowers 8, approx. equal in length to sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 2-2.6 x 0.9-1.2mm, glabrous; apical appendage pyramidal-acute or -obtuse, 0.2mm long, with simple hairs; stamens in female flowers rarely present, rudimentary, 0.6-0.7mm long. Ovary in female flowers (3-)4(-5)-carpellate, ovoid to oblong, angled, 1-1.6 x 1-1.5mm, glabrous, viscous, completely surrounded by thick layer of resin; styles (3-)4, connate, 2.7-8mm long, glabrous, viscous, separating at the apex, each free arm 0.1-0.2mm long, usually straight, sometimes recurved; in male flowers rudimentary ovary usually present. Capsule (3-)4(-5)-angled, in lateral view transversely oblong, 4-5 x 5.5-8(-10)mm, crustaceous, thickened, with sessile glands, sparsely puberulent, dark red to brown at maturity, base & apex truncate; carpel navicular, excluding appendage 3.5-4(-4.5) x 2.5-3.5mm, including appendage (when present) 4-5 x 3.5-4mm; appendage sometimes present, a narrow wing, above middle of capsule only, 0.5-1mm broad, much narrower than the valve, crustaceous; dehiscence septifragal. Seeds 1-2, lenticular, 2-2.4 x 1.7-2.3mm, black, dull; aril apparently absent, enlarged funicle brown, bi-lobed & globular, 0.5mm long. Seedling glabrous, hypocotyl 5-8mm long; cotyledons linear, 10-12 x 1.2mm, acute, glabrous; epicotyl 1mm long; first 2-6 leaves simple, alternate, petiolate, obovate or spatulate, base attenuate, tapering to the petiole, margin entire, apex 3-lobed, the lobes sometimes further divided, obtuse.

Chromosome number: n=14 (West 1738)

TYPIFICATION:

D. baueri was described by Endlicher from material collected and/or illustrated by Bauer - "Salt Island, South Coast (Ferd. Bauer)". It is not known whether Bauer illustrated this species, or whether Endlicher's citation refers to a specimen collected by Bauer or an illustration by him. Bauer accompanied R. Brown on the Flinders Expedition (1801-1805) and his illustrations were mostly based on material collected by or in the care of Robert Brown (BM) (Stafleu and Cowan, 1976). Bauer completed only 236 drawings of Australian plants of the 2073 sketches of items of natural history which he began while associated with Brown and Flinders. These completed illustrations are held at BM and do not include *D. baueri* (R.J. Henderson, BRI, pers. comm. 1979). The remaining sketches are probably those referred to by Britten (1909) as being held at Vienna (W). Apparently some of these were filed with the herbarium specimens (Dr. P. Green, K, pers. comm. 1979), many of which were destroyed during world war II. It is not known whether Sapindaceae was among the dicot families which were affected by war action. There is no Bauer illustration of this species at W now (Riedl, W, pers. comm. 1979), but this does not preclude the possibility that he did sketch *D. baueri*.

Endlicher's protologue includes details of the capsules, and so he must have had access to fruiting specimens (or illustration). Bauer's herbarium is housed at W, but no *D. baueri* specimens collected by him have been located there or in any other of the major European or Australian herbaria.

Hügel's collections were acquired by W in January, 1839 (Stafleu and Cowan, 1976), but the Vienna herbarium does not contain any *D. baueri* specimens from his collections now.

Stearn's introduction to the 1960 facsimile edition of Robert Brown's "Prodromus Florae Novae Hollandiae" gives no clue as to the identity or location of Salt Island. Brown's manuscript of descriptions of Australian plants and Flinder's account of the "Voyage to Terra Australis" (Flinders, 1814) make no mention of such an island. Given the present distribution of *D. baueri* and the locations on the "South Coast" at which Brown is known to have collected (Stearn, 1960), the type location could be anywhere between Fowler's Bay on the west coast of South Australia and the eastern end of Kangaroo Island.

Three Robert Brown specimens of *D. baueri* which were collected on the Flinders expedition have been found. Two of these (MEL, BM) are annotated "South Coast, Inlets XII and XIV, 10.iii.1802", and the third specimen from K, of which I have seen a photograph only, includes a label stating "Dodonaea repanda Inlets XII and XIV". Although flowers are present, none of these specimens contain fruit. Radlkofer (1933) cited a Robert Brown fruiting specimen, which he saw: "R Brown! (South Coast, Inlets XII and XIV fr.; Hb. Berol. ex Hb. Kew.)", but this specimen is not at B now. It too may have been destroyed through war action.

Since it appears that neither an illustration nor specimen(s) on which Endlicher's description was based is extant, a neotype should be chosen. The neotype must be in accordance with the protologue and therefore should at least include fruit. If the type locality was known it would be possible to select a neotype from that population, or one in close proximity to it. Given that Salt Island has not been located consideration should be given to collections of this species which were made during the Flinders expedition. The Robert Brown *D. baueri* specimens from inlet XII mentioned above, were collected on the same day that both Bauer and Brown went to Mt. Brown (23km east of Port Augusta) (Brown, ms. unpubl. ; Flinders, 1814). Since this is the only area from which it is

definitely known that *D. baueri* was collected during the journey, the neotype has been chosen from a population also in the Southern Flinders Ranges, i.e. near Mt. Remarkable which is slightly south of Mt. Brown.

Lectotypification is necessary for the name *D. deflexa* F. Muell., as Mueller did not designate any one specimen (or locality) as the type and at least two specimens now at MEL were almost certainly available to him when he described this species. The Behr collection is chosen as the lectotype as it is dated and the sheet bears a label in Muellers' handwriting.

DISTRIBUTION (Fig. 7.34):

D. baueri is endemic to the southern districts and Flinders Ranges of South Australia. It is widespread on Eyre Peninsula, extending to Fowler's Bay in the west, on Yorke Peninsula and northwards into the Flinders Ranges. It is also found on Kangaroo Island and was locally common in the vicinity of the Murray River mouth, an area which has suffered greatly from the spread of human habitation and recreational activities.

ECOLOGY:

The distribution of this species fairly closely matches the 250-500mm annual rainfall zone in temperate South Australia. It usually grows on rocky hillsides and exposed sites on mountain ridges and in the more arid areas of its distribution it is confined to isolated hills or mountains, e.g. Mt. Whyalla and the Gawler Ranges of Eyre Peninsula. In the Flinders Ranges *D. baueri* is often found in gorges or along rocky creek beds. In north-central Yorke Peninsula and the Murray region it grows as a low understorey shrub on red-brown sandy loam in mallee scrub, often associated

with *Eucalyptus porosa*, *E. oleosa*, *Melaleuca lanceolata* and *M. uncinata*. On the north-west coast of Yorke Peninsula *D. baueri* assumes a prostrate cliff-hugging form on exposed granitic-gneissic cliffs.

Flowering time varies over the distributional range of the species, but most populations flower in summer, usually December to March or April. Mature fruit is present from approximately August to November.

NOTES:

D. baueri has been recorded previously from Victoria, New South Wales and Western Australia, but all of these localities are considered to be extremely doubtful.

Ewart (1931) recorded *D. baueri* in Victoria as "'on the Murray' and very rare, if Victorian". There are no specimens from Victoria in Australian or major overseas herbaria, nor has it been found in that state during field work associated with this study. One NSW specimen collected by Betcher cites the locality as "Murray River". Given that *D. baueri* does not occur east of 140°E it is most likely that this specimen was collected on the Murray River in South Australia (west of 140°E) and not in Victoria.

In the "Fragmenta" (1875) Mueller included *D. baueri* with *D. bursariifolia* - "ad flumina Darling's River et Murrumbidgee". However, these localities probably refer to *D. bursariifolia*, a species which is found on these rivers now.

One extremely doubtful Western Australian record of *D. baueri* exists, viz. Phillips 320A, 21 miles from Balladonia Homestead, W.A., towards Norseman, 3.ix.1968 (CBG38538, PERTH). This number has been added to Phillips' field notebook in ink (probably at a later date), the other collections at the same locality (Phillips 318-326) being in pencil. The notebook also records the locality as "21 miles from Balladonia Motel towards Norseman" (M.D. Crisp, CBG, pers. comm. 1978). Balladonia Motel

is c. 43.2ml (27km) by road west of the homestead. (The PERTH duplicate cites the locality as "21 miles from Balladonia towards Norseman"). There is no guarantee that this specimen was collected in Western Australia. There are no other records west of Fowlers Bay in S.A., and in 1978 the species was not located during extensive searches at all possible distance permutations from Balladonia Motel and Homestead.

AFFINITIES:

D. baueri is a distinct species showing little close relationship to any others. The fruit occasionally shows similarities to those of *D. bursariifolia*, from which *D. baueri* can be distinguished by the complete, although narrow wing of *D. bursariifolia* capsules. The leaves of the two species differ greatly. *D. baueri* leaves most closely resemble those of *D. intricata* in shape, size and texture, but the latter species has a well developed wing on the fruit. In the Gawler Ranges where these two species are sympatric they exhibit a similar habit, and apart from *D. intricata* occupying slightly higher slopes they are found in a very similar habitat.

SPECIMENS EXAMINED: selection only, including historical collections
(203 collections examined).

SOUTH AUSTRALIA:- Blaylock 1566, Southern Yorke Peninsula, Hundred of Ramsay, 10.x.1970. fr. (AD).- Brown 5429, Spencer's Gulf, (Bay 12), 10.iii.1802. m.fl. (BM).- Brown s.n., Inlets XII & XIV, s.dat. f.buds (MEL84078).- Donner 3758, Finniss, 55km SSE of Adelaide, 15km W of Milang, 26.x.1971. fr. (AD).- Lothian 1240, Northern Flinders Ra., Edeowie Ck., 55km N of Hawker, 24.vii.1955. fr. (AD).- Rohrlach 85, Eyre Peninsula, 20km S of Kimba, 31.i.1959. m.fl. (AD).- West 1171, Southern Flinders Ra., Mt. Remarkable N.P., 3km SW of Black Hill on northern scarp of Davey's Ck., 11.x.1975. fr. (AD).- West 1274, Kangaroo Is., 4km S of Macgillivray &

25km S of Kingscote, 22.xii.1975. m.fl. (AD).- West 1275, loc. cit.,
22.xii.1975. f.fl., fr. (AD).- West 1738, 9km N of Monarto South on rd.
to Rockleigh, 16km NW of Murray Bridge, 27.ii.1976. m.fl. (AD).- West
1739, loc. cit., 27.ii.1976. f.fl. (AD).- West 2163, Gawler Ras., Barber
Hill, 7km SE of Hiltaba HS., 30.viii.1977. f.fl. (AD).

31. *Dodonaea tepperi* F. Muell. ex Tepper, Append. Pl. Ardrossan, Yorke Pen. in Trans. Roy. Soc. S. Aust. 3:176,178 (1880); Radlkofer, Pflanzenreich IV.165:1398 (1933); Eichler, Suppl. to Black, Fl. S. Aust. 215 (1965).
 TYPE: "on a stony hillside, near Ardrossan". Lectotype (here designated): J.G.O. Tepper 957, Yorke Peninsula, s.dat. fr. (MEL84140). Isolectotypes: Tepper 957, s.loc., s.dat. fr. (MEL); Tepper 957, Ardrossan, very rare on Tertiary ground adjoining Silurian, vi.1880. fr./f.fl. (AD97732739). Probable syntypes: Tepper s.n., Ardrossan, 1880. f.fl./m.fl. (AD96234011); Tepper s.n., Yorke Peninsula, s.dat. f.fl./m.fl. (MEL84141); Tepper s.n., Ardrossan, Yorke Peninsula, s.dat. immat.fr. (BRI71904).

DESCRIPTION (Fig. 7.35):

Dioecious or rarely polygamo-dioecious shrub, to 0.6m high, spreading. Branches dense, intricate; branchlets angular, puberulent. Leaves simple, sessile, linear, oblong or narrow-elliptic, (0.8-)1-1.2(-1.4) x (0.1-)0.2-0.3cm, thick, coriaceous, appearing striate when dry, with brown verruculose glands, viscous especially when young, glabrous, base attenuate, margin thickened, revolute, entire or irregularly sinuolate or repand, apex acute or obtuse, midvein impressed above, sometimes conspicuous below, lateral venation obscure. Flowers unisexual & rarely bisexual, monadic, axillary; pedicels (1-)1.5-2.6mm long, glabrous. Sepals 3-4, ovate, (1.8-)2.5-3(-3.3) x (1-)1.5-2(-2.4)mm, acute, viscous, outer surface glabrous, with verruculose glands, inner margin villous, inner surface becoming glabrous towards base, persistent; at anthesis the sepals in male flowers are spreading, in female & bisexual flowers they are erect, valvate, surrounding the ovary, strongly recurved in fruit. Stamens in male & bisexual flowers 6-8, approx. equal in length to the sepals, erect; filaments 0.3-0.5mm long, glabrous; anther lobes oblong and curved, 2-2.4 x 0.6-1mm, glabrous; apical appendage broad-triangular, 0.2mm long,

with short bristle-like hairs; stamens in female flowers absent. Ovary in female & bisexual flowers 3-4-carpellate, oblong, 3-4-angled, 1-1.5 x 0.6-1mm, glabrous, viscous with a thick layer of resin; styles 3-4, connate, to 8mm long, glabrous, separating unequally near the apex, each free arm up to 0.3mm long, recurved; in male flowers rudimentary ovary present. Capsule 3-4-angled, in lateral view broad-obovate, 4-5 x 5-5.5mm, crustaceous, glabrous, dark red-brown & irregularly orange speckled at maturity, base broad-cuneate, apex truncate; carpel broad-navicular, excluding appendage 4-5 x 1.5-2.5mm; appendage often absent, narrow, lobe-like, at apex only, usually less than 0.5mm long, much narrower than the valve, crustaceous; dehiscence septifragal. Seeds 0-2, lenticular, 2-2.3 x 1.5-1.8mm, dark grey to black, dull; aril apparently absent, enlarged funicle brown, 1-1.2mm broad. Seedling not seen.

Chromosome number: $n = 14$ (West 1342)

TYPIIFICATION:

Since the diagnosis distinguishes this species on its speckled fruits the type collection must include mature fruit. Six sheets of *D. tepperi* specimens collected by Tepper from Ardrossan or Yorke Peninsula in 1880 (or possibly that year) have been found (two at AD, three at MEL and one at BRI). BRI71904, which is undated, contains one immature fruit, AD96234011 consists of one specimen with female flowers and another with male flowers, and MEL84141, which is not dated, also includes one specimen with male flowers and two with female flowers. The three remaining sheets are all annotated by Tepper as number 957 and each of them contains mature fruit. Of these three, MEL84140 and MELs.n. each consist of three separate specimens which appear to be uniform and are almost certainly of the same collection, while AD97732739, which is part of Tepper's reference herbarium, contains two *D. tepperi* specimens, one with two fruit and one with female flowers.

Associated with one of the Melbourne herbarium fruiting specimens (MEL84140) is a letter from Tepper to Mueller dated '14th September 1880', in which Tepper mentions that he is sending fruiting material of the *Dodonaea* ("bei *Dodonaea*") to Mueller. The reference to the *Dodonaea* in this letter and on the label accompanying MELs.n., which indicates that Tepper had recollected the plant, implies that previous correspondence regarding this species had taken place between the two gentlemen. It is likely that Tepper had previously sent flowering material to Mueller who indicated that fruits were needed for a certain identification. Subsequently Tepper collected fruits and sent them to Mueller in September, 1880.

Tepper attributes the name of this taxon to Mueller. The diagnosis published by Tepper distinguishes the species primarily on the mature fruit and Tepper made reference to the peculiar speckled nature of the fruit in the above-mentioned letter to Mueller with (presumably) the first fruiting specimens Mueller had seen. Flowers are not mentioned in the diagnosis, probably because they were not different from those of other species and not because they had not been seen at that time. In fact it seems likely that Tepper collected female flowers in June, 1880. The label in Tepper's handwriting (in German) on the fruiting MELs.n. sheet refers to the flowers collected in June and AD97732739, consisting of one female-flowered specimen and one with fruit is dated June, 1880. This may be the collection that was first sent to Mueller.

It therefore appears as though these six sheets of specimens are syntypes. Since Tepper's diagnosis states that only one plant was known at the time of publication it is very likely that the female-flowering and the fruiting specimens were separate collections from the same plant and that the male specimens (on MEL84141 & AD96234011) were collected from a different individual at a later date, probably after publication. This species is polygamo-dioecious and has a very small number of bisexual flowers

on some predominantly male plants, but never any male flowers on female plants. Thus, the male-flowering specimens have been collected from a separate individual.

The MEL84140 material is here chosen as the lectotype, with MELs.n. & AD97732739 being isolectotypes, for the following reasons:

- it contains the best specimen of the only collection which can be definitely allied to the diagnosis - i.e. the fruiting material containing Tepper's no. 957;
- the sheet was seen by both Mueller and Tepper;
- Tepper's letter regarding the fruiting specimen being sent to Mueller accompanies this sheet;
- the fruiting specimen (AD97732739) from Tepper's reference collection is very small and contains only two fruits. (Tepper collected for Mueller and it is likely that he sent the better specimens to the botanist and kept only a representative of it for himself).

The other three specimens are regarded as probable syntypes, as BRI71904 is not dated and may have been collected after the publication of the diagnosis and both MEL84141 & AD96234011 include male-flowering specimens which were probably not collected before the publication. However, the female specimens on these sheets (the AD one is dated 1880), which are in a different growth phase, were probably available to Tepper at the time he described the taxon.

DISTRIBUTION (Fig. 7.35):

D. tepperi is an endemic and extremely rare South Australian species, which is now known from one locality only, i.e. in the Monarto area (35°03'S 139°08'E) in the Murraylands of South Australia. Even at this

site the "population" appears to consist of one plant only. Fig. 7.35 indicates the small number and disjunct nature of the localities from which the species has been collected in the past.

J.G.O. Tepper in 1880 was the first to collect the species at Ardrossan ($34^{\circ}26'S$ $137^{\circ}55'E$) on the east coast of Yorke Peninsula. He subsequently collected it in "Spencer's Gulf", and other early collectors found *D. tepperi* in localities as widespread as the "Gawler Ranges", "Port Lincoln" & "Port Elliott". It was not until 1975 that the species was rediscovered in the Monarto area. However, extensive searches have not located it anywhere else in South Australia.

ECOLOGY:

The only habitat data available for this species is that of the Monarto area. This is a disturbed agricultural site, but natural regeneration of some of the indigenous flora has given some insight into the type of plant community in which the species probably grew in the past.

The Monarto area is regarded as semi-arid with a 250mm annual rainfall, and the only known *D. tepperi* individual is growing in a *Eucalyptus dumosa* mallee shrubland community. Several larger shrubs such as *Acacia microcarpa*, *Acacia argyrophylla* & *Eremophila glabra*, and many smaller chenopodiaceous species, e.g. *Maireana brevifolia*, *Enchylaena tomentosa* & *Rhagodia crassifolia* are found in the understorey. This site is a disturbed roadside bounded on both sides by cleared grazing land. The soil is a grey sandy clay overlying limestone.

It is very likely that the Ardrossan habitat where Tepper found this species on Tertiary sandy clays over limestone was of a similar nature to the Monarto area. However, the east coast of Yorke Peninsula and particularly around Ardrossan has suffered greatly under man's agricultural pursuits and no natural vegetation occurs in this area now.

The one live plant available for study consistently flowered during summer, i.e. December to March. Fruit development takes place during winter and mature fruit, when they are produced, are present from August to November.

NOTES:

This species is obviously in danger of becoming extinct. Until 1975 when it was rediscovered during this study it had not been collected since 1894. It is now represented by one individual which is predominantly male, but which produces a small number of bisexual flowers each year.

This plant has been studied for 4½ years in an attempt to gather data on its reproductive biology. A tagging system was used to follow the development of the bisexual flowers. In two seasons a small number of fruit with viable seed was collected. Although some of this seed germinated, the seedlings did not survive beyond the cotyledon stage. Further discussion relating to the reproductive strategies of *D. tepperi* is included in Chapter 4.

Vegetative propagation has been successful, but plants originating in this manner are necessarily all derived from the one source of genetic variation. If re-establishment of the species in the field were to be attempted it would be desirable to have a female plant of different stock. This, however, is not mandatory as the species is probably self-compatible (see Chapter 4).

Several extensive searches of previous localities and similar habitat types have been made during this study, but no other plants have been found. On Yorke Peninsula two amateur botanists have been attempting to locate the species for more than 20 years. From the notes accompanying several of his herbarium specimens it is obvious that Tepper regarded *D. tepperi* as being a rare species when he collected it even in 1886

(AD97732734), and only one plant was known at the time the diagnosis was written. Further destruction of the habitat has occurred with land clearance for agricultural purposes. Hartley & Leigh (1979) included *D. tepperi* as an endangered and restricted endemic.

There is a possibility that *D. tepperi* is actually of hybrid origin, with the parent species being *D. baueri* & *D. viscosa*. This hypothesis is being investigated and will not be further discussed here.

AFFINITIES:

D. tepperi shows affinities to *D. baueri*, with which it shares such features as the development of an enlarged funicle, and similar solitary, axillary flowers. With *D. hexandra* this species shows similarities in fruit shape, but it can be clearly distinguished on leaf characters, especially leaf shape, and its speckled fruit.

SPECIMENTS EXAMINED:

SOUTH AUSTRALIA:- Hussey s.n., Port Elliot, 1894. fr. (MEL).- Schomburgk s.n., Port Lincoln, s.dat. m.fl. (AD96234012).- Spooner 4534, Monarto, Hundred of Mobilong, 20.i.1976. m.fl. (AD).- Spooner 5134, loc. cit., 24.ii.1977. m.fl. (AD).- Sullivan s.n., Gawler Ranges, s.dat. fr. (MEL).- Tepper 957, Ardrossan, Yorke Peninsula, vi.1880. fr. (MEL84140 - lectotype, MELs.n. & AD97732739 - isoelectotypes).- Tepper s.n., loc. cit., 1880. m.fl./f.fl. (AD96234011 - probable syntype).- Tepper s.n., Spencer's Gulf, 1880. immat.fr. (MEL, NSW108364).- Tepper s.n., Ardrossan, Fields Rivieri, 9.vii.1884. f.fl. (AD).- Tepper s.n., Ardrossan, 28.xi.1886. st. (AD97732734). Tepper s.n., Yorke Peninsula, s.dat. m.fl./f.fl. (MEL84141 - probable syntype).- Tepper s.n., Ardrossan, Yorke Peninsula, s.dat. immat.fr. (BRI71904 - probable syntype).- West 1342, Monarto, 9km N of Monarto South on rd. to Rockleigh, 16km NW of Murray Bridge, 27.ii.1975 - 24.ix.1978. m.fl., fr. (AD).

32. *Dodonaea hexandra* F. Muell., Trans. Vic. Inst. 1:117 (1855); published again in Hooker's J. Bot. Kew Gard. Misc. 8:33 (1856); Bentham, Fl. Aust. 1:483 (1863); Radlkofer, Pflanzenreich IV.165:1400 (1933); Black, Fl. S. Aust. edn 1. 363, fig.160N (1926), edn 2. 542, fig.693N (1952); Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956).

TYPE: "In the scrub near Port Lincoln, on limestone. C. Wilhelmi."

Lectotype (here designated): C. Wilhelmi s.n., Port Lincoln, s.dat.

immat.fr. (MEL). Isolectotypes: BM, W (2 sheets). Probable syntype:

Wilhelmi s.n., Port Lincoln, ex h. bot. Melb. mas. & foem., s.dat.

m.fl./f.fl. (MEL).

FIGURES: Black, Fl. S. Aust. edn 2. 539, fig.693N (1952).

DESCRIPTION (Fig. 7.36):

Dioecious shrub, to 0.6m high, spreading. Branches intricate; branchlets angular & furrowed, usually puberulent, red. Leaves simple, appearing clustered at the shoot apices, sessile, linear, channelled below, upper surface convex, (0.6-)0.8-1.4(-3.5) x 0.1(-0.2)cm, bright green, coriaceous, glabrous, with verruculose glands, viscous, base attenuate, with raised leaf scar, margin entire, strongly revolute, apex acute, venation obscure. Flowers unisexual, monadic, rarely diadic, axillary & terminal; pedicels 1-1.5mm long, usually reflexed, viscous. Sepals 3, ovate, (1.5-)1.8-2.5(-3.6) x 1-1.6mm, acuminate, viscous, outer surface glabrous, with brown verruculose glands, inner margin glutinous & puberulent, inner surface glabrous, persistent; at anthesis the sepals in male flowers are spreading, in female flowers they surround the ovary, are free at the apex only, valvate below. Stamens in male flowers 6, approx. equal in length to the sepals, erect; filaments 0.2-0.4mm long, glabrous; anther lobes oblong, 2-2.2 x 0.8-1mm, glabrous; apical appendage trian-

gular, 0.3-0.4mm long, pubescent; stamens in female flowers absent. Ovary in female flowers 3-carpellate, globose or oblong, sometimes 3-angled, 1-1.3 x 0.8-1.2mm, glabrous, viscous with thick resin layer; styles 3, connate, 3.5-8.5mm long, glabrous, separating unequally near the apex, each free arm up to 0.3mm long, recurved; in male flowers rudimentary ovary usually present. Capsule 3-angled, globose, in lateral view angular-obovate, 5-7 x 5-7(-8)mm, crustaceous, glabrous, viscous when young, with verruculose glands, often scurfy when dry, brown at maturity, base broad-cuneate or rounded, rarely truncate, apex acute, sometimes rounded; carpel broad-navicular, excluding appendage 5-7 x 2-3mm; appendage usually absent, narrow, lobe-like, at apex only, to 0.5mm long, acute, much narrower than the valve, crustaceous; dehiscence septifragal. Seeds 2-3, subglobose, 1.6-2 x 1.6-2mm, black, shiny; aril white, infundibular, 1mm long. Seedling not seen.

Chromosome number: n=14 (Short 229, West 1350)

TYPIIFICATION:

Mueller based this species on a collection of Wilhelmi from Port Lincoln, of which four specimens, all with immature fruit, have been seen (MEL, BM, & two from W). Since the author did not designate any one of these specimens as the type, a lectotype must be selected for this name. All four specimens are in equally good condition. The BM sheet includes a number (#4263), which appears to have been added while it was in the possession of H. F. Hance, from whose herbarium this specimen originated. The MEL specimen is here chosen as the lectotype, as it is housed in the herbarium in which Mueller worked.

Another MEL sheet, containing one specimen with female flowers & a second with male flowers, is probably a syntype. This sheet bears a

label in Mueller's hand which gives the locality as Port Lincoln and Wilhemi as the collector. In addition this label states "ex. h. bot. Melb.", which probably indicates that the specimen was from cultivated material in Melbourne botanic gardens which originated from a Wilhemi field collection near Port Lincoln. This specimen is undated, but as Wilhemi collected around Port Lincoln mainly in 1851 and 1854 (Wilhemi, 1857) it is likely that this material was available to Mueller in 1855. The protologue includes details of the anthers so he must have seen flowers before describing the species.

DISTRIBUTION (Fig. 7.36):

D. hexandra is primarily a South Australian species with a probable extension into the Victorian mallee regions (see Note 1). There is also one Western Australian record which requires authentication (see Note 2).

Within South Australia the species is found in the southern mallee regions. It grows over a wide expanse of both Eyre and Yorke Peninsulas (apart from the extreme south of each) and in the Murraylands. *D. hexandra* is uncommon on the eastern end of Kangaroo Island and does not occur in the wetter south-east of South Australia.

ECOLOGY:

This species is typically an undershrub of mallee scrub communities, and it is commonly found in mallee broombush associations. The dominant species with which *D. hexandra* is associated vary over its distributional range. *Eucalyptus incrassata*, *E. porosa*, *E. oleosa*, *E. socialis*, *E. foecunda*, *E. anceps* & *E. diversifolia* are the most common mallee tree species. The understorey may vary from dense broombush with dominants of *Melaleuca uncinata* & *Baeckea behrii*, to heath dominated by *Hakea*, *Leptospermum* & *Lasiopetalum* species, to open mallee scrub with a sparse understorey of

small shrubs such as species of *Astroloma* & *Pomaderris*. In low-lying areas *D. hexandra* often grows in open *Eucalyptus cladocalyx* woodlands with *Callistemon macropunctatus*.

D. hexandra is most commonly found on alkaline soils and often in sandy loams overlying limestone. The *Eucalyptus diversifolia* mallee scrub, in which this species sometimes grows, is usually associated with sandy soils.

The absence of *D. hexandra* from the south-east of South Australia is probably because of the higher rainfall of that region.

This species flowers in early winter, i.e. May to July, and fruits are usually present from September to November.

NOTES:

1. The only record of *D. hexandra* occurring in Victoria is a specimen at NSW of Althofer with locality data of "Victorian mallee". The species is found in the upper south-east region of South Australia in mallee heath and mallee broombush communities which extend across the border into Victoria. It is possible that thorough collecting in the western Victorian mallee associations adjoining the South Australian Scorpion Springs and Mt. Shaugh Conservation Parks would locate populations of *D. hexandra*.

2. This species was apparently collected in Western Australia on the Elder Scientific Expedition in 1891. AD holds a Gwynne specimen collected "85m NE by E of Esperance Bay" and a 'duplicate' with Helms as collector is at MEL (both dated 2.xi.1891). No other material of *D. hexandra* has been collected from W.A. The locality given with these specimens is calculated to be in the vicinity of Mt. Ragged ($33^{\circ}27'S$ $127^{\circ}28'E$), east-north-east of Esperance. The most southern camping place of the Elder Expedition is Camp No. 68 at Fraser Range Station ($31^{\circ}57'44"S$

122° 35'E) (Mueller & Tate, 1896; Steele & Steele, 1978), which is considerably further north than the location of the Gwynne & Helms specimens. Steele & Steele (1978) reported Lindsay, the leader of the expedition, travelling south to Esperance by horseback while the remainder of the expedition was at Fraser Range Station. They mentioned only one aboriginal accompanying Lindsay. It is possible that the specimens were collected by Lindsay and given to Helms, the naturalist and/or the assistant, Gwynne on Lindsay's return from Esperance. It is not known whether Helms & Gwynne made additional collecting trips from Fraser Range while Lindsay was further south. Intensive searches of the region between Fraser Range and Esperance need to be carried out to determine whether this species does occur in the area. The mallee habitat of this part of W.A. would seem to be suitable for the species.

PUTATIVE HYBRIDS

D. hexandra x *D. humilis*

Populations of *D. hexandra* & *D. humilis* occur together in several areas of South Australia. In two localities in the Murray mallee putative hybrids between these two species have been found. Usually *D. humilis* flowers earlier than *D. hexandra*, but occasional overlap has been observed in populations other than those showing hybridisation.

Although fruit has been collected from the hybrid plants no male flowers have been observed at anthesis. Revisits to populations near Malinong (south-east of Murray Bridge) have shown that female hybrids flower at the same time as the parent species. One female plant originating in the field has flowered profusely in cultivation, and in isolation has produced a small amount of fertile seed. The possibility of some form of apomixis in these hybrid plants, as observed in other species (see Chapter 4), may account for the apparent lack of and necessity for male flowers.

The hybrid individuals are intermediate in several characteristics which distinguish the two species. Most leaves are flat and irregularly toothed or lobed, some have opposite pairs of leaflets, while others are simple and linear. Other intermediate features include the general indumentum, leaf texture, recurvature of the leaf margin, leaf apex shape, inflorescence structure, sepal shape, carpel number, style length and seed characteristics.

No male flowers have been observed and so pollen sterility tests have not been possible. The fruiting specimens which have been observed both in the field and on herbarium sheets have not contained any viable seed, although the capsules have dehisced naturally.

Specimens:

SOUTH AUSTRALIA:- Sharrad 337 & 340, 6km W of Malinong, 45km SE of Murray Bridge, 3.xi.1959. fr. (AD).- Sharrad 568-569, loc. cit., 20.iv.1960. st. (AD).- Sharrad 595-596, loc. cit., 22.v.1960. mature f.fl. (AD).- West 1861, 3.4km N of Ki Ki on Dukes Hwy. between Tailem Bend & Tintinara, 16.v.1977. st. (AD).- West 1870 & 1872, 14km SW of Coomandook, 3km S of Two Sisters hills, 16.v.1977. st./f.fl. (AD).

AFFINITIES:

D. hexandra is most closely related to *D. pinifolia* from Western Australia. Both species have similar narrow, revolute leaves, although those of *D. pinifolia* are often toothed or lobed. The fruits are also similar, except that *D. hexandra* capsules rarely show any appendage development, whereas *D. pinifolia* fruits are horned.

D. tepperi & *D. hexandra* show general similarities in leaf and fruit, but the latter can be readily distinguished by its linear leaves, and being 3-merous it consistently has six anthers.

SPECIMENS EXAMINED: selection only (206 collections examined)

SOUTH AUSTRALIA:- Alcock 16A, Eyre Pen., Hundred of Mortlock, Pillana Siding, 43km NNW of Port Lincoln, 7.v.1964. f.fl. (AD).- Alcock 1577, Eyre Pen., Hundred of Hincks, 8km W of Mt. Verran, 29.x.1967. fr. (AD).- Copley 274, Northern Yorke Pen., 10km N of Bute on Port Broughton rd., 8.v.1966. f.fl. (AD).- Eichler 15441, Kangaroo Is., nr. Birchmore Lagoon, 20km SW of Kingscote, 13.xi.1958. fr. (AD).- Haegi 699, Murray Mallee, 5km SE of Halidon, 85km ENE of Murray Bridge on Loxton rd., 12.x.1975. fr. (AD).- Hunt s.n., Murray Mallee, between Coomandook & Yumali, 15.xii.1964. fr. (AD96501048).- Kuchel 1296, Southern Eyre Pen., Hundred of Blesing, 22.x.1963. fr. (AD).- Orchard 2228, Gawler Ras., Yandinga Gorge, 5km N of Minnipa, 26.ix.1969. fr. (AD).- Rohrlach 198, Eyre Pen., Hundred of Cortlinye, 15km NW of Kimba, 1.iii.1959. m.fl. (AD).- Short 307, Yorke Pen., Stansbury, 24.iv.1977. m.fl. (AD).- Smith 569, Southern Lofties, O'Sullivan's Beach, 20km SSW of Adelaide, 4.x.1967. fr. (AD).- West 1348, Murray Mallee, S of Mallee View H.S., Monarto, 27.ii.1976. fr. (AD).- West 1452, Yorke Pen., 2.6km N of Winulta, 4.viii.1976. f.fl. (AD).- West 1993, Eyre Pen., 13.5km ESE of Cummins on Stokes rd, 5km W of Stokes, 20.viii.1977. immat.fr. (AD).

33. *Dodonaea ericoides* Miq. in Lehm., Pl. Preiss. 1:227 (1845); Bentham, Fl. Aust. 1:483 (1863); Mueller, Fragm. 9:88 (1875); Radlkofer, Pflanzenreich IV.165:1400 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).
 TYPE: "Crescit in regionibus interioribus Australiae austro-occidentalis, raro !! Herb. Preiss No. 2435." Lectotype (here designated): L. Preiss 2435, in Nova Hollandia merid. austr. regionibus interioribus, raro!!, s.dat. st. (U91926). Isolectotype: MEL84093.

D. cryptandroides Diels in L. Diels et E. Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:347 (1904); Radlkofer, Pflanzenreich IV.165:1401 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956) - syn. nov.
 TYPE: "in distr. Darling ad pedes collium pr. Bellevue in fruticetis humilibus solo glareoso flor. m. April. (E. PRITZEL Pl. Austr. occ. 295; D. 2724)." Lectotype (here designated): E. Pritzel 295, District Swan: in silvis subumbrosis montium Darling Range, iv.1901. m.fl. (AD96232217). Isolectotypes: G (3 sheets), NSW, P and W. Syntype: Diels et Pritzel 86, Swan Distr.: Bellevue, iii.1901. f.fl. (PERTH).

DESCRIPTION (Fig. 7.37):

Dioecious shrub, 0.3-0.5(-0.8)m high, erect. Branches opposite, slender, intricate; branchlets angular, or furrowed, red, usually densely pubescent. Leaves simple, opposite, rigid, erect, sometimes recurved above the middle, sessile, linear, rarely narrow-oblongate, (0.2-)0.5-1.0(-1.5) x 0.1-0.2cm, olive-green, often tinged with purple, coriaceous, thick, pubescent, rarely almost glabrous, base almost decurrent, with raised leaf scar, margin strongly revolute so that only the midrib of the lower surface is visible, entire or often with 2(3-4) lobes or teeth at or above

the middle, apex acute, midvein prominent on lower surface, slightly impressed above, lateral venation inconspicuous. Flowers unisexual, monadic, terminating branchlets; pedicels 0.5-1.5(-2)mm long, recurved, pubescent. Sepals 4, ovate, 2.5-4.5(-5.5) x 1.5-2mm, acuminate, outer surface concave, pubescent, inner margin villous, inner surface glabrous, persistent; at anthesis the sepals in male flowers are spreading, in female flowers they are erect, surrounding the ovary & free only at the apex where the style protrudes. Stamens in male flowers 8, approximately equal in length to sepals, widely divergent; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, twisted at anthesis, 2.5-3.2 x 0.5-1mm, glabrous; apical appendage triangular-acuminate, 0.2-0.3mm long, pubescent; stamens in female flowers absent. Ovary in female flowers 4-carpellate, oblong, 0.8-1 x 0.7mm, pubescent, rarely glabrous; styles 4, connate, flattened, sometimes twisted in upper part, 6-11mm long, glabrous, red, separating unequally near the apex, each free arm 0.1-0.2mm long, recurved; in male flowers rudimentary ovary usually present. Capsule 4-angled, subglobose, (4-)4.5-8(-9) x 5-8mm, crustaceous & thickened, densely pubescent, grey tomentose (sometimes hoary) at maturity, base broad-cuneate to truncate, apex obtuse to truncate; carpel lunate, rarely navicular, excluding appendage (4-)4.5-8(-9) x 1.5-3(-3.5)mm; appendage lobe-like, at or above middle of capsule only, 0.5-1mm long, rounded, much narrower than the valve, crustaceous; dehiscence septifragal. Seeds 1-2, lenticular, 2.2-2.7 x 2.0-2.5mm, black, dull; aril white, infundibular, 1-1.2mm long. Seedling not seen.

Chromosome number: not known.

TYPIIFICATION:

Two specimens of the type collection (Preiss 2435), on which Miquel based his description of *D. ericoides* have been seen. Both of these

specimens, one of which is housed at U & the other at MEL, are in poor condition. Miquel did not designate either specimen as the type and so it is necessary to select a lectotype for this name. Although the U material is sterile it is larger and in better condition than the scrappy MEL specimen, which contains only a few leaves and one damaged immature fruit. Since Miquel's herbarium and types are housed at U the specimen from that herbarium, which he must have seen is here chosen as the lectotype. Neither specimen appears to be annotated by Miquel.

Diels based *D. cryptandroides* partly on Pritzel's collection 295 and partly on Diels no.2724. The latter specimen has not been found and may have been destroyed at B through war action. Seven sheets of Pritzel 295 have been seen - three from G & one from AD, NSW, P and W. Each of these specimens contains male flowers and four of them are in good condition. Since there is no material available from the herbarium at which the author worked the AD specimen (AD96232217) is here chosen as the lectotype of *D. cryptandroides*. The protologue includes details of female flowers. The only specimen available bearing female flowers is that of Diels & Pritzel 86 (PERTH), which is regarded as a syntype.

DISTRIBUTION (Fig. 7.37):

D. ericoides is now restricted to a small number of populations in the south-west of Western Australia. It exhibits a north-south distribution pattern running from north of Geraldton to Wannamal (ca. 90km north-north-east of Perth) in the south, and ranging from 20-100km inland from the coast. Collections by Diels and Pritzel in 1901 and Williams in 1932 indicate that this species extended into the Darling Ranges east of Perth earlier this century.

ECOLOGY:

The present day rarity of *D. ericoides* is partly due to its occurrence in woodland habitats. These communities have been widely cleared in the past for agricultural expansion with the result that this species is now known only from a very small number of populations, which occupy land considered unsuitable for agricultural purposes. Attempts were made during this study to relocate previously collected populations, but several of these natural plant communities have been destroyed in the intervening years. *D. ericoides* occurs as an undershrub of *Eucalyptus wandoo* woodlands in the southern part of its distribution. It is also found in low heath shrublands such as at Mt. Lesueur (George 12898) or Howatharra Hills (West 3299-3308). The species usually grows on rocky lateritic hill-sides or lateritically derived soils.

Flowering time appears to vary from April through winter to the early summer months of November and December. The skeletal nature of the soils in which *D. ericoides* grows probably makes it very susceptible to seasonal climatic conditions and this may be responsible for some of the variation in the time of flowering. Mature fruit are most often found from September to November.

NOTES:

1. After examining the type material of *D. cryptandroides* Diels this taxon has been found to be conspecific with *D. ericoides* Miq. and is therefore regarded as a synonym of the latter (Stafleu et al., 1978, Art. 11). Following the descriptions in the protologue of *D. cryptandroides* Diels noted that this species could be distinguished from *D. ericoides* on its narrower leaves and sparser indumentum. He added that the distinction would be clearer if the fruits were known (the material available to him lacked fruits). Even without capsules it is quite clear that these two

taxa are conspecific. They share such features as opposite, linear, revolute leaves, relatively large ovate, acuminate sepals which are pubescent outside and glabrous on the inner surface, reflexed pedicels, solitary flowers and similar indumentum.

2. The labels on the specimens from the type collection of *D. ericoides* indicate that Preiss regarded this species as being rare at the time of collection, which was probably 1839 (cf. *D. aptera* Preiss 2439). Some reasons have been discussed above which account for a relatively recent restriction in the distribution of *D. ericoides*. Hartley and Leigh (1979) included this species in the category of rare species, occurring only in small populations, which are often restricted to specific habitats.

AFFINITIES:

D. ericoides is the only species of the genus with opposite leaves, and can therefore be readily distinguished from all other species. Several other features, such as the hairy nature and shape of the fruit and the leaf shape, indicate that it does not appear to be closely related to any other species. The leaves vaguely resemble *D. tepperi*, although the two can be easily recognised by the teeth and pubescence of *D. ericoides* leaves. Some forms of *D. triangularis* have fruits of similar shape and pubescence to this species, but *D. triangularis* has flat, obovate leaves quite different from the linear, revolute ones of *D. ericoides*.

SPECIMENS EXAMINED:

WESTERN AUSTRALIA:- Drummond 726, W.A., 1843. m.fl. (BM,MEL).- Fitzgerald s.n., Mogumber, x.1903, xi.1903. fr. (NSW).- Gardner 9090, Mt. Lesueur, 25.viii.1948. fr. (PERTH).- Gardner 10273, Mount Peron,

11.x.1951. fr. (PERTH).- Gardner 12846, Howatharra Hills, 27.ix.1960.
 fr. (PERTH).- George 5938, 7ml E of Wannamal, 8.xi.1963. fr. (PERTH).-
George 6194, Quin's Hill, W of Mogumber, 11.iv.1964. m.fl./f.fl. (PERTH).-
George 7849, 27ml SE of Walkaway, 4.ix.1966. fr. (PERTH).- George 12898,
 S side of Mt. Lesueur, 13.x.1974. fr./st. (PERTH).- Griffin 1009, 8km SSE
 of Eneabba, 31.v.1978. m.fl. (PERTH).- Griffin 1492, loc. cit., 7.xi.1978.
 fr. (PERTH).- Keighery 330, 20ml E of Greenhead, 10.xi.1974. buds. (PERTH).-
McFarland 1043, Moresby Ra., 21 rd. ml N of Geraldton, 26.v.1977. m.fl.
 (PERTH).- Mueller s.n., W.A., s.dat. fr. (NSW).- Royce 7709, Jurien Bay,
 3.xi.1962. fr. (PERTH).- Royce 9748, Watheroo N.P., W of Watheroo,
 8.x.1971. fr. (PERTH).- West 3299-3308, McFarland's Howatharra Hills
 Reserve, 33.6km (by rd.) NE of Geraldton, 7.xii.1978. m.fl., buds, fr. (AD).-
Williams s.n., nr. Darlington, 20.iv.1932. m.fl. (PERTH).- Willis s.n.,
 S of Mt. Lesueur, 7.x.1961. fr. (MEL).

34. *Dodonaea triangularis* Lindl. in Mitchell, Journ. Exped. Trop. Aust. 219 (1848); Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 31.I:407 (1858); [Mueller, Pl. indig. Col. Vic. 1:88 (1862) pro syn.]; Bentham, Fl. Aust. 1:481 (1863); Mueller, Fragm. 9:87 (1875); Bailey, Fl. Qld. 1:316 (1899); Radlkofer, Pflanzenreich IV.165:1402 (1933); Beadle et al., Fl. Syd. Reg. 386 (1972).
 TYPE: leg. Mitchell, Mount Faraday area, 1.vii.1846. Lectotype (here designated): Lieut.-Col. Sir T.L. Mitchell 198, Sub-tropical New Holland, 1.vii.1846. m.fl. (CGE). Isolectotype: NSW.

D. mollis Lindl. in Mitchell, Journ. Exped. Trop. Aust. 212 (1848); [Bentham, Fl. Aust. 1:481 (1863) pro syn.; Mueller, Pl. indig. Col. Vic. 1:88 (1862) pro syn.; Radlkofer, Pflanzenreich IV.165:1402 (1933) pro syn.]
 TYPE: leg. Mitchell, Maranoa River, near Mt. Owen, 22.ix.1846. Lectotype (here designated): Lieut.-Col. Sir T.L. Mitchell 308, Sub-tropical New Holland, 22.ix.1846. fr. (CGE). Syntypes: Mitchell 165, Sub-tropical New Holland, vi.1846. f.fl. (CGE); Mitchell 216, Sub-tropical New Holland, 17.vii.1846. m.fl. (CGE, ?NSW); Mitchell 274, Sub-tropical New Holland, 31.viii.1846. immat.fr. (CGE, L809.269-234).

D. trigona Lindl. in Mitchell, Journ. Exped. Trop. Aust. 236 (1848); [Bentham, Fl. Aust. 1:481 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1402 (1933) pro syn.]
 TYPE: leg. Mitchell, Balmy Creek, 16.vii.1846. Holotype: Lieut.-Col. Sir T.L. Mitchell 178, Sub-tropical New Holland, vii.1846. fr. (CGE).

D. lindleyana F. Muell., Pl. indig. Col. Vic. 1:88 (1862), nom. illeg. (Stafleu et al., 1978, Art. 63).

DESCRIPTION (Fig. 7.38):

Dioecious or rarely polygamo-dioecious shrub, 1.5-3m high, erect. Branches spreading, erect; branchlets angled, often flattened, pubescent, very rarely glabrous. Leaves simple, sessile or with petiole 1-3mm long; lamina variable, mostly obovate, sometimes oblanceolate, obtriangular or angular-obovate, rarely spatulate or elliptic, usually tri-dentate or 3-lobed at the apex, (1.2-)2-3.5(-6) x (0.6-)0.8-2(-3)cm, dull green, coriaceous, usually pubescent, with adpressed hairs, sometimes on midrib & margin only, rarely glabrous, base attenuate to broad-cuneate, margin entire, thickened & revolute, apex acute, usually tri-dentate or 3-lobed, rarely 5-lobed, sometimes entire, rarely truncate, mid-vein prominent, lateral venation obscure. Flowers unisexual and rarely bisexual, monadic to 3-6-flowered botryoidal, in axillary & terminal compound inflorescences; pedicels (3.5-)4-8(-10)mm long, jointed near the base, reflexed in female flowers & fruit, erect in male flowers, pubescent, very rarely glabrous. Sepals 4(-5), narrow-lanceolate to lanceolate, (1.2-)1.5-2(-3) x 0.6-1mm, acute, outer surface pubescent, inner surface glabrous, rarely glabrous both surfaces, persistent; at anthesis the sepals in male & bisexual flowers are widely spreading or recurved, in female flowers they surround the ovary & are free. Stamens in male & bisexual flowers 6-8, far exceeding the sepals, divergent; filaments 0.6-0.8(-1)mm long, glabrous, rarely pubescent; anther lobes oblong, twisted at anthesis, 2.5-3.5 x 0.6-0.8mm, usually glabrous, rarely sparsely pubescent; apical appendage broad-triangular, 0.1-0.3mm long, usually pubescent, sometimes glabrous; stamens in bisexual flowers deciduous soon after anthesis; stamens in female flowers absent. Ovary in female & bisexual flowers 3(-4)-carpellate, oblong, sometimes angled, 0.8-1.4 x 0.8-1mm, densely pubescent; styles 3, connate, twisted spirally in upper part, 5-15(-25)mm long, pubescent at the base, separating unequally near

the apex, each free arm 0.2-0.4mm long, recurved; in male flowers rudimentary ovary usually present. Capsule 3(-4)-angled, in lateral view broad-obovate, 6-9 x 8.5-10.5(-11.5)mm, crustaceous & thickened, usually sparsely pubescent when mature, sometimes glabrous, dark brown to red at maturity, base rounded or truncate, apex truncate or obtuse; carpel deeply navicular, excluding appendage 6-9 x 3-3.5(-4)mm, appendage usually present, narrow, lobe-like, usually above middle of capsule only, 1-2mm long, much narrower than the valve, crustaceous or coriaceous; dehiscence septifragal, very rarely septicidal. Seeds 2-4, lenticular, 2.3-2.5 x 1.8-2.2mm, black, shiny, with hyaline membrane lifting at the margin; aril absent. Seedling not seen.

Chromosome number: not known.

TYPIFICATION:

Lindley based *D. triangularis* on material collected by Mitchell on July 1st, 1846 near Mt. Faraday. Two specimens of this collection have been found (CGE & MEL). Both of these specimens agree with the protologue in having male flowers and obtriangular leaves, and both bear notes in Lindley's handwriting. The author did not designate either as a type, so the CGE specimen is here chosen as the lectotype. This sheet is held in the herbarium where Lindley's types and original herbarium are kept.

Lectotypification was necessary for the synonymous name *D. mollis*, as five syntypes have been found and Lindley did not nominate any one of them as the type. The label of each of these specimens (4 from CGE and one from L) includes notes in Lindley's hand and it is likely that they were all available to him when he described this species. The protologue includes capsule details, and so the only specimen with mature fruit (i.e. Mitchell 308) is chosen as the lectotype. Another sheet from NSW annotated

as Mitchell 216 contains immature fruit and looks more like a duplicate of the CGE Mitchell 274 specimen than of the male-flowered CGE 216 sheet. It is possible that this NSW specimen is a syntype, but it does not bear Lindley's hand writing and may not have been seen by him.

DISTRIBUTION (Fig. 7.38):

D. triangularis occurs in the upper Hunter Valley region of New South Wales and in south-eastern Queensland on the Dividing Range. In Queensland its distribution extends as far as Tambo in the west and Pentland ($20^{\circ}32'S$ $145^{\circ}24'E$) in the north. The area near Rockhampton, where the ranges extend further towards the coast, is the locality at which *D. triangularis* occurs in closest proximity to the coastline.

ECOLOGY:

D. triangularis appears to be restricted to the skeletal granitic and sandstone soils of the Great Dividing Range. It is commonly found on rocky hillsides as an understorey shrub of dry sclerophyll forest or woodland communities. In open forests *D. triangularis* occurs in associations dominated by *Eucalyptus trachyphloia*, *E. sp. aff. paniculata* with a *Callitris sp.* understorey. *Eucalyptus wilkinsoniana*, *E. maculata* & *E. acmenioides* often form the upper canopy of dry sclerophyll forests in which this species is found. Other shrub species associated with *D. triangularis* include *Acacia fimbriata*, *A. conferta*, *A. juncifolia*, *Leucopogon muticus* & *Olearia elliptica*.

The time of flowering seems to vary over the distributional range of this species, but late summer, autumn and early winter are the most common seasons. Fruits take five to seven months to mature so that shrubs bear mature fruit from September through to December.

NOTES:

D. triangularis exhibits a large amount of variation in indumentum density and leaf morphology (Fig.7.38). There is no evident correlation of either of these features with the geographical or ecological distribution of the species. Furthermore, since the total range of both of these varying characters can be found in one locality, e.g. at Sandy Hollow in the Hunter Valley of New South Wales, it appears that the variation may not be environmentally induced. However, ecophysiological experiments may show correlations of indumentum density with certain micro-environmental variables, such as hours of sunlight received, depth of soil in rock crevices and the water holding capacity of such crevices, in which this polymorphic species grows.

AFFINITIES:

D. triangularis is most closely related to *D. trifida* of Western Australia. These two species are both pubescent, features of the ovary and fruit are similar and both possess seeds with the hyaline membrane lifting at the margin. They can be distinguished by the smaller, regularly tri-dentate leaves and stamens, which only slightly exceed the sepals, of *D. trifida*.

SPECIMENS EXAMINED: selection only (137 collections examined).

NEW SOUTH WALES:- Boorman s.n., Wallangra, xi.1912. fr. (NSW140617).- Burgess s.n., Sandy Hollow, 4.viii.1963. fr. (CBG9824).- Constable 4020, Gungahlin, 10ml SE of Merriwa, 9.viii.1962. fr. (NSW).- Coveny s.n., 5ml S of Bulga, 11.ii.1968. m.fl., bisex.fl. (NSW140615).- Crisp 2264 & Telford, Goulburn River Valley, Murrumbo Gap, 28.x.1976. fr. (CBG).

QUEENSLAND:- Durrington 762, Moreton District, Mt. French, 14.5km W of Boonah, 6.viii.1973. immat.fr. (BRI).- Johnson 7128 & Briggs, Callide open cut, 25km NE of Biloela, 2.vi.1971. m.fl.,bisex.fl.s.,fr. (NSW).- Smith 11332, 4ml W of Weranga, Tara Line, 3.v.1961. m.fl./f.fl. (BRI).- Tindale 721, 2.4ml NW of Kogan, 1.vi.1971. f.fl. (NSW).- White 10804, Callide Valley, iv.1937. f.fl. (BRI).

35. *Dodonaea trifida* F. Muell., *Fragm.* 9:88 (1875) - based on *D. humifusa* Miq. var. *hirtella* Benth.; Radlkofer, *Pflanzenreich* IV.165:1403 (1933); Blackall and Grieve, *W. Aust. Wildfls.* 2:325 (1956).

D. humifusa Miq. var. *hirtella* Benth., *Fl. Aust.* 1:483 (1863); [Radlkofer, *Pflanzenreich* IV.165:1403 (1933) pro syn.]

TYPE: "Drummond, 5th Coll. n.249." Holotype: J. Drummond 249, S.W. Australia, s.dat. m.fl./f.fl. (K-photograph!). Isotypes: Drummond 249, W.A. s.dat. f.fl., immat.fr. (BM); Drummond 249, de Swan River au Cape Riche, 1848. st. (G); Drummond 249, W.A., s.dat. m.fl./f.fl. (MEL84142).

DESCRIPTION (Fig. 7.39):

Dioecious shrub, to 1m high, erect. Branches spreading, densely pilose & puberulent; branchlets terete or biconvex. Leaves simple, sessile, angular-obovate, sometimes obtriangular, tri-dentate or 3-lobed above the middle, rarely the three lobes dividing again, (0.7-)0.8-1(-1.2) x (0.4-)0.5-0.8(-1)cm, coriaceous, sparsely pilose on margin & midrib, rarely on the lamina, or glabrous, base cuneate, margin slightly revolute, entire & thickened, apex teeth or lobes obtuse or acute, midvein conspicuous, lateral venation usually obscure. Flowers unisexual, crowded in terminal, 3-5-flowered botryoids; pedicels 1-2mm long, longer in female than male flowers, pilose or glabrous. Sepals 4-6, linear to lanceolate, rarely elliptic in female flowers, (1.6-)2.5-3.5(-4.3) x 0.6-1(-1.2)mm, longer and narrower in male flowers, acute or obtuse, pilose on margin, persistent, & erect in fruit; at anthesis the sepals in male flowers are strongly recurved, in female flowers they surround the ovary & are free for their entire length. Stamens in male flowers 8, just exceeding the sepals, erect or divergent; filaments 0.6-1.5mm long, glabrous; anther lobes oblong, 2-3 x 0.7-0.9mm, glabrous; apical appendage acuminate,

0.3mm long, pilose; stamens in female flowers absent. Ovary in female flowers 3-carpellate, oblong, 3-angled, 1.2-1.5 x 0.8-1.2mm, densely long-pilose; styles 3, connate, twisted spirally in upper part, 10-20mm long, long-pilose at base, separating unequally near the apex, each free arm 0.1-0.6mm long, usually recurved; ovary in male flowers absent. Capsule 3-angled, in lateral view obovate or broad-angular-obovate, (7-) 8-9.5(-10) x 7.5-9.5(-10)mm, crustaceous, sparsely pilose, dark red or brown tinged with purple at maturity, base truncate or rounded, apex truncate, rarely emarginate, style base persistent; carpel navicular, excluding appendage 7-9 x 2.5-4.5mm; appendage usually lobe-like, above middle of capsule only, 1-2.5mm long, narrower than the valve, coriaceous; dehiscence septifragal. Seeds 1-4, lenticular, 2-2.4 x 1.8-2.2mm, black, shiny, with hyaline membrane lifting at the margin; aril absent. Seedling not seen.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.39):

D. trifida is known from only four populations along the south coast of Western Australia. It is found in a restricted coastal strip from Albany to Kundip (17km SE of Ravensthorpe), and with the exception of the Kundip population, within a few kilometres of the coastline.

ECOLOGY:

This species is found as an undershrub of coastal scrub or low forest, such as in *Melaleuca* sp. thicket amongst *Eucalyptus redunca*. The very small number of collections and little information available indicate that *D. trifida* grows in grey loamy sand or gravelly, granite-derived soils, and it is most often found on hillsides.

Flowering occurs in the spring and early summer months of September to November. The fruit develops relatively quickly and can be found in early summer, i.e. November to early January.

NOTES:

The rarity of this species has been recognised by Hartley and Leigh (1979), who classified it in the category of rare species occurring only in small populations, within a particular habitat.

AFFINITIES:

D. trifida is a very distinct species showing most affinity to *D. triangularis* in ovary, fruit and wing shape, pubescence and the black seeds with the membrane lifting at the margin. The small, regularly tri-dentate or 3-lobed leaves and the pilose pubescence of *D. trifida* readily distinguish it from all other species.

SPECIMENS EXAMINED:

WESTERN AUSTRALIA:- Anon. s.n., Fitzgerald R. N.P., s.dat. fr. (PERTH).- Canning WA/68 7469A, Miller's Point, 9.xi.1968. m.fl. (CBG).- Canning WA/68 7469B, loc. cit., 9.xi.1968. f.fl. (CBG).- Newbey 1447, Miller's Point, Beaufort Inlet, 18.x.1964. fr. (PERTH).- Newbey 2630, Kundip, 20.xi.1966. fr. (PERTH).- Newbey 2729, near Thumb Peak, E of Ongerup, 27.x.1967. fr. (PERTH).- Newbey 3046, Mount Melville, Albany townsite, 22.xi.1964. fr. (PERTH).- West 3035-3046, Beaufort Inlet, 0.5km N of Miller's Point on road to Bremer Bay road, 25.xi.1978. m.fl./f.fl., fr./st. (AD).

IV. Sect. *Cornutae* (Benth.) West, stat. nov.

Ser. *Cornutae* Benth., Fl. Aust. 1:480 (1863), p.p. (excl. *D. baueri*),
basionym.

Ser. *Aphanopterae* Radlk. subser. *Appendiculatae* Radlk., Pflanzenreich
IV.165:1356 (1933), p.p.

TYPE SPECIES: Lectotype (here designated): *D. pinifolia* Miq.

DIAGNOSIS:

Leaves simple, sessile, margin revolute, entire or with (1-)2(-4)
irregular teeth above the middle; capsule globose, crustaceous, appendage
above middle of capsule only, narrow & horn-like, 1-3(-6)mm long; seed
arillate.

TYPIFICATION:

The lectotype must be chosen from among those species included in
series *Cornutae* by Bentham, excluding *D. baueri* Endl., which does not
have capsules with horn-like appendages (i.e. *D. pinifolia*, *D. ceratocarpa*
& *D. divaricata*). *D. pinifolia* has been selected since Bentham saw
several specimens of this species and he placed it first in the group.

DISTRIBUTION:

The section is confined to south-west Western Australia.

D. caespitosa Diels

D. ceratocarpa Endl.

D. divaricata Benth.

D. pinifolia Miq.

KEY TO SPECIES OF SECTION *CORNUTAE*

- 1a. Leaves flat, > 0.3cm broad (rarely 0.3cm broad), usually oblanceolate to obovate, rarely narrow-elliptic; pedicels clavate, ribbed
 36. *D. ceratocarpa*
- 1b. Leaves convex above, ≤ 0.3cm broad, usually linear or terete, rarely narrow-elliptic or obovate; pedicels filiform, not ribbed, or ±absent . . 2
- 2a. Leaves appearing clustered at nodes, ≤0.1cm broad, revolute & appearing 2-grooved below, apex obtuse & recurved; branchlets red; stamen filaments 0.5-0.8mm long 37. *D. caespitosa*
- 2b. Leaves solitary at nodes, usually > 0.1cm broad, revolute but not 2-grooved below, apex acute, not recurved; branchlets brown; stamen filaments < 0.3 or usually > 0.7mm long 3
- 3a. Leaves ≤ 0.8cm long; pedicels < 0.5mm long; sepals ≤ 0.5mm broad; stamens 6, filaments 0.2-0.3mm long 38. *D. divaricata*
- 3b. Leaves > 0.8cm long (rarely 0.8cm long); pedicels > 1mm long; sepals > 1mm broad; stamens 8, filaments 0.7-1mm long 39. *D. pinifolia*

36. *Dodonaea ceratocarpa* Endl. in Enum. Pl. Hügel 13 (1837); Bentham, Fl. Aust. 1:481 (1863); Mueller, Fragm. 9:88 (1875); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:346 (1904); [Radlkofer, Pflanzenreich IV.165:1396 (1933) pro syn.]; Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).

TYPE: "King Georges Sound. (Hügel.)." Holotype: C. Hügel s.n., King Georges Sound, s.dat. fr. (W).

D. pterocaulis Miq. in Lehm. Pl. Preiss. 1:225 (1845); [Bentham, Fl. Aust. 1:481 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1396 (1933) pro syn.]

TYPE: "in rupestribus montis prope Tjallop reg. Kent. 17. Nov.1840. Herb. Preiss. No. 2440." Lectotype (here designated): L. Preiss 2440, in Nova Hollandiae ora occid. in rupestribus montis prope Tjallop (Kent), 17.xi.1840. fr. (U91922). Isolectotype: L. Preiss 2440, in Col. Swan River, 1843, fr. (G).

[*D. oblongifolia* auct. non Link : Radlkofer, Pflanzenreich IV.165:1396-7 (1933).]

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956)

DESCRIPTION (Fig. 7.40):

Dioecious shrub, 0.5-2.5m high, spreading. Branches spreading, angled; branchlets strongly angular or ribbed, sometimes almost winged, glabrous or rarely puberulent. Leaves simple, sessile, oblanceolate to obovate, rarely narrow-elliptic, (1.4-)1.8-3(-5.6) x (0.3-)0.5-1(-1.2)cm, coriaceous, with sessile glands, glabrous, base attenuate, with raised leaf scar, margin entire & revolute, apex acute or mucronate, midvein

prominent, lateral venation usually obscure. Flowers unisexual, in 3-4-flowered botryoids, terminating branchlets; pedicels 1.5-2.5(-3)mm long, erect, clavate, weakly ribbed. Sepals 4, ovate, (2-)2.5-3.5 x 1-2mm, acuminate, viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrous, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they surround the ovary & are free at the apex only. Stamens in male flowers 8, approx. equal in length to sepals, divergent; filaments 0.5-0.7mm long, glabrous; anther lobes oblong, 1.5-2.5 x 0.6-0.8mm, glabrous; apical appendage acuminate, to 0.3mm long, pubescent; stamens in female flowers absent. Ovary in female flowers (3-)4-carpellate, oblong, sometimes angled, 0.8-1.1 x 0.7-1mm, viscous, sparsely pubescent; styles 4, connate, (8-)10-15mm long, glabrous, separating unequally at the apex, each free arm being less than 0.5mm long; ovary in male flowers absent. Capsule (3-)4-angled, excluding appendages globose, or sometimes oblong, including appendages (4.5-)5-6.5(-8) x (5-)5.5-8.5(-11)mm, crustaceous, with sessile glands, glabrous, sometimes scurfy when dry, light brown to dark purple-brown at maturity, base truncate, apex (excluding appendages) usually truncate, sometimes emarginate; carpel broad-navicular, excluding appendage (4-)4.5-6(-7) x 1.5-3mm; appendage horn-like, at apex only, usually spreading, sometimes erect, 1-3mm long, usually shorter than the valve, crustaceous; dehiscence septifragal. Seeds 3-4, lenticular-globose, (1.8-)2-2.2 x (1.6-)2-2.2mm, black, dull; aril white, infundibular, 1-1.3mm long. Seedling sparsely puberulent; hypocotyl 5-8mm long; cotyledons linear, (12-)15-20 x 1-2mm, acute, glabrous; epicotyl 0.5-2mm long; first 6-8 leaves simple, alternate, petiolate, obovate, or angular-obovate & deeply 3-lobed, each lobe usually tri-dentate, base cuneate, margin entire, or 2-lobed above the middle, apex acute & tri-dentate; later leaves without lobes.

Chromosome number: not known.

TYPIFICATION:

Two specimens of the type collection for the synonymous name *D. pterocaulis* Miq. (Preiss No.2440) have been seen. Miquel did not nominate a single specimen as the type for this species and so it is necessary to select a lectotype. As Miquel worked at U the specimen from that herbarium is here chosen as the lectotype (U91922). The label on this sheet states the Preiss no. as 2240 (and not 2440). This is presumably a mistake as all the other label data is in agreement with the type citation. The other specimen available at this time is from G and is regarded as an isolectotype.

DISTRIBUTION (Fig. 7.40):

D. ceratocarpa is restricted to the coastal area of south-west Western Australia. This shrub extends from the Serpentine River south of Perth to the Cape Naturaliste & Cape Leeuwin areas on the west coast and along the south coast as far east as Israelite Bay on the Great Australian Bight.

ECOLOGY:

This species grows along the south-western coastal granite and limestone outcrops of Western Australia. *D. ceratocarpa* appears to be restricted to granite hills or rocky outcrops such as Boyatup or Howick Hills east of Esperance or the granite hills near Albany, and in the Cape Naturaliste area it is more commonly found on sandy loam and limestone. As well as the more inland and isolated hill habitats this species tolerates coastal conditions on headlands and cliffs right on the coast line, where it associates with large paperbark *Melaleuca* species & *Eucalyptus spathulata* var. *spathulata*.

D. ceratocarpa grows in low forests of *Eucalyptus calophylla* often with dense understorey of *Anthrotroche* sp., *Agonis flexuosa*, *Jacksonia furcellata*, *Lasiopetalum* sp., *Phyllanthus calycina*. It is also found in *Eucalyptus tetraptera* mallee heath communities with *Kunzea baxteri*, *Calothamnus* sp., & *Lepidosperma* sp.

The flowering season extends from August through to the early summer months of December and January. Fruit are usually present from September to January.

NOTES:

Dodonaea oblongifolia Link (= *D. viscosa* Jacq.) superficially resembles *D. ceratocarpa* so that without fruits the two species could be confused. When Radlkofer monographed the genus in 1934 he had only male-flowering specimens of *D. oblongifolia* available and it seems that he must have mistakenly identified these as being conspecific with *D. ceratocarpa*. The type of the former name cannot be located at B where Link's herbarium is held, but Link's protologue and the description and illustration by Lindley in Bot. Reg. 13:1051, t.1051 (1827) more closely resemble the *D. viscosa* complex than *D. ceratocarpa*. *D. oblongifolia* Link is here regarded as a synonym in the *D. viscosa* Jacq. complex.

AFFINITIES:

D. ceratocarpa shows most affinity to *D. humifusa*, with which it shares a similar leaf shape, similar sepal shape and indumentum and in some individuals the fruits also show resemblances. The two species can be distinguished by the usually narrower, toothed leaves of *D. humifusa*, which also has longer and thinner pedicels; and fruits with lobe-like appendages. Plants of this last-mentioned taxon are prostrate and rarely polygamodioecious, whereas *D. ceratocarpa* is greater than 0.5m high and dioecious.

D. aptera sometimes resembles *D. ceratocarpa* in leaf shape, but the two can be separated on the longer pedicels, more complex inflorescences and petiolate leaves of *D. aptera*. The capsule appendages of *D. ceratocarpa* are horn-like, while those of *D. aptera* are smaller and lobe-like.

Without fruit and on a superficial examination *D. ceratocarpa* could be confused with the *D. viscosa* complex. There are several characters which will distinguish *D. ceratocarpa* from *D. viscosa*, e.g. the latter species has winged fruit, longer pedicels, more complex inflorescences and lacks arillate seeds.

SPECIMENS EXAMINED: selection only (93 collections examined)

WESTERN AUSTRALIA:- Butler s.n., Esperance, ix.1956. fr. (PERTH).-

George 7487, Lucky Bay, E of Esperance, 21.i.1966. m.fl., fr. (PERTH).-

Goadby 313, near King George's Sound, iv.1899. m.fl. (NSW).- Newbey 1925,

Willung, 28.xi.1965. fr. (PERTH).- Royce 3219, Yallingup, 31.vi.1950.

f.fl. (PERTH).- Royce 5645, Cowaramup Bay N.P., 21.x.1956. fr. (PERTH).-

West 2937, Howick Hill, 80km E of Esperance, 23.xi.1978. fr. (AD).-

West 3034, Beaufort Inlet, Miller's Point, 110km NE of Albany, 25.xi.1978.

fr. (AD).- West 3048, Mt. Melville, Albany, 26.xi.1978. fr. (AD).-

West 3238, 2.5km SE of Cape Naturaliste, 3.xii.1978. fr. (AD).

37. *Dodonaea caespitosa* Diels in L. Diels et E. Pritzel, *Fragm. Phytogr. Aust. occid.* in Engler's *Bot. Jahrb.* 35:347, fig.43A,B (1904); Radlkofer, *Pflanzenreich* IV.165:1401, fig.44A,B (1933); Blackall & Grieve, *W. Aust. Wildfls.* 2:324 (1956); Beard, *W. Aust. Pl. edn 1.* 60 (1965), edn 2. 81 (1970).

TYPE: "ad distr. Coolgardie fines australes pr. Graspach septentrionem versus in fruticetis lutoso-arenosis fruct. m. Nov. (D. 5309)." Lectotype (here designated): illustration - fig.43A,B in Diels et Pritzel, *Fragm. Phytogr. Aust. occid.* in Engler's *Bot. Jahrb.* 35:348 (1904).

FIGURES: Diels in Diels et Pritzel, *Fragm. Phytogr. Aust. occid.* in Engler's *Bot. Jahrb.* 35:347, fig.43A,B (1904); republished in Radlkofer, *Planzenreich* IV.165:1388, fig.44A,B (1933); Blackall & Grieve, *W. Aust. Wildfls.* 2:324 (1956).

DESCRIPTION (Fig. 7.41):

Dioecious shrub, 0.2-0.5m high, spreading, compact & rounded. Branches rigid, intricate, dense; branchlets angular or furrowed, red, viscous, puberulent. Leaves simple, usually 3-4 clustered at the nodes, sessile, linear, sometimes almost terete, (0.2-)0.4-0.8(-1)cm long, less than or equal to 0.1cm broad, bright green, thick & coriaceous, viscous, glabrous or sparsely puberulent, base sessile, with raised leaf scar, margin revolute & thickened, entire or with (1-)2(-4) irregular teeth up to 1.5mm long, usually above the middle, apex obtuse, recurved, midvein prominent below so that (with revolute margins) leaf appears 2-grooved below, lateral venation obscure. Flowers unisexual, monadic, axillary; subsessile. Sepals 3, ovate, 1.5-2.3 x 1-1.3mm, acute or acuminate, viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrous, caducous; at anthesis the sepals in male flowers

are spreading, in female flowers they surround the ovary & are free. Stamens in male flowers 6, approx. equal in length to the sepals or just exceeding them, erect; filaments 0.5-0.8mm long, glabrous; anther lobes oblong, 1-1.5 x 0.4-0.7mm, glabrous; apical appendage acuminate, 0.2-0.3mm long, pubescent; stamens in female flowers sometimes present, rudimentary, to 0.6mm long. Ovary in female flowers 3(-4)-carpellate, globose, angled, 0.6-0.8 x 0.5-0.8mm, with sessile glands, glabrous; styles 3, connate, 6-6.5mm long, glabrous, separating near the apex, each free arm being less than 0.1mm long, recurved; ovary in male flowers absent. Capsule 3(-4)-angled, excluding appendages globose, including appendages 4.5-6 x 5-9mm, crustaceous, with sessile glands, viscous, glabrous, dark red to brown at maturity, base truncate or rounded, apex (including appendages) truncate or broad-emarginate; carpel navicular, excluding appendage (2.5-)3.5-5 x (1.5-)2-3mm; appendage horn-like, at apex only, erect, sometimes curved inwards, 1-3mm long, usually longer than the valve, crustaceous; dehiscence septifragal. Seeds 3-4, lenticular-globose, 1.4-1.5 x 1.4-1.6mm, dark grey to black, dull; aril white, infundibular, 0.7-0.8mm long. Seedling not seen.

Chromosome number: not known.

TYPIFICATION:

Diels based his description of this species on one of his own collections (No.5309) from near 'Graspatch'. Diels' herbarium was housed at B and Radlkofer (1933) indicated that he saw this fruiting specimen from "Hb. Berol.". This Diels specimen cannot be located at B now, and no duplicates of this collection are known. The illustration accompanying the protologue therefore, is here designated as the lectotype of *D. caespitosa*.

DISTRIBUTION (Fig. 7.41):

D. caespitosa occurs in south-western Western Australia in a north-west-south-east arc stretching from Koorda to the north-west of its distribution to the Mt. Ragged area east of Esperance.

ECOLOGY:

D. caespitosa is a shrub of the semi-arid mallee scrub and mallee heath communities of south-west Western Australia. It often grows at the base of large granite rocks, or on granitic soils and is also found in sandy loams or rocky clays overlying laterite and ironstone. This species appears to have some tolerance to saline conditions as it sometimes grows around salt lakes and in saline watercourses.

The mallee scrub in which *D. caespitosa* is mostly found is dominated by different eucalypt species over its distributional range. In the north it is often associated with mallee forms of *Eucalyptus wandoo*, *E. loxophleba* with *Callitris* & *Casuarina* species. The denser mallee scrub and heath further south variously includes *E. pileata*, *E. anceps*, *E. conglobata*, *E. leptocalyx*, *E. nutans*, *E. flocktoniana* & *E. tetragona*. The understorey may be dense and composed of heathy shrubs, or more open, often with *Melaleuca uncinata*.

D. caespitosa flowers in February or March and fruits are usually mature in October or November.

AFFINITIES:

D. caespitosa is most closely related to *D. divaricata*, but the former species exhibits several distinguishing features such as solitary, sessile flowers, clustered, linear and recurved leaves and very small seeds.

SPECIMENS EXAMINED: selection only (43 collections examined)

WESTERN AUSTRALIA:- Chinnock 4367, 48km W of Lake King, 12.xi.1978. fr. (AD).- George 4306, 24ml E of Hyden, 5.ii.1963. m.fl./f.fl. (PERTH).- Newbey 246, 2.5ml NW of Ongerup, m.fl. (PERTH).- Royce 10155, Cape Arid N.P., 5.xii.1971. fr. (PERTH).- West 2939, 1.3km N of Howick Hill, 23.xi.1978. fr. (AD). West 2947, Munglinup R. crossing, 81km E of Ravensthorpe, 24.xi.1978. fr. (AD).- West 2979, 13.8km N of Hopetoun, 24.xi.1978. fr. (AD).- West 3164, 9.3km E of Bending, 29.xi.1978. fr. (AD).- West 3187, 10.3km N of Kellerberrin, 30.xi.1978. fr. (AD).- Wilson 3493, 9km E of Southern Cross, 22.ix.1964. immat.fr. (AD).

38. *Dodonaea divaricata* Benth., Fl. Aust. 1:481 (1863); Mueller, Fragm. 9:87 (1875), p.p. (excl. ref. to "planta Drummondi fissifolia"); Radlkofer, Pflanzenreich IV.165:1398-1399 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).

TYPE: "Between Moore & Murchison rivers, Drummond, n.96, and 4th Coll. n.256." Lectotype (here designated): J. Drummond 96, between Moore and Murchison Rivers, West Australia. 1853. immat.fr. (K-photograph!). Isolectotypes: BM, MEL84091. Syntypes: J. Drummond 256, immat.fr. (BM,W).

[*D. ericoides* auct. non Miq.: Turcz., Bull. Soc. Imp. Naturalistes Moscou 31.I:407 (1858).]

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:325 (1956).

DESCRIPTION (Fig. 7.42):

Dioecious shrub, 0.2-0.5m high, spreading, to 1m diameter. Branches rigid, intricate, dense; branchlets terete or weakly furrowed, dark red or brown, with verruculose glands, puberulent. Leaves simple, sessile, linear, rarely narrow-elliptic or obovate, convex on upper surface, (0.3-) 0.5-0.7(-0.8) x 0.1-0.2(-0.3)cm, olive-green, coriaceous, thick, viscous, with brown verruculose glands, puberulent, base attenuate, margin revolute, entire or with (1-)2(-4) irregular teeth up to 1mm long, apex acute, mid-vein prominent, lateral venation obscure. Flowers unisexual, monadic, terminating branchlets or axillary; subsessile or with pedicels 0.5mm long. Sepals (3-)5, linear, 1.5-2 x 0.3-0.5mm, acute, viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrous, caducous; at anthesis the sepals in male flowers are

spreading, in female flowers they are erect & free. Stamens in male flowers 6, just exceeding the sepals, divergent; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 1.7-2 x 0.7-0.8mm, glabrous; apical appendage acute, 0.1mm long, pubescent; stamens in female flowers absent. Ovary in female flowers 3-carpellate, globose, 0.5 x 0.5mm, viscous, glabrous or pubescent; styles 3, connate, slightly twisted, 5-7mm long, glabrous, separating unequally near the apex, each free arm 0.1-0.5mm long, recurved; in male flowers rudimentary ovary present. Capsule 3-angled, excluding appendages globose, including appendages 3-3.5(-5.5) x 4-4.5(-6)mm, crustaceous, with sessile glands, glabrous, often pubescent when immature, dark red-brown at maturity, base truncate, apex emarginate; carpel globular-navicular, excluding appendage 2-2.5 x 1.5-2.5mm; appendage horn-like, at apex only, spreading, 1-1.5(-3)mm long, shorter than the valve, crustaceous; dehiscence septifragal. Seeds 2-4, lenticular-globose, 1.4 x 1.4mm, black, dull; aril white, infundibular, 0.5mm long. Seedling not seen

Chromosome number: not known.

TYPIIFICATION:

The choice of a lectotype is necessary as two collections were cited with the original description. The three specimens of Drummond 96 (from BM, K and MEL) contain immature, pubescent fruit. Five sheets of the Drummond 256 collection have been seen - the MEL, K and G specimens contain male flowers, while the W and BM specimens have immature fruit. Bentham mentions in the protologue that he had not seen flowers, and so it is presumed that Bentham did not have the MEL, K and G male-flowering specimens available to him. The Drummond 96 collection most closely fits the protologue and the K specimen, which was certainly available to Bentham,

is here chosen as the lectotype.

The male-flowering Drummond 256 specimens, not seen by Bentham are technically not syntypes.

DISTRIBUTION (Fig. 7.42):

D. divaricata is restricted to an area of south-west Western Australia. It extends from Three Springs at the north-western limit of its distributional range to the Narembeen area further south-east.

ECOLOGY:

D. divaricata usually grows on clay or loam and sometimes in stony soils. It is often associated with mixed open mallee scrub with *Eucalyptus stoadii*, *E. celubris* & *E. wandoo* in low wandoo woodlands and in mallee heath with species such as *Melaleuca uncinata*.

This species usually flowers late winter or early spring and fruits are mature by December.

NOTES:

The collection Wilson 3832 differs from most other specimens in having a greater proportion of toothed leaves, slightly larger horns on the capsules and an indumentum of longer hairs. However, its general habit, leaf shape, inflorescence structure, and the pubescent immature fruit place it in this species.

AFFINITIES:

D. divaricata most closely resembles, and has often been confused with *D. pinifolia*, especially in leaf shape, a character in which the two taxa sometimes overlap. The larger leaves, the ovate, acuminate sepals, the larger, mostly 4-angled fruits and the cymose arrangement of flowers of *D. pinifolia* serve to distinguish it from *D. divaricata*.

SPECIMENS EXAMINED:

WESTERN AUSTRALIA:- Demarz 5257, 242ml peg Great Eastern Highway, 10.x.1974. fr. (PERTH).- George 8074, 13ml W of Quairading on rd. to York, 20.ix.1966. m.fl./immat.fr. (PERTH).- Ising s.n., Wongan Hills, 11.viii.1925. m.fl. (AD96935444).- Ising s.n., loc. cit., 17.viii.1925. immat.fr. (AD966100217).- Keighery 332, 2km S of Ballidu, 8.xi.1974. immat.fr. (PERTH).- Keighery 340, S of Minnivale, 7.xi.1974. fr. (PERTH).- Melville 4108 & Calaby, 7ml N of Watheroo, 18.vii.1953. m.fl. (NSW).- Melville 4109 & Calaby, loc. cit., 18.vii.1953. fr. (NSW).- Phillips s.n., between Three Springs & Arrino, 14.ix.1968. m.fl. (CBG57259).- Royce 2139, 12ml E of Ballidu, 11.ix.1947. m.fl. (PERTH).- Royce 2140, loc. cit., 11.ix.1947. f.fl. (PERTH).- West 1068, 1070, 1071, 1073-1074, 11.2km N of Three Springs on rd. to Morawa, 14.viii.1975. f.fl./fr. (AD).- West 3165-3167, 10km NW of Narembeen, 29.xi.1978. fr./st. (AD).- West 3218-3221a, Pithara, 1.xii.1978. fr./m.fl. (AD).- West 3277-3280, 11.2km N of Watheroo, 6.xii.1978. fr./m.fl. (AD).- West 3284-3286, 11.3km NW of Three Springs, 6.xii.1978. m.fl./st./fr. (AD).- Wilson 3832, 15km N of Bodgingarra, 2.xi.1965. immat.fr. (PERTH).

39. *Dodonaea pinifolia* Miq. in Lehm., Pl. Preiss. 1:227 (1845); Benth., Fl. Aust. 1:480 (1863); Mueller, Fragm. 9:88 (1875) incl. broad-leafed form cited under *Dodonaea ceratocarpa*; Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:346-347 (1904); Domin, Mém. Soc. Sci. Bohême 1921-22, 2:62 (1923); Radlkofer, Pflanzenreich IV.165:1399-1400 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).
 TYPE: "in glareosis montis prope St. Ronan's-well, reg. York et in planitie arenosa Quangen, reg. Victoria, 12.Apr.1840. Herb. Preiss. No. 2438". Lectotype (here designated): L. Preiss 2438, Australasia, s.dat. m.fl.,fr. (W). Isolectotypes: G, L, MEL84125, MEL84126, U91925.

Empleurosma virgata Bartl. in Lehm., Pl. Preiss. 2:228 (1848); [Benth., Fl. Aust. 1:480 (1863) pro syn.; Domin, Mém. Soc. Sci. Bohême 1921-22, 2:62 (1923) pro syn.; Radlkofer, Pflanzenreich IV.165:1399-1400 (1933) pro syn.]

TYPE: "in rupestribus ad latus meridionale montis Curric (York) 15.April. 1840. Herb. Preiss. No.2166^b." Syntypes: L. Preiss 2166, G, MEL84150, MEL84151, W (2 sheets).

D. pinifolia Miq. var. *submutica* Benth., Fl. Aust. 1:480 (1863)-basionym of *D. submutica* (Benth.) Domin; Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:347 (1904); [Domin, Mém. Soc. Sci. Bohême 1921-22, 2:62 (1923) pro syn.]; Radlkofer, Pflanzenreich IV.165:1399-1400 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956) -syn. nov.

D. submutica (Benth.) Domin, Mém. Soc. Sci. Bohême 1921-22, 2:62 (1923) in obs. - based on *D. pinifolia* Miq. var. *submutica* Benth.; [Radlkofer, Pflanzenreich IV.165:1399 (1933) pro syn.]

TYPE: "Drummond, 4th Coll. n.255." Holotype: J. Drummond 255, Swan River, s.dat. fr. (K-photograph!). Isotypes: G, BM, MEL84124, W.

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:324 (1956).

DESCRIPTION (Fig. 7.43):

Dioecious or rarely polygamo-dioecious (see Note 3) shrub, 0.2-1m high, spreading, to 1.5m diam. Branches dense or sometimes open, intricate; branchlets angled or ribbed, dark red-brown, viscous, puberulent. Leaves simple, sessile, linear, sometimes terete, rarely oblong or obovate, (0.8-)1.5-2.5(-3.5) x 0.1-0.2(-0.3)cm, coriaceous, with sessile or verruculose glands, viscous, glabrous or very rarely puberulent, base attenuate, margin revolute, entire or with 1-4 irregular teeth or lobes up to 2mm long, apex acute, rarely obtuse, midvein prominent, lateral venation obscure. Flowers unisexual, rarely bisexual (see Note 3), monadic, or diadic to triadic, axillary; pedicels 1-2(-4)mm long, usually longer in female flowers, erect. Sepals 4, ovate, rarely lanceolate, 2-3(-3.5) x 1.5-2.5mm, acuminate, viscous, outer surface glabrous, with sessile glands, inner margin villous, inner surface glabrous, caducous; at anthesis the sepals in male flowers are recurved, in female flowers they surround the ovary, are free towards the apex & valvate below. Stamens in male flowers 8, divergent; filaments 0.7-1mm long, glabrous; anther lobes oblong, 1.8-2.3 x 0.6-0.8mm, glabrous; apical appendage acuminate & curved inwards, 0.3-0.5mm long, puberulent; stamens in female flowers usually present, rudimentary & less than 1mm long. Ovary in female flowers (3-)4-carpellate, globose, angled, 1 x 1mm, with sessile glands, viscous, pubescent; styles 4, connate & twisted spirally in upper part, 5-8mm long, pubescent at the base, separating unequally near the apex, each free arm 0.1-0.5mm long, recurved; in male flowers rudimentary ovary usually present. Capsule

(3-)4-angled, excluding appendages globose or obovoid, including appendages (4.5-)5.5-10(-11.5) x (5-)8-11.5(-20)mm, crustaceous, with sessile glands, viscous when young, glabrous, light to pinkish-brown at maturity, base broad-cuneate or truncate, apex (excluding appendages) truncate; carpel shallow-navicular, excluding appendage (4.5-)5.5-8(-10.5) x 1.5-2.5(-3)mm; appendage usually horn-like, sometimes lobe-like, at apex only, spreading or erect, (0.5-)2.5-6(-8)mm long, usually longer than the valve, crustaceous or rarely \pm membranous; dehiscence septifragal. Seeds 2-4, lenticular-globose, 1.8-2.2(-3) x 1.8-2(-3)mm, black, dull; aril white, infundibular, 0.7-1mm long. Seedling glabrous except for puberulent stem & branchlets; hypocotyl 10-15(-35)mm long; cotyledons linear, 15-20(-40) x 1.3-2mm, acute, glabrous; epicotyl 1-2.5mm long; first 5-6 leaves simple, alternate, sessile, linear, or angular-obovate & 3-lobed near the apex, base sessile or attenuate, margin entire, or 2-3-lobed above the middle, apex acuminate or acute; later leaves without lobes.

Chromosome number: $n = 14$ (West 3193, West 3372)

TYPIIFICATION:

Miquel based *D. pinifolia* on Preiss collection no. 2438, of which six specimens have been seen (i.e. G,L,MEL (2 sheets), U & W). The L,U & W sheets each contain more than one specimen, some with male flowers and some with fruit dissepiments. The sheet from W contains one specimen with old capsules only and another with both male flowers and fruit dissepiments attached. The latter specimen indicates that Preiss collected from a male plant which contained some bisexual flowers (see Note 3). All the other specimens of the type collection appear to be uniform vegetatively and the W specimen is evidence that, although some sheets contain only male flowers or remains of capsules, they are probably all of the same collection. For this reason

and because the W sheet contains specimens in good condition and closely corresponding with the protologue, it is here chosen as the lectotype.

No lectotype has been chosen from among the five available sheets of the Preiss no. 2166 collection on which Bartling based *Empleurosma virgata*, as it is likely that there is more material of this collection in other European herbaria. Bartling's herbarium and types are housed at GOET and sets were distributed to several herbaria whose material has not been seen during this study.

DISTRIBUTION (Fig. 7.43):

D. pinifolia is widespread in the south-west of Western Australia. It extends from Cue and the Geraldton area in the north, to the Wongan Hills and further south to Stirling Ranges and Ravensthorpe. Peak Charles and the Cape Arid National Park east of Esperance form the eastern limit of its distribution.

ECOLOGY:

This species is usually found growing in rocky situations, especially granite and laterite, or in sandy and gravelly soils and occasionally sandy loam. *D. pinifolia* grows in a range of vegetation associations including open mallee scrub, mallee heath, woodland and dry sclerophyll forests. Near Hopetoun it is found in mallee heath with *Eucalyptus leptocalyx*, *E. anceps*, *E. conglobata* and *E. spathulata* var. *glandiflora* and with the shrubs *Melaleuca uncinata*, *Acacia alata* and *Hakea laurina*. The forest of the Stirling Ranges in which *D. pinifolia* has been collected is dominated by *Eucalyptus wandoo*,

E. occidentalis & *E. falcata*. *Casuarina campestris* is a common associate in drier areas, and proteaceous shrubs form dense heath communities with *D. pinifolia*.

D. pinifolia appears to be an initial coloniser of disturbed sites. Several collections were made during this study of populations colonising disturbed roadsides, and sites such as creek crossings. After fire it regenerates from seed, or if the bush is not subjected to a high intensity fire it is capable of reshooting from the base. In these cases the foliage is deeply lobed and resembles the juvenile foliage of the seedlings.

Flowering occurs over summer, usually December to March, and capsules are present from late August through to November.

NOTES:

1. *D. pinifolia* is a morphologically variable species. The shape of the leaves, the size and shape of the fruits and the capsule appendages and the flower arrangement vary widely in the large range of specimens examined. In many cases the extremes of a character are exhibited by a single individual and often within a population. There is a tendency towards a geographical cline of fruit size and leaf shape from north to south, but this breaks down in many places. In the arid Cue and Payne's Find area is a very woody form with large fruits with long appendages and small flat leaves. The populations near Ravensthorpe and west of that town usually have linear, almost terete leaves and small fruits with the appendage reduced to a lobe-like structure. Neither of these forms however, is constant either morphologically or geographically and, as all intermediate stages are represented it seems appropriate to consider *D. pinifolia* a single polymorphic species incapable of satisfactory subdivision.

2. Examination of the four sheets of the type collection of *D. pinifolia* var. *submutica* indicates that this variety and the species

D. pinifolia are the same taxon. The capsules of Drummond 255 contain long horn-like appendages up to 2.5mm and the branchlets are no more angular than the type collection of *D. pinifolia*. Bentham cast doubt on the validity of this infraspecific taxon when he described it - "capsules apparently almost without horns, but not perfect in our specimens". *D. pinifolia* var. *submutica* is therefore regarded as a synonym of *D. pinifolia*. (Stafleu et al., 1978, Art. 11).

3. There is some evidence of polygamo-dioecy in this species. Although no bisexual flowers have been seen in the field or on herbarium specimens a small number of male-flowering specimens also contain a few fruit or fruit dissepiments. The type collection, Preiss no. 2438, appears to be an example of this.

AFFINITIES:

D. pinifolia is most closely related to *D. divaricata*, with which it shares 'horned' fruit, arillate seeds and small linear leaves. The two species have been confused in the past, but they can be distinguished on the sessile, solitary flowers, very small stamen filaments, linear sepals, and leaves less than 1cm long in *D. divaricata*. This species also has smaller, 3-carpellate fruits and puberulent leaves.

D. ceratocarpa sometimes resembles *D. pinifolia*, but the former species has oblanceolate to obovate, flat leaves, with sessile glands, clavate pedicels and shorter stamen filaments.

SPECIMENS EXAMINED: selection only (91 collections examined)

WESTERN AUSTRALIA:- George 9829, 4ml SSW of Ravensthorpe, 7.iii.1970. m.fl./f.fl., fr. (PERTH).- Haegi 968, Peak Charles, 15.ix.1976. fr. (AD).- Kenneally 2308, Wongan Hills, 21.ix.1974. fr. (PERTH).- Knox 651045, 16ml S of Pithara, x.1965. fr. (PERTH).- West 3011-3016, West River crossing

on Ravensthorpe/Jerramungup rd., 25.xi.1978. fr. (AD).- West 3021-3027,
16.5km S of Jerramungup, 25.xi.1978. fr. (AD).- West 3090-3099, 21.2km
NW of Katanning, 27.xi.1978. fr. (AD).- West 3189-3194, 15 km N of
Kellerberrin, 30.xi.1978. fr./m.buds. (AD).- West 3226-3230, Mogumber,
2.xii.1978. fr./m.fl. (AD).- West 3324-3327, Cue, 9.xii.1978 fr./m.fl.
(AD).- West 3371-3375, 10km E of Southern Cross, 11.xii.1978. fr./m.fl.
(AD).- Wilson 4389, 48km N of Bremer Bay, 2.x.1966. fr. (PERTH).-
Wilson 5423, 32km W of Ravensthorpe, 3.x.1966. fr. (PERTH).- Wilson 5881-
5882, 1km S of Ravensthorpe, 21.v.1967. m.fl./fr. (PERTH).

V. Sect. *Pinnatae* (Benth.) West, stat. nov.

Sect. *Remberta* Miq. in *Linnaea* 18:94 (1844).

Ser. *Pinnatae* Benth., Fl. Aust. 1:483 (1863), p.p. (excl. *D. humilis*,
D. megazyga & *D. inaequifolia*).

Ser. *Cyclopterae* subser. *Oospermae* Radlk., Pflanzenreich IV:165:1352 (1933),
p.p.

TYPE SPECIES: Holotype: *D. pinnata* Sm.

DIAGNOSIS:

Leaves usually imparipinnate, rarely paripinnate, petiolate, leaflet margin entire, apex acute to obtuse, often toothed or lobed, terminal leaflet usually shorter than laterals, sometimes \pm absent; capsule in lateral view oblong to obovate, to transversely broad-elliptic or broad-oblong, apex usually obcordate, rarely emarginate, carpel membranous or coriaceous, rarely crustaceous, wing membranous or coriaceous, rounded, approx. equal width from apex to base, extending from apex to base of carpel; seed exarillate.

TYPIIFICATION:

D. pinnata is the holotype of this section since Bentham based his series *Pinnatae* on this specific epithet (Stafleu et al., 1978, Art. 22.4).

DISTRIBUTION:

Members of this section occur in almost all parts of Australia. Several show restricted distributions in eastern and southern Australia while other species are widespread across the continent.

D. adenophora Miq.
D. boroniaefolia G. Don
D. concinna Benth.
D. larreoides Turcz.
D. microzyga F. Muell.
D. multijuga G. Don
D. oxyptera F. Muell.
D. physocarpa F. Muell.

D. pinnata Sm.
D. polyzyga F. Muell.
D. rupicola C.T. White
D. sinuolata West
D. stenozyga F. Muell.
D. subglandulifera West
D. uncinata West
D. vestita Hook.

KEY TO SPECIES OF SECTION *PINNATAE*

- 1a. Leaflets terete or linear & < 2mm broad, glabrous or puberulent, never pubescent or hirsute, with sessile glands, never with sunken glands & if verruculose glands are present then on lower surface only, apex acute to obtuse 15
- 1b. Leaflets various shapes, mostly narrow- to broad-obovate, usually \geq 2mm broad, pubescent to hirsute, rarely glabrous, hirsute or with sunken, sessile or verruculose glands, apex usually toothed or lobed 2
- 2a. Lateral leaflets \geq 10, if 10 then leaves hirsute, leaves imparipinnate 3
- 2b. Lateral leaflets usually \leq 10, rarely 12 & then leaves paripinnate & terminated by a very small tooth or lobe, glabrous or pubescent, never hirsute 10
- 3a. Capsule glabrous or sparsely pubescent, wing margin entire; plant at least in part glabrous (e.g. inner sepal surface or capsule) . . . 4
- 3b. Capsule densely hirsute, wing margin denticulate; whole plant hirsute to pubescent 9
- 4a. Capsule carpel (excluding wing) \geq 12.5mm long; leaves hirsute, glands absent; flowers monadic 40. *D. pinnata*
- 4b. Capsule carpel (excluding wing) < 12.5mm long; leaves glabrous or pubescent, not hirsute, with sessile, verruculose or sunken glands; inflorescence botryoidal to paniculate, never monadic 5
- 5a. Petiole \leq 8mm long, leaflets angular-obovate to obovate, rarely oblong, with large, sunken glands near margin of upper surface & usually below, pubescent with arched or curved hairs; seed compressed towards the margin 6
- 5b. Petiole > 8mm long, leaflets oblong to oblanceolate, without sunken glands, glabrous or pubescent, the hairs straight or strongly adpressed, not arched; seed not compressed towards the margin 7
- 6a. Leaflets \geq 16; capsule 3-winged; inflorescence a many-flowered panicle 41. *D. multijuga*
- 6b. Leaflets < 16; capsule 4-winged; inflorescence a 2-5-flowered botryoid 42. *D. boroniaefolia*
- 7a. Leaves (excluding petiole) > 7cm long, leaflets \geq 28; sepals > 3mm long; seeds lenticular-globose, \geq 2.4mm long 43. *D. polyzyga*
- 7b. Leaves (excluding petiole) < 7cm long, leaflets usually < 28; sepals \leq 3mm long; seeds lenticular, < 2.4mm long 8

- 8a. Leaves (excluding petiole) usually < 3cm long, leaflets < 2mm broad, isobilateral, margin irregularly sinuate; capsule > 9mm long
 44. *D. sinuolata*
- 8b. Leaves (excluding petiole) usually > 3cm long, leaflets \geq 2mm broad, darker above than below, margin entire; capsule \leq 9mm long
 45. *D. larreoides*
- 9a. Capsule \geq 16mm broad, wing 5-7mm broad; leaves (excluding petiole) \leq 2cm long; sepals usually > 1.5mm broad 46. *D. vestita*
- 9b. Capsule < 16mm broad, wing 3-4mm broad; leaves (excluding petiole) > 2cm long; sepals \leq 1.4mm broad 47. *D. rupicola*
- 10a. Leaves paripinnate, with a small terminal lobe or tooth usually \leq 1mm long, leaflets usually > 7.5mm long, (rarely < 7.5mm long & then branchlets densely pilose), pubescent with adpressed hairs, glands absent; branchlets pilose 11
- 10b. Leaves imparipinnate, terminal leaflet smaller than laterals, but not tooth- or lobe-like & usually > 1mm long, leaflets \leq 7.5mm long, glabrous or puberulent, rarely pubescent & then hairs arched, with sessile, verruculose or sunken glands; branchlets puberulent to pubescent, never pilose 12
- 11a. Capsule 5-6-winged, > 10mm long, inflated, not readily dehiscent; pedicel 8-13mm long; petiole > 8mm long 48. *D. physocarpa*
- 11b. Capsule 4-winged, < 10mm long, not inflated, dehiscence septifragal; pedicel < 3mm long; petiole \leq 7mm long 49. *D. oxyptera*
- 12a. Capsule < 8mm long, dehiscence septicidal; leaflets \leq 1.5mm broad
 50. *D. adenophora*
- 12b. Capsule \geq 10mm long, dehiscence septifragal; leaflets \geq 1.5mm broad
 13
- 13a. Leaves with large sunken glands, pubescent, the hairs arched; inflorescence diadic or triadic 42. *D. boroniaefolia*
- 13b. Leaves with verruculose glands, never with sunken glands, glabrous or puberulent; inflorescence monadic or diadic 14
- 14a. Leaves puberulent, terminal leaflet apex obtuse to rounded, not hooked; sepals \geq 1.3mm broad, caducous 51. *D. microzyga*
- 14b. Leaves glabrous, terminal leaflet apex acute, recurved & hooked; sepals \leq 1.4mm broad, persistent 52. *D. uncinata*
- 15a. Petiole \leq 3mm long, with verruculose glands below; leaflets with verruculose glands below only; capsule \leq 7mm long 53. *D. subglandulifera*
- 15b. Petiole usually > 3mm long, rarely < 3mm long & then without verruculose glands; leaflets with sessile or verruculose glands above & below; capsule > 7mm long 16

- 16a. Leaflets usually > 10, irregularly sinuate; style \geq 5mm long; branchlets \pm terete, with verruculose glands 44. *D. sinuolata*
- 16b. Leaflets usually < 10, entire; style < 5mm long; branchlets angular, lacking verruculose glands 17
- 17a. Branchlets glabrous; petiole > 9mm long, leaflets usually > 9mm long 54. *D. stenozyga*
- 17b. Branchlets puberulent; petiole \leq 6mm long, leaflets \leq 9mm long 55. *D. concinna*

40. *Dodonaea pinnata* Sm. in Rees, Cyclop. 12 (1809); DC., Prodr. 1:617 (1824); G. Don, Gen. hist. 1:674 (1831); [Steudel, Nom. bot. 522 (1840) pro syn. sub *Serjania australis*]; Miq. in Linnaea 18:95 (1844); Bentham, Fl. Aust. 1:484 (1863); Moore, Fl. N.S.Wales 95 (1893); Radlkofer, Pflanzenreich IV.165:1383-1384 (1933); Beadle et al., Fl. Syd. Reg. 387 (1972).
 TYPE: "Communicated by earl St. Vincent, who received it from New South Wales." - n.v.

Serjania australis Spreng., Syst. 2:248 (1825); [Rادلkofer, Pflanzenreich IV.165:1383 (1933) pro syn.]

TYPE: "Nov. Holl." - n.v.

FIGURES: Martin, Aust. J. Bot. Suppl. 6:18, fig.75 (1973)- pollen only.

DESCRIPTION (Fig. 7.44):

Dioecious shrub, 0.5-1.5m high, spreading. Branches spreading; branchlets terete or slightly angular, hirsute. Leaves imparipinnate, (1.35-)1.8-3(-3.8)cm long (excluding petiole); petiole 4-5(-5.5)mm long, densely hirsute; rhachis winged, 1-1.5mm broad, channelled above; lateral leaflets 10-16(-26), opposite or irregularly alternate, narrow-angular-obovate to narrow-obovate, sometimes linear-oblongate or ovate, (4-)5-7.5(-9) x 2-2.5mm; olive-green above, usually paler below, scabrous, viscous, densely hirsute, the hairs white or clear in colour, base cuneate, sessile, or rarely with petiolule to 0.2mm long, margin entire, revolute, apex acute, midvein prominent below, impressed above, lateral venation obscure; the terminal leaflet small, lobe-like, otherwise similar to lateral leaflets. Flowers unisexual, in few-flowered compound inflorescences composed of monads, terminal or terminating branchlets; pedicels (3.5-)5-6.5(-9)mm long, hirsute. Sepals 4-5, ovate, sometimes ovate-lanceolate, (1.6-)2-3.6(-4.5) x (1.1-)1.3-1.7(-2)mm, acute, viscous, outer surface sparsely hirsute, inner surface glabrous, persistent; at anthesis

the sepals in male flowers are spreading, in female flowers they are free, erect, imbricate near the base, surrounding the ovary. Stamens in male flowers 8-10(-12), approx. equal in length to the sepals, spreading; filaments 0.1-0.2mm long, glabrous; anther lobes broad-oblong, twisted at anthesis, 1.8-2(-2.2) x 0.8-1mm, pubescent to hirsute, the hairs denser towards the apex; apical appendage a broad, obtuse lobe, to 0.2mm long, hirsute; stamens in female flowers absent. Ovary in female flowers 4-carpellate, broad-oblong or elliptic, angled, 1-1.2 x 1-1.1mm, viscous, densely hirsute; styles 4, connate, twisted above the middle, 8-15mm long, pubescent or hirsute near the base, separating unequally near the apex, each free arm to 0.8mm long, divergent; in male flowers rudimentary ovary usually absent. Capsule 4-winged, in lateral view transverse- to broad-elliptic, or broad-obovate, 14-18(-21) x 15.5-18(-22)mm, coriaceous, viscous, glabrous, or rarely with a few hairs on wing margins, red-brown to purple at maturity, base broad-cuneate to truncate, rarely rounded, apex emarginate; carpel excluding wing transverse-oblong, broad-navicular, (12.5-)13.5-16 x 3.5-5(-5.5)mm, with sparse sessile glands; wing 3.5-5 (-6)mm broad, undulate, extending from apex to base of carpel, broadest at the capsule apex, broader than or equal to the valve; dehiscence septi-fragal. Seeds 2-4, lenticular, compressed towards the margin, 2.7-3.2 (-3.8) x 2.4-2.8mm, black, dull; aril absent. Seedling hirsute; hypocotyl 15-18mm long; cotyledons linear, 18-22.5 x 1.5-2mm, acute, glabrous; epicotyl 0.5-1mm long; the first 2-4 leaves imparipinnate, with 3-5 leaflets, the leaflets obtuse, otherwise as in mature leaves, later leaves with increasing numbers of leaflets.

Chromosome number: not known.

TYPIFICATION:

Material from the Smith herbarium, now held at LINN has not been seen, and so no comments can be made on the state of the type of *D. pinnata*. Bentham (1863) cited "Port Jackson, R. Brown (Hb. R.Br. and Smith)", indicating that he saw Brown specimen(s) collected at Port Jackson from the Smith and Brown herbaria. A sheet of Brown (No. 5439) *D. pinnata* specimens from Port Jackson, now held at BM, has been examined and is probably of the same collection as that seen by Bentham, but it is uncertain whether this is type material. It contains male-flowering specimens only and in that way agrees with Smith's protologue. Attempts will be made to examine the material held at LINN or a microfiche copy of the Smith herbarium, and to clarify the typification for this name.

DISTRIBUTION (Fig. 7.44):

D. pinnata is confined to the Hawkesbury and Nepean River systems near Sydney on the central coast of New South Wales.

ECOLOGY:

This species grows on sandstone or on sandy soil in dry sclerophyll forest. Associated species include *Eucalyptus eximia*, *E. gummifera*, *E. punctata*, *E. piperita*, *Angophora bakeri*, *Acacia linifolia*, *Hakea dactyloides*, *Lambertia formosa*, *Isopogon anemonifolius* and *Boronia mollis*.

D. pinnata flowers in spring (August to October) and fruit is mature during summer (November to February).

AFFINITIES:

D. pinnata shows close relationships to *D. multijuga* of eastern New South Wales and southern Queensland and *D. vestita* of central Queensland. It shares similar leaves and indumentum with *D. vestita* although the hairs of *D. vestita* are usually golden-coloured. The capsules and flowers of

these two species differ in *D. vestita* having hirsute capsules, long pedicels, sepals on the inner surface glabrous at the base only, and longer filaments and anthers.

D. multijuga is similar to *D. pinnata* in leaf morphology and some capsule characters. Besides the size difference in sepals and anthers these two species can be distinguished by the pubescent indumentum of short, curved hairs, the longer, ±glabrous fruiting pedicels, caducous sepals, the 3-winged capsules, axillary inflorescences and large sunken glands on the leaves of *D. multijuga*.

SPECIMENS EXAMINED: selection only (41 collections examined).

NEW SOUTH WALES:- Blakely s.n., 1ml NW of Berowra, ix.1935. f.fl.,fr. (NSW140580).- Blakely s.n., Kangaroo Point, Hawkesbury R., x.1918. m.fl. (NSW140585).- Blakely s.n., Patonga, 6.xii.1925. fr. (NSW140588).- Brown 5439, Port Jackson, 1802-5. m.fl. (BM).- Cleland s.n., Wiseman's Ferry, on Hawkesbury R., 8.viii.1915. m.fl. (AD96233017).- Ellen s.n., Middle Creek, Narrabeen Lake, xii.1916. fr. (NSW140592).- Fairley-Cunninghame s.n., Boorai Creek, Colo River area, 30.x.1966. mature f.fl.,fr. (NSW84404).- Hamilton s.n., Hawkesbury R. (Brooklyn), v.1912. fr. (NSW140598).- West 2561-2565, E bank of Nepean R., 5km NW of Mulgoa, 25.iv.1978. st. (AD).- Winter s.n., Glenorie, ix.1929. m.fl. (NSW140590).

41. *Dodonaea multijuga* G. Don, Gen. hist. 1:674 (1831); Bentham, Fl. Aust. 1:485-586 (1863); Mueller, Fragm. 9:86 (1875); Moore, Fl. N.S.Wales 95 (1893); Radlkofer, Pflanzenreich IV.165:1385-1386 (1933); Beadle et al., Fl. Syd. Reg. 387 (1972).
 TYPE: "Native of New Holland (v.s. herb. Lamb.)." Lectotype (here designated): A. Cunningham s.n., Liverpool Plains, 1825. m.fl. (W). Isolectotypes: G (2 sheets).

[*D. hirtella* auct. non Miq.: Mueller, Pl. indig. Col. Vic. 1:89 (1862).]

DESCRIPTION (Fig. 7.45):

Dioecious shrub, 1-1.5m high, erect. Branches slender; branchlets angular, densely covered with bent & adpressed hairs. Leaves imparipinnate, (2-)3-4.5(-4.8)cm long (excluding petiole); petiole (3.5-)5-7(-8)mm long, pubescent; rhachis winged, 1-1.2mm broad, channelled above; lateral leaflets (16-)20-28(-32), opposite or irregularly alternate, oblong to broad-obovate, sometimes obtriangular or angular-obovate, rarely linear, (1.5-)4-6(-7) x (1-)2-4mm, dark or bright green above, paler below, scabrous, viscous, with 5-10 large, sunken glands around margin on upper surface, & sometimes visible on midvein below, pubescent, the hairs bent & adpressed, sometimes sparse on upper surface, base cuneate, oblique, sessile, margin entire or sinuate, revolute, apex obtuse to broad-acute, sometimes mucronate, sometimes obscurely 2-3-toothed, recurved & often appearing truncate or emarginate from above, midvein prominent below, impressed above, lateral venation obscure; the terminal leaflet lobe-like, otherwise as in lateral leaflets. Flowers unisexual, in many-flowered, axillary panicles composed of monads to metabotryoids; pedicels (7-)8-13(-14)mm long, viscous, sparsely pubescent, becoming glabrous in fruit. Sepals 4(-5), lanceolate to narrow-lanceolate, 3-3.5(-4) x 0.8-1.4mm, acute to acuminate, viscous, outer surface sparsely pubescent, inner

surface pubescent at the apex, glabrous towards the base, caducous; at anthesis the sepals in male flowers are recurved, in female flowers they are free, erect, sometimes recurved at the apex, surrounding the ovary. Stamens in male flowers 8(-10), shorter than the sepals, divergent; filaments 0.2-0.3mm long, glabrous; anther lobes linear-oblong, twisted at anthesis, 2.5-2.8 x 0.7-0.9mm, pubescent, the hairs denser towards the apex; apical appendage a broad, obtuse lobe, to 0.1mm long, pubescent to hirsute; in female flowers rudimentary stamens sometimes present. Ovary in female flowers 3-carpellate, oblong to ellipsoid, angled, 1-1.3 x 0.8-1.1mm, viscous, densely pubescent; styles 3, connate, twisted in upper half, (7-)11-13mm long, pubescent near the base, separating unequally near the apex, each free arm 0.2-0.5(-2)mm long, divergent; in male flowers rudimentary ovary present. Capsule 3-winged, in lateral view broad-to transverse-obovate, slightly inflated, (13-)14.5-16(-16.5) x (15-)16-20mm, coriaceous, viscous, with sparse sessile glands on carpel, sparsely pubescent, red-brown to red at maturity, base cordate, apex obcordate; carpel excluding wing transverse-oblong, navicular, (9.5-)10-12(-13) x (3.5-)4-5.5mm, thickened; wing 3-4mm broad, usually undulate, extending from apex to base of carpel, broadest at the capsule apex, narrower than the valve; dehiscence septifragal. Seeds 2-4, lenticular, strongly compressed towards the margin, 2.4-3.4 x 2.4-2.7mm, black, dull; aril absent. Seedling pubescent; hypocotyl 9-15mm long; cotyledons linear, (17-)20-23 x 1-2mm, acute, glabrous; epicotyl 2-3mm long; the first 2 leaves imparipinnate, with 5-7 leaflets, sunken glands absent, otherwise as in mature leaves, later leaves with increasing numbers of leaflets.

Chromosome number: not known.

TYPIFICATION:

G. Don described *D. multijuga* from material in the Lambert herbarium. Enquiries have been made and/or material has been borrowed from the majority of European herbaria known to hold Australian material from the Lambert herbarium (Miller, 1970). Three sheets of specimens (G (2 sheets), W) collected by Allan Cunningham in 1825, which were part of the Lambert herbarium, have been located. All three specimens have male flowers, which would have enabled Don to include the inflorescence structure, together with details of the leaves, in the brief protologue. The W specimen is chosen as the lectotype as it is a larger specimen in better condition than the G material.

DISTRIBUTION (Fig. 7.45):

D. multijuga occurs mainly in the central coast and tablelands regions of New South Wales, and it also grows in the N.S.W. northern tablelands and in south-east Queensland. Earlier this century it was common near the George's River (south of Sydney) and further south-west towards Goulburn, but these areas have suffered greatly from the urban and agricultural sprawl. *D. multijuga* is now found in the more inaccessible tablelands areas from Nerriga in the south to Scone, with a slight disjunction to the Casino area, and in the Queensland Moreton district near Brisbane.

ECOLOGY:

D. multijuga grows on sandstone or in sandy soils often associated with creek and river banks. It usually occurs in dry sclerophyll forest and may be associated with *Eucalyptus ovata*, *E. cypellocarpa*, *E. urceolaris*, *Acacia parramattensis*, and shrubs such as *Grevillea baueri* and *G. evansiana*.

Flowers reach anthesis in late summer to autumn (February to early May) and fruits are usually present from October to December.

AFFINITIES:

D. multijuga is most closely related to *D. pinnata*. The two species share similar fruit shapes and general leaf morphology, but they differ by *D. pinnata* having a longer indumentum of straight hairs, shorter, pubescent fruiting pedicels, smaller persistent sepals, 4-winged capsules, and flowers in terminal inflorescences.

The large sunken glands on the margin of the leaflets are also found in *D. boroniaefolia*, which has a leaflet shape resembling that of *D. multijuga*. *D. boroniaefolia* has a smaller number of leaflets, few-flowered inflorescences, 4-winged capsules and smaller seeds.

SPECIMENS EXAMINED: selection only (86 collections examined).

NEW SOUTH WALES:- Blaxell & Briggs 3001, Boolijah Creek, 3km ESE of Sassafras on Nowra-Nerriga rd., 15.iii.1969. m.fl. (NSW).- Boorman s.n., Berrima, vii.1906. f.fl. (NSW140562).- Carrick 3235, Khyber Pass, Mt. Sheridan, 90km E of Rylestone, 26.x.1972. immat.fr. (AD).- Crisp 2048 & 2049, highest peak on Cabbage Tree Creek, 22km NW of Bateman's Bay, 22.iv.1976. m.fl. (AD,CBG).- Fletcher s.n., Woronora R., x.1894. fr. (NSW140560).- Rupp s.n., Mt. King William, Copmanhurst, x.1911. fr. (NSW140550).- Telford s.n., Yadboro S.F., 13.ii.1968. m.fl. (CBG22682).- West 2579-2586, on Endrick R. crossing, 5km E of Nerriga on Nowra-Braidwood rd., 30.iv.1978. f.fl./st. (AD).- Wrigley s.n., Endrick R., between Braidwood and Nerriga, 4.xii.1967. fr. (CBG22156).

QUEENSLAND:- Lavarack s.n., Moreton distr., TR374, (Mt. Beerburum), vi.1974. fr. (BRI223822).

42. *Dodonaea boroniaefolia* G. Don, Gen. hist. 1:674 (1831); Bentham, Fl. Aust. 1:485 (1863); Mueller, Fragm. 9:86 (1875), Native Pl. Vic. 1:123 (1879); Bailey, Fl. Qld. 1:318 (1899); Moore, Fl. N.S.Wales 95 (1893); Domin, Biblioth. Bot. 22(89^h):912 (1927), p.p. (excl. "South Australia"); Ewart, Fl. Vic. 739 (1931), p.p. (excl. "South Australia"); Radlkofer, Pflanzenreich IV.165:1387 (1933), p.p. (excl. South Aust. occurrence); Galbraith, Wildfls. Vic. 88 (1967); Beadle et al., Fl. Syd. Reg. 387 (1972); Willis, Hdbk. Pl. Vic. 2:359 (1972), p.p. (excl. "W.A.").

TYPE: "Native of New Holland (v.s. herb. Lamb.)". Lectotype (here designated): A. Cunningham s.n., Interior of New S. Wales, 1825. fr. (G).

Isolectotypes: G (folder of fr.); G (m.fl.); A. Cunningham 74, in vicinity of Bathurst and western Interior and country north from that settlement, xii.1825. fr. (BM); A. Cunningham 74, Bathurst, 1825. fr. (CGE); A Cunningham s.n., in the vicinity of Bathurst, 1825. fr./m.fl. (W).

D. caleyana G. Don, Gen. hist. 1:674 (1831); [Bentham, Fl. Aust. 1:485 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1386 (1933) pro syn.]

TYPE: "Native of New Holland (v.s. herb. Lamb.)", n.v.

D. hirtella Miq. in Linnaea 18:94 (1844); Mitchell, Journ. Exped. Trop. Aust. 191 (1848); Mueller, Pl. indig. Col. Vic. 1:89 (1862); [Bentham, Fl. Aust. 1:485 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1386 (1933) pro syn.]

TYPE: "Crescit in New South Wales Novae Hollandiae. (Herb. Watson.no.G)".

Lectotype (here designated): A. Cunningham s.n., Australia, s.dat. fr. (U91878). Isolectotype: CGE.

DESCRIPTION (Fig. 7.46):

Dioecious, or rarely polygamo-dioecious shrub, 0.5-2m high, spreading or erect. Branches dense, spreading; branchlets terete, or angular in

the ultimate branchlets, densely covered with simple, arched hairs strongly curved towards the branchlets, or sometimes puberulent. Leaves imparipinnate, (0.6-)0.85-2(-2.8)cm long (excluding petiole); petiole (1-)2-5.5(-8)mm long, viscous, glabrous to pubescent; rhachis winged, 1-1.5mm broad, channelled above; lateral leaflets (6-)8-12(-14), opposite or irregularly alternate, narrow-angular-obovate or narrow-obovate to angular-obovate or obovate, rarely broad-obovate or oblong, 3(-6)-toothed or-lobed at the apex, (2.5-)3.5-6.5(-9) x (1.5-)2-3.5(-4.5)mm, bright green, coriaceous, viscous, with sunken glands on margin on upper surface and on midvein below, sometimes visible on lateral veins below, glabrous to pubescent, the hairs usually arched or curved towards the leaf surface, rarely straight, base cuneate, margin entire, revolute or recurved, apex 3(-6)-toothed or-lobed, the teeth broad-acute to obtuse, the central one often recurved, midvein prominent below, impressed above, lateral venation usually obscure, rarely visible below; the terminal leaflet lobe-like & entire, otherwise similar to lateral leaflets. Flowers unisexual, or rarely bisexual, diadic or triadic, axillary; pedicels (4-)4.5-6.5(-8)mm long, often longer in female flowers, viscous, pubescent, rarely glabrous. Sepals 4, lanceolate in female flowers, ovate in male flowers, (2-)2.5-3(-4) x 1-1.7(-2)mm, long-acute to acuminate, viscous, outer surface pilose to pubescent, sometimes sparsely so, inner surface sparsely pubescent to glabrous, often glabrous towards the base, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are free, erect, surrounding the ovary. Stamens in male & bisexual flowers 8, exceeding the sepals, spreading; filaments 0.3-0.4mm long, glabrous; anther lobes narrow-oblong, twisted at anthesis, 2-2.5(-3) x 0.7-1mm, pilose or pubescent above the middle, rarely at the apex only; apical appendage a broad, obtuse lobe, to 0.1mm long, pubescent; stamens in female flowers absent. Ovary in female & bisexual flowers 4-carpellate, oblong to globose, 0.7-1

x 0.7-1mm, viscous, densely pilose; styles 4, connate, 9-18mm long, pubescent at the base, separating unequally near the apex, each free arm up to 1.7mm long, divergent; in male flowers rudimentary ovary usually present. Capsule 4-winged, in lateral view broad- to transverse-elliptic, (10-)11-15(-20) x 12-16(-18)mm, membranous, viscous, glabrous or sometimes pubescent, red to pink-purple at maturity, base cordate, apex deeply obcordate, with the wings overlapping; carpel excluding wing lunate & transverse-oblong, 7-9(-12) x (2-)3-4.5mm; wing 2.5-4.5(-5)mm broad, extending from apex to base of carpel, broadest at the capsule apex, approx. same width as the valve; dehiscence septifragal. Seeds 2-4, lenticular, strongly compressed towards the margin, 2.1-2.6 x 1.8-2.4mm, black, dull; aril absent. Seedling glabrous or sparsely puberulent; hypocotyl (10-) 15-20mm long; cotyledons linear, 20-26 x 1.5-2mm, acute, glabrous; epicotyl 1-4mm long; the first 2 leaves imparipinnate, with 3-5 leaflets, sunken glands absent, otherwise as in mature leaves, later leaves with increasing numbers of leaflets.

Chromosome number: not known.

TYPIIFICATION:

G. Don described *D. boroniaefolia* from material in the Lambert herbarium. Enquiries made to the majority of European herbaria known to hold Australian material from that herbarium (Miller, 1970) have located five sheets of specimens collected by Allan Cunningham in 1825 (BM, CGE, G (2 sheets), W), one of which was certainly part of Lambert's herbarium. Four of the six specimens involved are from the same fruiting plant and the other two are from another plant bearing male flowers. The W sheet contains one of each of these specimens (i.e. it has both a male-flowering and a fruiting specimen mounted together), and the BM and CGE material is from

the plant in fruit. The G material, which was part of the de Candolle herbarium, is composed of two sheets, one with male flowers and the other with fruit, in the same folder. The fruiting specimen from G, here chosen as the lectotype, is accompanied by a label with locality and date of collection as well as "E. Lamb. herb.". The G male-flowering specimen in the same folder exactly matches the specimen with male flowers on the W sheet. So, although the two G specimens are mounted separately and the label accompanying the second specimen only indicates that it was collected by Cunningham, it is very likely that they were both in the Lambert herbarium and that Don used them in describing *D. boroniaefolia*. Mounted on the same sheet as the G specimen with male flowers is a small folder containing capsules and capsule fragments, and seeds and leaflets, all of which obviously belong to the lectotype. Since this material is mounted on a separate sheet it is regarded as an isolectotype, as are the B, CGE and W specimens. The G specimen with capsules is chosen as the lectotype primarily because it is the only one that was definitely part of the Lambert herbarium.

Lectotypification is necessary for the synonymous name *D. hirtella*, as neither of the two specimens of the type collection, which have been examined, were nominated by Miquel as the type. Since the fruiting specimen (U91878) agrees more closely with the protologue and it is housed in the herbarium in which Miquel worked and which holds his main collection and types, it is here chosen as the lectotype. It seems likely that Miquel did not see the isolectotype held at CGE as he makes no specific mention of its hirsute female flowers, which might have been expected in such a detailed protologue.

DISTRIBUTION (Fig. 7.46):

D. boroniaefolia is widespread in eastern Australia from western Victoria, through New South Wales to the Charters Towers area of north-

eastern Queensland. In New South Wales it occurs on the western plains, the western slopes and tablelands and on the central coast. Its distribution extends into the Maranoa and Warrego districts of southern Queensland and northwards into the central Mitchell district on the western side of the Great Dividing Range.

ECOLOGY:

The communities in which *D. boroniaefolia* grows vary considerably throughout its extensive distribution. For instance, in N.S.W. it occurs on sandstone in dry sclerophyll forest dominated by *Eucalyptus rossii* in the central tablelands, in dry woodland with *Acacia implexa* on the quartzites of the Cocopara Range north-east of Griffith, and as a codominant with *Micromyrtus* sp. in heath in the Warrumbungle Ranges. Further north in Queensland it is mostly found on sandy soils, frequently in *Eucalyptus populnea*, *E. melanophloia* and *Callitris* sp. woodlands, as well as in *Eucalyptus melanophloia* - *Acacia aneura* open woodlands.

D. boroniaefolia flowers mainly in winter to spring (i.e. May to October), but the flowering season appears to vary over its geographical range. Mature capsules are usually present in late spring to summer (September to January).

NOTES:

1. *D. boroniaefolia* exhibits a certain amount of morphological variation, especially in leaf and leaflet size and indumentum density. There appears to be no obvious correlation of changes in leaflet size along a gradient such as a geographical cline, but it seems that much of the variation in indumentum density is environmentally induced. Individual plants from the same locality, which are ecologically isolated can vary considerably in the density of hairs on the leaves.

2. One specimen from Jobs Gate on the Queensland/N.S.W. border (Purdie 561D) differs from most *D. boroniaefolia* material in having entire, acute leaflets. A small number of collections from Victoria (e.g. Beauglehole 55247, Canning CBG21406) differ from the majority of material of this species in having broader leaflets with more teeth (up to 6) at the apex. In all other features these plants belong to *D. boroniaefolia* and until further field work is done relating to the consistency of this different form, both morphologically and geographically, it is not formally recognized at any infraspecific level.

3. The erroneous records of the occurrence of *D. boroniaefolia* in South Australia (e.g. Mueller, 1889; Domin, 1927 and Radlkofer, 1933) probably emanate from a misidentification of a small specimen of *D. humilis* from Ardrossan on Yorke Peninsula by Tepper (1880). Sheet AD97732733 contains a number of specimens of Sapindaceae species including one of *D. humilis* collected in 1879 which is labelled *D. boroniaefolia*.

PUTATIVE HYBRIDS:

1. *D. boroniaefolia* x *D. viscosa* ?ssp. *cuneata*

In eastern Australia *D. viscosa* is sympatric with *D. boroniaefolia*. A few collections from the central western slopes and one from the Warrumbungle Mts. of New South Wales appear to be intermediate between *D. boroniaefolia* and *D. viscosa* probably ssp. *cuneata*. These putative hybrids are usually glabrous and have imparipinnate leaves with 2-3 pairs of opposite lateral leaflets and a broader terminal leaflet resembling the apex of *D. viscosa* ssp. *cuneata* leaves. The leaves are usually viscous with sessile glands and the inflorescences are terminal. The male flowers and capsules of these specimens have features characteristic of both suggested parent species.

Three specimens, which appear to be from the same collection (MEL, L908.269-912, U91875) and another from Buffalo Range, may be hybrids between the broader-leaved Victorian form of *D. boroniaefolia* and *D. viscosa*.

Specimens:

NEW SOUTH WALES:- Althofer s.n., Barren Jack Mt., nr. Dripstone, x.1949. st. (NSW141170).- Althofer s.n., Ben Bullen (Pearson's Lookout), vi.1946. f.fl. (NSW141171).- Boorman s.n., Capertee, xi.1900. m.fl. (CGE,G,PERTH).- Gaudichaud 191, Port Jackson, s.dat. st. (W).- Giles s.n., Black Ra., Four Mile Creek, 20ml S of Orange, x.1962. f.fl. (NSW141168); xi.1962. fr. (NSW141169).- Johnson & Constable s.n., head of Tooraweenah Creek, Warrumbungle Mts., 18.iv.1952. m.fl. (NSW29309,AD97236270,BRI141347).- McLellan s.n., Yeoval, 2.ix.1956. st. (NSW141209).
 VICTORIA:- Anon. s.n., Buffalo Ra., 10.ii.1853. st. (MEL).- Anon. s.n., s.loc., s.dat. f.fl., fr. (MEL, L908.269-912, U91875).

2.*D. triquetra* x ?*D. boroniaefolia*, see *D. triquetra*

AFFINITIES:

D. boroniaefolia is most closely related to *D. multijuga*. The two species have leaflets of similar shape and with sunken glands on the margin of the upper surface, but *D. multijuga* has a larger number of leaflets, many-flowered inflorescences, 3-winged capsules and larger seeds.

D. uncinata shows resemblance to *D. boroniaefolia*, but it can be distinguished by its puberulent branchlets, the verruculose glands on the leaves, the hooked terminal leaflet, the acute apical teeth of the lateral leaflets, and the glabrous ovary and anthers.

SPECIMENS EXAMINED: selection only (182 collections examined).

NEW SOUTH WALES:- Boorman s.n., Como, xi.1899. fr. (NSW141125).-

Boorman s.n., Manildra, xi.1906. fr. (NSW141204).- Cheel s.n., Nattai

R., nr. Colo, xi.1911. fr. (NSW131467).- Fraser s.n., 40ml NW of

Walgett, on Goodooga rd. (southern), 18.iv.1963. f.fl. (NSW141161).-

Hamilton s.n., Katoomba, xii.1902. m.fl. (NSW131466).- Mckie s.n.,

Yellow Gap, 22.xii.1942. f.fl.,fr. (NSW141183).- Wrigley s.n., 49ml

from Narrandera towards West Wyalong, 17.xii.1971. f.fl. (CBG42122).

QUEENSLAND:- Purdie & Boyland 284, 39km E of Cunnamulla on rd. to Bollon,

27.iii.1976. f.fl. (BRI).- C.T. White 8681A, Torrens Creek, 19.iii.1933.

m.fl. (BRI).- K. Williams 57, 12ml WNW of St. George on St. George-Bollon

rd., 22.ix.1968. fr. (BRI).

VICTORIA:- Aston 648, Strathbogie Ras., nr. Kelvin View, 12.x.1960. fr.

(NSW).- Canning s.n., Beechworth Gorge, 30.x.1967. m.fl./fr. (CBG21406).

43. *Dodonaea polyzyga* F. Muell., North-Aust. Exped. in Hooker's J. Bot. Kew Gard. Misc. 9:197 (1857), Fragm. 1:74-75 (1859); Bentham, Fl. Aust. 1:483 (1863); Ewart & Davies, Fl. N. Terr. 175 (1917); Radlkofer, Pflanzenreich IV.165:1384-1385 (1933); Beard, W. Aust. Pl. edn 1. 61 (1965), edn 2. 81 (1970); Chippendale, Proc. Linn. Soc. N.S.Wales 96:246 (1972).

TYPE: "Secus margines rupestres rivulorum sicut secundum valles petraes fluvii Victoriae superiores." Holotype: F. Mueller s.n., rocky gullies of the Upper Victoria River, i.1856. fr. (MEL84128).

DESCRIPTION (Fig. 7.47):

Polygamous shrub, 2-3m high, diffuse. Branches scraggly, spreading; branchlets terete, or angled, sometimes ribbed, viscous, pilose. Leaves imparipinnate, (7.4-)10-14(-15)cm long (excluding petiole); petiole 12-18(-21)mm long, with sessile glands, viscous, sparsely pilose-pubescent; rhachis twinged, 1-1.5mm broad, channelled above; lateral leaflets 28-46, opposite or irregularly alternate, oblong to oblong-lanceolate, (10.5-)12-18.5(-21.5) x 3-5(-6)mm, olive-green above, paler below, viscous, with sessile glands, sparsely pubescent, the hairs denser on the margin, base cuneate, oblique, sessile or with a petiolule 0.1-0.3mm long, margin entire, thickened, apex acute, acuminate or mucronate, midvein prominent, lateral venation usually conspicuous; the terminal leaflet narrow-elliptic or lanceolate, 9-15(-23) x 2-2.5(-4)mm, with a long-acute apex, otherwise similar to lateral leaflets. Flowers unisexual, or bisexual, (female flowers not seen), in terminal panicles composed of monads to metabotryoids; pedicels 7-11mm long, viscous, pilose-pubescent. Sepals 4-6, ovate, (3.3-)3.6-5(-6) x 1.4-2(-2.6)mm, acute, viscous, pilose-pubescent & villous, persistent; at anthesis the sepals in male flowers are spreading, in bisexual flowers they are erect, valvate, surrounding the ovary & immature stamens. Stamens in male & bisexual flowers 10-12(-16), exceeding or

equal in length to the sepals, divergent; filaments (0.6-)0.8-1.1(-1.5)mm long, glabrous; anther lobes narrow-oblong, 2.3-2.8(-3) x 0.7-0.9mm, pilose-pubescent; apical appendage triangular-acuminate, incurved, 0.4-0.5mm long, pubescent. Ovary in bisexual flowers 3-carpellate, obovate, angled, 1.5-2 x 1.4-1.9mm, viscous, sparsely pubescent; styles 3, connate for almost entire length, 5.5-12.5mm long, glabrous, shortly lobed at the apex; in male flowers rudimentary ovary present. Capsule 3-winged, in lateral view transverse-obovate, 12-14(-17) x 21-24 (-27)mm, coriaceous, viscous, sparsely pubescent, red-brown or pink at maturity, base cordate, apex emarginate; carpel excluding wing 8-10 x 4-6mm, thickened; wing 7-9(-10)mm broad, extending from apex to base of carpel, broadest at the capsule apex; dehiscence septifragal. Seeds 2-4, lenticular-globose, 2.4-2.6 x 2.3-2.5mm, black, shiny; aril absent. Seedling pubescent, the hairs curved; hypocotyl 15-19mm long, red; cotyledons oblong, 17-19.5 x 4mm, acute, glabrous; epicotyl 2-3mm long; the first 8 leaves imparipinnate with 3-11 leaflets, the leaflets usually 2-3-toothed at the apex, otherwise as in mature leaves.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.47):

D. polyzyga is confined to the Kimberleys region of north-east Western Australia and the Victoria River area of Northern Territory.

ECOLOGY:

This species grows in skeletal soils on rocky slopes (sometimes of limestone) and is often associated with *Eucalyptus brevifolia* and *Plectrarchne* sp.

Flowering occurs from May to August and mature capsules are usually present at the same time.

NOTES:

Although a number of flowering specimens have been examined no female flowers have been seen. *D. polyzyga* appears to produce mainly bisexual flowers. Some individuals have bisexual flowers only, but usually a smaller number of male flowers occur in the same inflorescence. Pollen fertility tests on a small number of herbarium specimens with only bisexual flowers tend to suggest low fertility for this genus. This polygamous species probably represents a significant step in the trend to dioecism within the genus (see Chapter 4 for further discussion). Field work on a population basis is necessary to determine sex ratios both within and between individuals.

AFFINITIES:

D. polyzyga shows resemblance to *D. megazyga* in having a large number of leaflets, although the leaflets of the latter species are lanceolate and puberulent and the fruits and flowers are quite different. *D. polyzyga* exhibits several characters that distinguish it from all other species including large sepals and capsules, large, compound inflorescences, pilose-pubescent anthers and its polygamous nature.

SPECIMENS EXAMINED: selection only (33 collections examined)

NORTHERN TERRITORY:- Dunlop 3527, Limbunya, 29.iv.1974. fr. (CANB,NSW,NT, PERTH).- Gittins 2334b, 32km from Wave Hill towards Hooker Creek, viii. 1971. m.fl.,bisex.fl.,fr. (BRI,NSW).- Perry 2139, 7ml S of Victoria Downs Stn., 12.vi.1949. bisex.fl.,fr. (BRI,CANB).

WESTERN AUSTRALIA:- Beard 4234, Brooking Gorge, 26.v.1965. m.fl.,
bisex.fl. (NSW).- Beaglehole 11175, Fitzroy R., Geike Gorge, NE of
Fitzroy Crossing, 3.viii.1965. fr. (BEAUGL,AD).- Burbidge 5131, Martin's
Gap, E of Ord R., 14.iv.1956. fr. (CANB,U).- Hutchinson 28, Texas Downs
Stn. on Ord R., S of Kununurra, 20.vi.1968. fr. (PERTH).- Jackson 1001,
Fitzroy R. basin, Geike Gorge, 20km NE of Fitzroy Crossing, 28.v.1967.
m.fl.,bisex.fl.,fr. (AD).- Lazarides 6308, 12ml SW of Lamboo Stn.,
13.vii.1959. bisex.fl.,fr. (AD,CANB.NSW).- Mirrington 710905, Geike
Gorge, ix.1971. bisex.fl.,fr. (PERTH).

44. *Dodonaea sinuolata* West, sp. nov.

[*D. tenuifolia* auct. non Lindl.: Bentham, Fl. Aust. 1:486 (1863) pro syn. sub *D. adenophora* Miq.; Mueller, Fragm. 9:85-86 (1875), p.p. (in ref. to Lau, Leichhardt & Cunningham specimens only); Maiden et Betche, Proc. Linn. Soc. N.S.Wales 24:641 (1899); Radlkofer, Pflanzenreich IV.165:1387-1389 (1933), p.p. (excl. Mitchell, Belyando R.); Black, Fl. S. Aust. edn 2. 542, fig.698 (1952), p.p. (to New South Wales & Queensland material only).]

[*D. adenophora* auct. non Miq.: Bentham, Fl. Aust. 1:486 (1863) p.p. (as to Leichhardt & Cunningham specimens only); Bailey, Fl. Qld. 1:318 (1899).]

Species nova Sect. *Pinnatarum*, *D. tenuifoliae* Lindl. *folioliis angustis linearibus et floribus inflorescentiisque similaribus affinis, sed differt capsulis in aspectu laterali late ellipticis usque late oblongis, alis carpellorum rotundatis, et folioliis paucioribus, plerumque sinuolatis usque denticulatis, raro integris.*

TYPE: Holotype: J.L. Boorman s.n., Queensland, Texas, ix.1910. fr. (NSW142640). Isotype: W9370.

DESCRIPTION (Fig. 7.48, 7.49 & 7.76):

Dioecious shrub, 1-3m high, spreading, multistemmed. Branches slender, spreading; branchlets faintly angled, or terete, viscous, with verruculose glands, glabrous. Leaves imparipinnate, (1.2-)1.5-2.8(-3.6)cm long (excluding petiole); petiole (6-)8-17(-20)mm long, glabrous or rarely very shortly puberulent; rhachis rarely winged, 1(-1.5)mm broad, channelled above, lateral leaflets (8-)10-14(-22), opposite or irregularly alternate, linear or rarely narrow-oblong, or oblanceolate to linear-obtriangular, (5-)6-12(-15.5) x 1-1.5(-2)mm, coriaceous, viscous, with sessile to verruculose glands, glabrous or sparsely puberulent, base narrow-cuneate to attenuate, sessile, or rarely with petiolule of 0.1-0.2mm long, margin irregularly sinuolate to entire, or sinuate or faintly so to denticulate,

apex obtuse to broad-acute or irregularly 3-toothed, the teeth acute & the central one recurved, midvein impressed above, prominent below, lateral venation obscure; the terminal leaflet much shorter, lobe-like, otherwise similar to lateral leaflets. Flowers unisexual, in 3-4-flowered botryoids & rarely metabotryoids, axillary; pedicels (4.5-)5-8(-10)mm long, viscous, glabrous. Sepals 4, ovate, (1.7-)2-2.7(-3) x (1-)1.2-1.4(-1.8)mm, obtuse to rounded, viscous, outer surface glabrous to sparsely pubescent, inner surface villous to tomentose, caducous; at anthesis the sepals in male flowers are spreading to recurved, in female flowers they are valvate, free at the apex only, surrounding the ovary. Stamens in male flowers 8, approx. equal in length to the sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 2.3-2.5 x 0.8-0.9mm, glabrous; apical appendage broad-triangular, to 0.2mm long, puberulent; stamens in female flowers absent. Ovary in female flowers (3-)4-carpellate, oblong to ovoid, angled, 1-1.3 x 0.8-1.1mm, viscous, with resin layer, glabrous; styles 4, connate, 5-8mm long, glabrous, separating at the apex into short lobes to 0.2mm long; in male flowers rudimentary ovary present. Capsule (3-)4-winged, in lateral view broad-elliptic to broad-oblong, (9.5-)10-12(-13) x 10-12(-15)mm, coriaceous, viscous, with sessile to verruculose glands on the carpels, glabrous, red to red-brown at maturity, base cordate, with the wings usually overlapping, apex deeply obcordate, with the wings overlapping; carpel excluding wing navicular & lunate, (4-)5-6 x 2-2.5(-3)mm, thickened; wing 3-4(-5.5)mm broad, extending from apex to base of carpel, usually broadest at the capsule apex, broader than the valve; dehiscence septifragal. Seeds 2-4, lenticular, 1.8-2.1 x 1.9-2mm, black, shiny; aril absent. Seedling with sparse verruculose glands, glabrous; hypocotyl 10-12mm long; cotyledons linear-lanceolate, 13-17 x 1.5-2.5mm, acute, glabrous; epicotyl 1-1.5mm long; the first 2-7 leaves impari-

pinnate, with (3-)7-11 leaflets, the leaflets oblong to oblanceolate, usually 3-6-lobed above the middle, otherwise as in mature leaves.

KEY TO SUBSPECIES OF *D. sinuolata*

Leaflets linear or rarely narrow-oblong, irregularly sinuate to entire, apex obtuse to broad-acute.

ssp. *sinuolata*

Leaflets oblanceolate to linear-obtriangular, irregularly sinuate or faintly so to denticulate, apex usually 3-toothed, rarely obtuse.

ssp. *acrodentata*

ssp. *sinuolata*

Leaves (1.4-)1.5-2.3(-3)cm long; petiole (6-)8-12(-13)mm long; leaflets linear, rarely narrow-oblong, irregularly sinuate to entire, obtuse to broad-acute.

DISTRIBUTION (Fig. 7.48):

D. sinuolata ssp. *sinuolata* occurs in north-eastern New South Wales and south-eastern Queensland. It grows on the tablelands and western slopes of the Great Dividing Range from Scone in the Hunter Valley and the Warrumbungle Mts. further west in N.S.W., northwards to Toowoomba in Queensland.

ECOLOGY:

Very little information is available on the habitats in which ssp. *sinuolata* grows. It appears to inhabit rocky sites in open forest or woodland. Associated species include *Eucalyptus microcarpa*, *E. maculata*, and *Acacia ixiophylla*. Field work is required to determine more accurately the habitats in which this subspecies is found.

D. sinuolata flowers in summer to autumn (January to May) and fruit is mature from July to November.

SPECIMENS EXAMINED: selection only (49 collections examined)

NEW SOUTH WALES:- Cabbage s.n., 15ml NE of Boggabri, xi.1909. fr. (NSW 142657).- Coveny 5603 & Jacobs, 5km SE of Mt. Wombo (23km WSW of Singleton), 17.ix.1974. immat.fr. (AD,CANB,NSW).- Forsyth s.n., Gunnedah, 31.x.1899. fr. (NSW142659).- Forsyth s.n., Warrumbungle Ras., x.1907. fr. (NSW142645).- Lambert s.n., The Pinnacles track (Mt. Playfair), 26.ix.1976. fr. (NSW142641).- Rupp s.n., Barraba & Horton Valley, iv.1913. m.fl./f.fl. (NSW142647).- Simmons, per Copley 5082, Looking Glass Mt., 18.x.1977. fr. (AD).- H.L. White s.n., Scone, ix.1899. fr. (NSW142643).
QUEENSLAND:- Gwythe s.n., Gladfield, i.1891. m.fl. (BRI72491).- McDonald 1156, Durikai S.F., W of Warwick, 3.ix.1975. fr. (BRI).

ssp. *acrodentata* West, ssp. nov.

Foliola oblanceolata usque lineari-obtriangularia, inordinatim sinuolata usque denticulata, apice plerumque 3-dentato, raro obtuso.

TYPE: Holotype: W.G. Trapnell & K.A. Williams 272, Queensland, Maranoa distr., 123km SE of Charleville, 30.viii.1973. fr. (BRI238994).

The subspecific epithet refers to the apex of the leaflets.

Leaves (1.7-)2-2.8(-3.6)cm long; petiole (9.5-)11.5-17(-20)mm long; leaflets oblanceolate to linear-obtriangular, irregularly sinuate or faintly so to irregularly denticulate, usually irregularly 3-toothed at the apex, the central tooth recurved, rarely obtuse.

DISTRIBUTION (Fig. 7.48):

D. sinuolata ssp. *acrodentata* occurs in south-west Queensland in the Warrego and Maranoa districts, from Quilpie to Thargomindah in the west to St. George in the east. Its distribution extends beyond Charleville in the north to the Tambo area.

One collection (Cadwell & Randall NSW84966) is from Hillston in southern New South Wales. This record is a great distance from all other collections of this taxon and requires verification.

ECOLOGY:

ssp. *acrodentata* grows in the red sandy loams and on stony ridges in arid and semi-arid areas of south-west Queensland. It commonly occurs in mulga (*Acacia aneura*) woodlands with *Eucalyptus melanophloia* and *E. populnea*, and it is also a shrub of *Acacia harpophylla* - *Eucalyptus cambageana* open woodlands.

SPECIMENS EXAMINED: selection only (31 collections examined)

QUEENSLAND:- Boyland 3078, Warrego distr., 12.8km NNW of Quilpie, 16.iv.1971. m.fl. (BRI).- Everist 3090, Maranoa distr., Boatman Stn., 17.vii.1947. fr. (BRI).- Everist 7484, Warrego distr., Bowalli, 55ml SW of Quilpie, 5.viii.1963. fr. (BRI).- Kay 9, 20km S of Cheepie, 28.vi.1978. mature m.fl. (BRI).- Purdie 672E, 4km S of Dillalah Siding on Mitchell Hwy., 29.vi.1977. immat.fr. (BRI).- Purdie & Boyland 75, 40km SE of Charleville along Boatman rd., 23.iii.1976. mature f.fl. (BRI).- Simmons, per Copley 5090, Eulo-Thargomindah rd., 18.x.1977. fr. (AD).- L.S. Smith 6315, Maranoa distr., Boatman rd., 28.v.1955. mature f.fl., fr. (BRI).- Trapnell & Williams 252, Warrego distr., 53km E of Quilpie, 28.viii.1973. fr. (BRI).- K. Williams 71, Maranoa distr., 111ml SW of Charleville, 22.ix.1968. fr. (BRI).

NOTES:

In the past material belonging to this species has been incorrectly known as *D. tenuifolia* Lindl. However, *D. tenuifolia* is a different species which was previously known as *D. macrozyga* F. Muell. (see *D. tenuifolia* for further explanation).

AFFINITIES:

D. sinuolata shows most resemblance to *D. tenuifolia* in leaf morphology. The two species can be distinguished on the long, flat capsule wings, the prominently angled branchlets, the winged rhachis of the leaves and the larger number of entire leaflets of *D. tenuifolia*.

D. subglandulifera was previously classified with material belonging to *D. sinuolata*. The two species can be distinguished by the capsule shape, the shorter leaves and petioles and the shorter entire leaflets with verruculose glands on the lower surface only of *D. subglandulifera*.

45. *Dodonaea larreoides* Turcz., Bull. Soc. Imp. Naturalistes Moscou 31.I:408 (1858); Bentham, Fl. Aust. 1:486 (1863); Mueller, J. Bot. 15:273 (1877); Mueller, Cens. Aust. Pl. 1:25 (1882), Sec. Cens. Aust. Pl. 1:43 (1889); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:348 (1904); Radlkofer, Pflanzenreich IV.165:1385 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:326 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).

TYPE: "Nova-Hollandia, Drum. III. n. 213." Syntypes: J. Drummond 213, Swan R., W.A., 1845. fr. (BM,CGE,G(5 sheets),MEL84105,W92010).

D. foliolosa F. Muell., Fragm. 2:182 (1861) - replacement name for *D. multijuga* F. Muell. non G. Don; [Bentham, Fl. Aust. 1:486 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1385 (1933) pro syn.]

TYPE: "In plagis petraeis ad fodinas Geraldine, Australiae occidentalis. A. Oldfield." Holotype: A. Oldfield s.n., Murchison R., s.dat. fr. (MEL).
Isotype: U91874.

D. multijuga F. Muell., Fragm. 1:219 (1859), nom. illeg., non G. Don, Gen. hist. 1:674 (1831).

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:326 (1956).

DESCRIPTION (Fig. 7.50):

Dioecious shrub, 1-3(-4)m high, erect. Branches rigid, spreading; branchlets angular, often 3-angled, viscous, with sessile glands, sometimes with verruculose glands, glabrous. Leaves imparipinnate, (2.5-) 3-4.5(-5)cm long (excluding petiole): petiole (7-)9-12(-13)mm long, glabrous; rhachis sometimes winged, 1-1.5mm broad, channelled above; leaflets 17-27(-31), opposite, sometimes irregularly alternate, oblong to obovate, 5-7 x 2-3mm, dark green above, light green below, coriaceous,

viscous, with sessile glands, glabrous or sparsely pubescent on the margin, the hairs short & closely adpressed, base cuneate, oblique, sessile, margin entire, recurved, apex acute to obtuse, rarely mucronate, recurved, often 2-3-toothed, the teeth acute or obtuse, midvein prominent, lateral venation obscure. Flowers (no male or female flowers available) in axillary botryoids & metabotryoids; fruiting pedicels 7-10mm long, viscous, glabrous. Sepals (of capsules only) 3(-4), ovate, 2.3-2.5 x 1.5-1.8mm, acute, outer surface glabrous, inner surface covered with short matted hairs, usually caducous, sometimes persistent. Stamens and ovary not seen. Capsule 3(-4)-winged, in lateral view transverse-obovate, (6.5-) 7.5-9 x (10-)11-13mm, coriaceous, viscous, glabrous, red to purple-brown at maturity, base cordate, apex obcordate; carpel excluding wing depressed-ovate, navicular (4-)4.5-5 x 2-2.5(-3)mm, with sessile glands; wing 3-4mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve; dehiscence septifragal. Seeds (slightly immature only available) 1-2, lenticular, 1.7-2 x 1.7-1.8mm, black, shiny; aril absent. Seedling not seen.

Chromosome number: $n = 14$ (West 3274)

TYPIFICATION:

Nine sheets of the type collection of *D. larreoides*, Drummond 3rd Series no. 213, have been examined (BM, CGE, G(5 sheets), MEL84105 and W92010). It has not been possible to determine whether there is another Drummond 213 specimen at KW, the herbarium in which Turczaninow's main herbarium is housed. The typification of this name will be clarified upon receiving information or material from KW.

The holotype sheet of *D. foliolosa* at MEL has a label with locality and collector in Oldfield's handwriting and the determination of 'D.

'*larraeoides* Turcz.' in Mueller's hand. The isotype sheet now held at U bears a label in Oldfield's hand with locality and collector and the determination of '*D. multijuga* F. Muell.'. It seems likely that Oldfield sent one specimen of his collection to Mueller, who in 1859 described it as a new species which he named *D. multijuga*. This, however, was a later homonym (Don, 1831), and in 1861 Mueller gave this species the replacement name of *D. foliolosa*. In the meantime Mueller probably communicated his name of 'multijuga' to Oldfield, who then sent the appropriately labelled duplicate to herbarium Rheno-Traject, which is now part of the U collections. Mueller must have discovered his species *D. foliolosa* was actually a synonym of Turczaninow's *D. larreoides* after 1861 (see e.g. Mueller, 1877) and then labelled the MEL specimen with the correct name.

DISTRIBUTION (Fig. 7.50):

D. larreoides occurs in south-west Western Australia. It extends from Ajana, north of Geraldton towards the south-east as far as Cunderdin, approx. 150km east of Perth.

ECOLOGY:

This species is a shrub of semi-arid mallee scrub and woodlands such as those dominated by *Eucalyptus salmonophloia*. Other associated species include *E. erythronema*, *E. celubris*, *E. dongarensis*, *Melaleuca pauperiflora*, many grass species and arid shrubs such as *Enchylaena tomentosa*, *Atriplex* sp. Soils vary from sandy or calcareous grey loams to conglomerates and laterites on small hills.

NOTES:

The original spelling of the specific epithet has been retained rather than the commonly used '*larraeoides*', as it is presumed

Turczaninow named this species for its resemblance to the genus *Larrea* Cav. (Zygophyllaceae). There is no indication that the spelling of this genus has been altered and so the author's spelling of the epithet is retained (Stafleu et al., Art. 73.1, 1978).

AFFINITIES:

D. larreoides shows resemblance to *D. inaequifolia* in some leaf characteristics, but the two species are readily distinguishable on leaflet and capsule shape.

SPECIMENS EXAMINED: selection only (33 collections examined)

WESTERN AUSTRALIA:- Ashby 305, nr. Yuna, 34km E of Northampton, 28.viii.1963. fr. (AD).- Ashby 2908, loc. cit., 8.viii.1969. fr. (AD).- Gardner 1999, Ajana, nr. Murchison R., 27.ix.1926. fr. (PERTH).- Gardner 2638, Eradu, 17.ix.1931. fr. (PERTH).- Gardner 7550, Wilroy, 29.viii.1945. fr. (PERTH).- Newbey 1988, 9ml E of Moonijin, E of Wongan Hills, 23.viii.1965. fr. (PERTH).- Royce 6641, Wongan Hills, E of Elphin, 11.ix.1961. fr. (PERTH).- West 3215-3217, 3km E of Dumbo Well, 8km N of Lake Hinds, 25km NW of Wongan Hills township, 1.xii.1978. fr. (AD).- West 3222, 3225, Pithara, 1.xii.1978. fr. (AD).- West 3274-3276, 11.2km N of Watheroo on Geraldton Hwy., 6.xii.1978. m.buds/?f.buds. (AD).

46. *Dodonaea vestita* Hook. in Mitchell, Journ. Exped. Trop. Aust. 265 (1848);
Bentham, Fl. Aust. 1:484 (1863); Mueller, Fragm. 9:86 (1875); Bailey,
Fl. Qld. 1:317 (1899); Britten in Banks & Solander, Ill. Bot. Cook's Voy.
1:16, t.43 (1900) - var. *glabrescens*; [Radlkofer, Pflanzenreich IV.165:
1383 (1933) pro syn. sub *D. pinnata*].

TYPE: leg. Mitchell, Belyando River area, 7.viii.1846. Holotype: Lieut.-
Col. Sir T.L. Mitchell 278, Sub-tropical New Holland, 31.viii.1846. fr.
(K).

D. paulliniaefolia A. Cunn. ex Steud., Nom. Bot. edn 2. 1:522 (1840), nom.
nud.

FIGURES: Banks & Solander, Ill. Bot. Cook's Voy. 1:16, t.43 (1900).

DESCRIPTION (Fig. 7.51):

Dioecious shrub, 0.5-1(-1.5)m high, multistemmed. Branches dense,
spreading; branchlets terete or ribbed or slightly angular, densely
hirsute or villous, the hairs often golden-yellow. Leaves imparipinnate,
(0.8-)1-2(-2.2)cm long (excluding petiole); petiole (1.5-)2-4(-4.5)mm
long, densely hirsute; rhachis winged, 1-2mm broad, channelled above;
leaflets (8-)10-14, opposite or irregularly alternate, obovate to oblong,
(3.5-)5-8(-9) x (2-)2.5-4(-5)mm, dark to olive-green above, paler below,
scabrous, viscous, with sessile glands sometimes visible, hirsute, the
hairs usually golden-yellow, base cuneate, sessile, or rarely with a
petiolule 0.1-0.3mm long, margin entire, revolute, apex acute to obtuse,
often 2-3-toothed, recurved, midvein prominent below, impressed above,
lateral venation usually obscure; the terminal leaflet lobe-like, other-
wise as in lateral leaflets. Flowers unisexual, in terminal compound
inflorescences composed of monads to botryoids, or sometimes in axillary
2-4-flowered botryoids; pedicels (7.5-)8-12(-13)mm long, hirsute.

Sepals 4(-6), ovate to ovate-lanceolate, 3-4.6(-5) x (1.2-)1.5-2(-2.3)mm, acute to acuminate, viscous, outer surface hirsute to villous, inner surface hirsute or pubescent, glabrous towards the base, persistent or sometimes caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are free & slightly spreading to form a cup-shaped structure around the ovary. Stamens in male flowers 8-10(-12), approx. equal in length to the sepals, spreading; filaments 0.5-0.6mm long, glabrous; anther lobes linear-oblong, 3.3-4 x 0.7-1mm, hirsute, the hairs denser towards the apex; apical appendage a broad, obtuse lobe, to 0.2mm long, hirsute; in female flowers rudimentary stamens usually present. Ovary in female flowers 4(-5)-carpellate, obovate, angled, 0.8-1 x 1mm, viscous, very densely hirsute, some hairs grouped into tufts between the small wings; styles 4(-5), connate, rarely twisted, (5-)6.5-16(-20)mm long, pubescent or hirsute near the base, separating at the apex into 4 short lobes of 0.1mm long, or into unequal arms up to 1mm long, recurved; in male flowers rudimentary ovary usually present. Capsule 4(-5)-winged, in lateral view transverse-elliptic, (8.5-)9-13(-15) x (16-)18-23(-24)mm, coriaceous, scabrous, hirsute, the hairs usually golden-yellow, red-brown to purple at maturity, base cordate, apex deeply obcordate; carpel excluding wing depressed-ovate to transverse-elliptic, navicular, 6-7 x (2.5-)3-4.5mm, densely hirsute; wing 5-7mm broad, margin undulate, sometimes irregularly denticulate, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve; dehiscence septifragal. Seeds 2-4, lenticular, 2.6-3 x 2.4-2.5mm, black, dull; aril absent. Seedling not seen.

Chromosome number: not known.

TYPIFICATION:

Five sheets of *D. vestita* specimens collected by Mitchell on the 1847 expedition into tropical Australia have been examined (BM,CGE,K,MEL,NSW). Only two of these sheets bear dates - the MEL one is dated '7 Aug.46' and corresponds to the date on which Hooker's protologue is included in Mitchell's Journal, and the K sheet is dated 31 August 1846. The protologue includes capsule details, but flowers are not mentioned. The K specimen and one of the specimens on the BM sheet contain capsules, while the other three (CGE, MEL,NSW) have mature female flowers. It appears that Hooker used only the K specimen and that he did not see any of the other four Mitchell collections, which were probably made at different localities and on various days during the journey. They are therefore not syntypes.

DISTRIBUTION (Fig. 7.51):

D. vestita occurs in eastern Queensland on the Great Dividing Range and western slopes. It extends from the Miles area of the Darling Downs to Aramac in the Mitchell district. Collections were made last century and in the first half of this century in the Cooktown region (see Notes).

ECOLOGY:

D. vestita usually grows on sandstone slopes in shallow rocky soil in open eucalypt forest or dry sclerophyll forest. It occurs with *Eucalyptus watsoniana*, *E. trachyphloia*, *E. baileyana*, *E. cloeziana*, *E. peltata* and *Angophora costata*. It occasionally is also found in *Eucalyptus microcarpa*, *Bothriochloa* woodland.

Flowering appears to take place during the winter (May to August) and capsules are usually present at the same time.

NOTES:

Three collections, namely those of Banks and Solander (MEL,NSW133689, W8263), D.D. Banks (BM), and Cunningham 45 (BM) from the Cook district, differ from typical forms of *D. vestita* in having linear-oblong leaflets, without teeth at the apex and capsules with less dense indumentum and narrower wings. On all other features these specimens belong to *D. vestita*. The disjunction in the distribution of these specimens may indicate geographical separation paralleling the morphological distinction of a sub-specific variant. Bentham (1863) recognised the differences of the Banks and Solander and Cunningham specimens and Britten (1900) described *D. vestita* var. *glabrescens* basing it on the Banks and Solander Endeavour River collection. Further material and field work is required to assess the position of these specimens in relation to *D. vestita*.

AFFINITIES:

D. vestita is most closely related to *D. rupicola* from the Glasshouse Mountains of south-east Queensland. The two species have similar hirsute indumentum and leaf and capsule shape. They differ in *D. rupicola* having larger leaves with the hairs usually white or clear (not golden as in *D. vestita*), flowers on shorter pedicels in many-flowered, terminal inflorescences, shorter filaments and anthers, and smaller capsules.

In leaf morphology *D. pinnata* resembles *D. vestita*, but the two taxa can be readily distinguished on flower and fruiting characters.

SPECIMENS EXAMINED: selection only (46 collections examined)

QUEENSLAND:- Banks & Solander s.n., New Holland, 1770. fr. (MEL,NSW133689, W8263).- Beeston 1137c, Mitchell distr., 45km SSE of Blackall, vii.1975. f.fl. (BRI).- Everist 8055, 8061, Leichhardt distr., Isla Gorge, 18ml SW of Theodore, 28.ix.1968. fr. (BRI).- Hockings s.n., Devil's Signpost,

Carnarvon Ras., vi.1962. m.fl./f.fl. (BRI33709).- L.A.S. Johnson 7196 & Briggs, 10km S of Isla Gorge Lookout, 37km (by rd.) S of Theodore, 3.vi.1971. f.fl. (AD,BRI,MEL,NSW).- R.W. Johnson 2801, Bauhinia Downs - Rolleston rd., 20ml W of Bauhinia Downs, 31.viii.1964. fr. (BRI).- McDonald 80, Stoney Creek, Blackdown Tableland, 19.iv.1974. f.fl.,fr. (BRI223820).- Trapnell & Williams 306, Gregory South distr., 59km NW of Quilpie, 3.ix.1973. fr. (BRI).- K.A.W. Williams 75055, Darling Downs distr., Gurulmundi - Woleebee rd., 3km W of Gurulmundi, 1.x.1975. fr. (BRI).- K.A.W. Williams 77129, Leichhardt distr., Quartz Creek - Buckland Gorge, 34km N of Tanderra Stn., 9.viii.1977. fr. (BRI).

47. *Dodonaea rupicola* C.T. White, Queensld. Nat. 6:13-14 (1926).

TYPE: "Queensland - growing between rocks, Saddle-back Mountain, Elimbah, Glass House Mountains district (about 30 miles north of Brisbane), C.T. White, Queensland Naturalists' Club Excursion, 11/9/1926." Lectotype (here designated): C.T. White 3225, Elimbah, Saddleback Mt., 11.ix.1926. fr. (BRI8526). Isolectotype: BRI72264. Probable syntype: White 3321, loc. cit., 29.xi.1926. m.fl./f.fl., fr. (BRI72265).

DESCRIPTION (Fig. 7.52):

Dioecious shrub, 0.6-1m high, spreading. Branches spreading; branchlets terete to slightly angular, densely hirsute. Leaves imparipinnate, (1.5-)2-3(-3.5)cm long (excluding petiole); petiole (3-)4-7(-8)mm long, densely hirsute; rhachis winged, 1-1.5mm broad; lateral leaflets 10-16 (-18), opposite, oblong to oblanceolate, (4-)5.5-8(-9.5) x 2-3.5(-4)mm, dark to olive-green above, paler below, scabrous, densely hirsute, base cuneate, sessile, margin entire, sometimes undulate, recurved or revolute, apex acute, often recurved, midvein prominent below, impressed above, lateral venation obscure; the terminal leaflet lobe-like, otherwise as in lateral leaflets. Flowers unisexual, in terminal, compound, multi-flowered inflorescences composed of monads to botryoids; pedicels 2-2.5mm long, hirsute. Sepals 4, lanceolate, sometimes ovate-lanceolate, (2.5-)3-3.8 (-4) x 1-1.4mm, acute, hirsute, sometimes glabrous on the inner surface near the base, persistent; at anthesis the sepals in male flowers are spreading, in female flowers they are free, erect & surrounding the ovary. Stamens in male flowers 8, approx. equal in length to the sepals, spreading; filaments 0.2-0.3mm long, glabrous; anther lobes oblong, 2.1-2.6 x 0.6-0.7mm, hirsute, the hairs denser towards the apex; apical appendage triangular-acute, to 0.5mm long, hirsute; stamens in female flowers absent. Ovary in female flowers 4-carpellate, obovate, angled, 1.2-1.3 x 1-1.3mm,

densely hirsute; styles 4, connate, twisted, 10-15mm long, sparsely pubescent at the base, separating unequally near the apex, each free arm to 1mm long, divergent; in male flowers rudimentary ovary present. Capsule 4-winged, in lateral view transversely broad-elliptic, 7.5-9 x 12-15mm, coriaceous, scabrous, densely hirsute, red-brown at maturity, base truncate to slightly cordate, apex emarginate to obcordate; carpel excluding wing depressed-ovate, navicular, 5.5-6.5 x 2.5-3.5mm; wing 3-4mm broad, margin undulate, irregularly denticulate, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve; dehiscence septifragal. Seeds 2-4, lenticular, 1.9-2.2 x 2mm, black, dull; aril absent. Seedling hirsute; hypocotyl 17-19mm long; cotyledons linear, 17 x 1.5mm, acute, glabrous; epicotyl 0.5-1mm long; the first 2-4 leaves imparipinnate, with (3-)5-7 leaflets, otherwise as in mature leaves.

Chromosome number: $n = 14$. (CBG 7708609 cult.)

TYPIFICATION:

Lectotypification for *D. rupicola* is necessary as White did not specify one of the two sheets of the type collection (White 3225) held at BRI as the type. Both sheets contain fruiting specimens and the same label data. BRI8526 is here chosen as the lectotype as it contains larger specimens in better condition.

White included details of flowers in his description and so he must have used specimen(s) other than those with fruit mentioned above. The label on sheet BRI72265 states "supplementary to White no. 3225" and contains flowering material collected two months later than White 3225. It appears that White returned to the Glasshouse Mts. in November to collect flowering material before drawing up the description of this species. BRI 72265 is the only sheet with flowering specimens held at BRI that were

collected prior to December 1926, and so White must have used it. Since this sheet was not cited with the protologue it is regarded as a probable syntype.

DISTRIBUTION (Fig. 7.52):

D. rupicola is an endemic Queensland species restricted to the Glasshouse Mountains area, approximately 60km north of Brisbane.

ECOLOGY:

D. rupicola grows in cracks among the rocks on top of or at the base of the mountains. It is associated with *Leptospermum speciosum*, *L. microcarpum*, *Calytrix tetragona*, *Baeckea camphorata* and *Cryptandra* sp.

Flowers and mature capsules are often present at the same time, usually September to November.

AFFINITIES:

The capsules of *D. rupicola* resemble those of *D. vestita* particularly in their hairiness. These two species can be differentiated on the smaller leaves covered with golden hairs, the longer pedicels, the longer filaments and anthers, and the larger capsules of *D. vestita*. In leaflet shape *D. rupicola* shows some affinities to *D. humilis*, but the hirsute indumentum of *D. rupicola* distinguishes it.

SPECIMENS EXAMINED:

QUEENSLAND:- Bevege & Webb s.n., Wildhorse Mt., (NE of Beerburrum), 18.v.1966. f.fl., fr. (NSW).- Elsol 149, Wildhorse Mt., in the Beerwah Forestry area, 16.vi.1977. f.fl., fr. (BRI).- Puxley s.n., Glasshouse Mts. district, s.dat. fr. (BRI72263).- Sharpe & Everist 1066, Saddleback, Glasshouse Mts., 5.ix.1974. fr. (BRI).- Shirley s.n., Beerburrum, s.dat.

f.fl.,fr. (BRI72262).- Stanley & Clarkson 8, Saddleback Mt. in Glasshouse Mts., 7.ix.1974. fr. (BRI).- Streimann & Telford 3415, Mt. Miketeebumulgrai (Saddleback Mt.), 5km W of Elimbah, 2.x.1973. fr. (CBG,NSW).- Telford 3417 & 3418, loc. cit., 2.x.1973. m.fl./f.fl. (CBG).- Webb s.n., Saddleback Mt., Elimbah, 18.v.1966. fr. (NSW).- K. Williams s.n., Saddleback Mt., 21.viii.1969. fr. (BRI86703).

48. *Dodonaea physocarpa* F. Muell., North-Aust. Exped. in Hooker's J. Bot. Kew Gard. Misc. 9:197 (1857), Fragm. 1:74 (1859), Pl. indig. Col. Vic. 1:85 (1862); Bentham, Fl. Aust. 1:484 (1863); Mueller, Fragm. 9:86 (1875); Bailey, Fl. Qld. 1:317 (1899); Ewart & Davies, Fl. N. Terr. 175 (1917); Domin, Biblioth. Bot. 22(89⁴):912, fig.154 (1927); Radlkofer, Pflanzenreich IV.165:1391 (1933); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970); Chippendale, Proc. Linn. Soc. N.S.Wales 96:246 (1972).

TYPE: "In campis aridis terrae Arnhemicae." Lectotype (here designated): F. Mueller s.n., Victoria River, s.dat. fr., immat. fr. (MEL84121). Isolectotypes: Mueller s.n., Victoria River, xii.1855. f.fl. (MEL84123); Mueller s.n., Victoria River, s.dat. fr. (MEL84122).

FIGURES: Domin, Biblioth. Bot. 22(89⁴):913, fig.154 (1927).

DESCRIPTION (Fig. 7.53):

Dioecious, or very rarely polygamo-dioecious shrub, 1-1.5(-2)m high, multistemmed, spreading. Branches dense, spreading; branchlets angular, ribbed, pilose-pubescent. Leaves paripinnate, (1.3-)1.6-2.6(-3.2)cm long (excluding petiole), terminated by a small tooth or lobe; petiole (4-)8-10(-14)mm long, pilose-pubescent; rhachis deeply channelled above; leaflets 6-10(-12), opposite or irregularly alternate, oblong to obovate, 9-12(-20) x (2-)3-4(-5)mm, light green, scabrous, viscous, pubescent, the hairs +adpressed, base cuneate, oblique, sessile, margin entire or slightly sinuate, recurved, apex acute or mucronate, often 2-3-toothed, midvein prominent, lateral venation obscure. Flowers unisexual, very rarely bisexual, in compound inflorescences composed of monads to botryoids, usually axillary, sometimes terminal; pedicels 8-13mm long, viscous, pilose. Sepals 4-6, lanceolate to ovate, 2.1-3.3(-3.6) x 1-1.5mm, acute, viscous, pubescent, caducous; at anthesis in male & bisexual flowers the

sepals are spreading, in female flowers they are free & spreading.

Stamens in male & bisexual flowers 10-12, exceeding the sepals, spreading; filaments 1-1.2mm long, glabrous; anther lobes oblong, 1.9-2.1 x 0.7mm, sparsely pubescent; apical appendage broad-triangular, to 0.2mm long, pubescent; stamens in female flowers absent. Ovary in female & bisexual flowers 4-6-carpellate, ovoid, angled, 2-2.4 x 1.3-1.7mm, viscous, pubescent; styles 4-6, connate, twisted, 12-16mm long, pubescent near the base, separating unequally at the apex, each free arm to 0.6mm long, divergent; in male flowers rudimentary ovary present. Capsule 5-6-winged, in lateral view broad-oblong to ellipsoid, greatly inflated, (18-)19.5-26 x 17-25mm, membranous or coriaceous, sparsely pubescent or glabrous, pink to red-brown at maturity, base cordate to broad-cuneate, apex emarginate, often with persistent style base; carpel excluding wing transverse-oblong, 16-22 x (5-)6.5-8mm; wing 1-2.5mm broad, extending from apex to base of carpel, usually same width over entire length, much narrower than the valve; not readily dehiscent, capsule splits longitudinally along central axis & carpel walls break down irregularly. Seeds 2-4, lenticular, ±compressed towards the margin, 2.4-2.5 x 2.2-2.5mm, black, shiny with hyaline membrane lifting over entire seed; aril absent. Seedling glabrous, with sessile glands; hypocotyl 8-10mm long, brown; cotyledons linear-lanceolate, 14.5-17 x 2.5-3.5mm, acute, glabrous; epicotyl 0.5-1.5mm long; the first 2 leaves imparipinnate, with 4-5 leaflets, otherwise as in mature leaves.

Chromosome number: not known.

TYPIFICATION:

Mueller's diagnosis of *D. physocarpa* does not include mention of any type. However, in 1859 in the 'Fragmenta', in which Mueller gave a

description of this species, he cited "aridis terrae Arnhemicae". On his 1855 expedition to northern Australia Mueller and his party travelled along the Victoria River, but they did not move further north into Arnhem Land (Willis, 1949). The three MEL sheets (MEL84121, MEL84122, MEL84123), which contain specimens collected by Mueller in 1855 on the Victoria River and which bear labels in his handwriting, must have been available to the author when the diagnosis of *D. physocarpa* was written. They are therefore types, and MEL84121 is here chosen as the lectotype because it bears fruit and most closely agrees with the diagnosis.

DISTRIBUTION (Fig. 7.53):

D. physocarpa is a northern Australian species ranging from the Kimberleys region of Western Australia to the east coast near Cairns, and north of latitude 20°S.

ECOLOGY:

D. physocarpa grows mainly on stony ridges or skeletal soils of laterite rises usually in shrubland or low woodlands. It often occurs with *Eucalyptus tectifica* and perennial grasses such as *Heteropogon contortus*, *Themeda australis* (e.g. in the Kimberleys). Other associated species include *Eucalyptus terminalis*, *E. brevifolia*, *Terminalia canescens*, *Petalostigma quadiloculare*, *Melaleuca acacioides* and sometimes *Plectrachne* sp. or *Triodia* sp.

It appears that *D. physocarpa* flowers October to January. Capsules are found on the plants from February to August.

NOTES:

1. Hartley (1979) included this species as an economic plant, probably because of reports of toxic effects (e.g. Ewart and Davies, 1917). No information is available on the poison properties (if any) of *D. physocarpa*.

2. The inflated capsule lacking a direct method of dehiscence is unique in this section of the genus. The release of the seed in *D. physocarpa* appears to rely on the eventual breakdown of the outer membranous carpel walls. Although the capsule seems to split longitudinally, the septa do not separate distinctly from the central axis or from the valves. The valves are persistent and the seed is released following irregular rupturing of the membranous walls.

AFFINITIES:

D. physocarpa is similar to *D. oxyptera* in leaf morphology, but the latter species has leaves with a longer pubescence, a winged rhachis, and shorter leaflets without teeth at the apex. The capsules and flowers of the two species are quite distinct.

The simple-leaved *D. petiolaris* is the only other member of the genus with an inflated capsule.

SPECIMENS EXAMINED: selection only (89 collections examined)

NORTHERN TERRITORY:- Chippendale s.n., 50ml S of Larrimah, 29.v.1958. fr. (NT4512).- Henshall 1909, Hayfield Stn., 10.i.1978. immat. fr. (AD, NT).- Must 428, 0.2ml S of Daly Waters turnoff, Stuart Hwy., 26.ii.1969. fr. (CANB, MEL, NT).- Robinson 320, 385ml S of Darwin, 1.iv.1964. m.fl. (NT).

QUEENSLAND:- Hinton 60, Cook distr., McLeod R., ii.1978. fr. (BRI).- Macdonald 11, Rookwood, Walsh R., i.1971. fr. (BRI, NSW).- Simon & Farrell 3106, Burke distr., 31km from Corinda on rd. to Westmoreland, 19.v.1976. fr. (BRI).

WESTERN AUSTRALIA:- Andrew 552, Kimberleys, 30.8km along Gibb River rd. W from junction with Wyndham rd., 5.5km W of King River, 4.vi.1979. fr.

(AD).- Beard 5515, between Dunham River Stn., and Pompey's Pillar, S
of Wyndham, 18.vi.1968. st. (PERTH).- Burbidge 5127, between Kimberleys
Research Stn. & Martin's Gap, 11.iv.1956. fr. (CANB,U).

49. *Dodonaea oxypetera* F. Muell., North-Aust. Exped. in Hooker's J. Bot. Kew Gard. Misc. 9:197 (1857), Fragm. 1:74 (1859); Bentham, Fl. Aust. 1:484-485 (1863); Bailey, Fl. Qld. 1:317 (1899); Ewart et Davies, Fl. N. Terr. 175 (1917); Radlkofer, Pflanzenreich IV.165:1383 (1933); Chippendale, Proc. Linn. Soc. N.S.Wales 96:246 (1972).

TYPE: "In collibus siccis scopulosis terrae Arnhemicae." Lectotype (here designated): F. Mueller s.n., Arnhems Land, s.dat. m.fl. (MEL84116).

Syntype: Mueller s.n., Fitzmaurice River, x.1855. m.buds. (MEL84117).

DESCRIPTION (Fig. 7.54):

Dioecious, or rarely polygamo-dioecious shrub, 1-2m high, spreading. Branches spreading, slender, sometimes scraggy; branchlets terete, angled or weakly ribbed, densely pilose, sometimes almost woolly. Leaves bipinnate, (0.3-)0.5-2(-3)cm long (excluding petiole), terminated by a very small tooth or lobe; petiole (3.5-)4-6(-7)mm long, pubescent; rhachis winged, 0.5-1mm broad, channelled above; leaflets 4-8(-12), opposite or sometimes irregularly alternate, oblong to oblanceolate, or obovate, (5.5-)7-11(-14) x (1.5-)2.5-4mm, dark green above, paler below, coriaceous, thick, viscous, densely pubescent, the hairs usually curved, base oblique-cuneate, sessile, margin entire, recurved, apex acute to short-acuminate, midvein prominent, lateral venation obscure. Flowers unisexual, rarely bisexual, monadic or diadic, axillary; pedicels 1.5-2(-2.5)mm long, viscous, sparsely pubescent. Sepals 4, ovate to lanceolate, 1.6-2.1 x 0.8-1.5 mm, narrower in female flowers, acute, viscous, outer surface pubescent, inner surface sparsely pubescent & villous near the apex, persistent; at anthesis the sepals in male & bisexual flowers are spreading, in female flowers they are free, erect & around the ovary. Stamens in male & bisexual flowers 6-8, approx. same length as the sepals, spreading; filaments 0.2-0.4mm long, glabrous; anther lobes oblong, 1.5-1.7 x 0.6-1mm,

glabrous or sparsely pubescent; apical appendage a broad, obtuse lobe, viscous, pubescent; stamens in female flowers absent. Ovary in female & bisexual flowers 4-carpellate, winged, angled, obovate, 0.7-1.2 x 0.8-1.1mm, viscous, densely pubescent or pilose; styles 4, connate, twisted, 7-9mm long, glabrous, separating at the apex, each free arm to 0.2mm long, recurved; in male flowers rudimentary ovary present. Capsule 4-winged, in lateral view transverse-obovate, 5.5-8 x 9.10-5mm, crustaceous, densely pilose-pubescent to villous, red-brown at maturity, base cordate to truncate, apex emarginate; carpel excluding wing navicular, (4-)4.5-5.5 x 2-2.5(-3)mm, crustaceous & thickened; wing 2-3.5mm broad, acute, rigid, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve, coriaceous, thick; dehiscence septifragal. Seeds 2-4, lenticular, 1.7-1.8 x 1.6-1.8mm, black, shiny, usually with hyaline membrane lifting over entire seed; aril absent. Seedling not seen.

Chromosome number: not known.

TYPIFICATION:

Mueller did not cite any type with the brief diagnosis of this species. However, in 1859 in the 'Fragmenta', in which he gives a more detailed description of *D. oxyptera*, he cited "terrae Arnhemicae". Two sheets now held at MEL (MEL84116, MEL84117) contain specimens collected by Mueller in Arnhem Land in 1855 on his north-west expedition (Willis, 1949). Both of these sheets bear labels in Mueller's writing and were available to him in 1857 at the time of writing to Dr. Hooker and giving the diagnosis. They are therefore syntypes. Each specimen has male flowers and MEL84116 also includes a bag of damaged material, including capsule fragments. Since capsules were mentioned in the diagnosis this sheet (MEL84116) is here selected as the lectotype.

DISTRIBUTION (Fig. 7.54):

D. oxyptera is confined to northern Australia. It occurs north of latitude 18°S in the Gulf of Carpentaria and Arnhem Land areas of the Northern Territory, and extends into north-western Queensland (Morrington Island) on the east and to the west, into the Kimberleys in Western Australia.

ECOLOGY:

This species usually grows on skeletal soils (lateritic podsols and skeletal shales) on stony rises or ridges. It occurs in eucalypt woodlands especially with *Eucalyptus brevifolia* and sometimes with spinifex.

From the small amount of material and information available *D. oxyptera* appears to flower in January and February and to fruit from May to August.

AFFINITIES:

D. oxyptera shows most resemblance to *D. physocarpa* in leaf morphology. Sterile material of the two species can be distinguished by the short pubescence of *D. physocarpa* leaves, and the longer leaflets with a toothed apex. The fruit are very different, with *D. physocarpa* having inflated capsules on long pedicels.

SPECIMENS EXAMINED:

NORTHERN TERRITORY:- Brass 418, Robinson R., vii.1925. (CANB).- Brown 5441, Port Blane, 27.i.1803. fr./m.fl./fr.,m.fl.,bisex.fl. (BM).- Byrnes 2531, 24ml S of Borroloola, 19.iii.1972. fr. (BRI, CANB,NSW,NT).- Byrnes 2684, Mitchell Ras., Arnhem Land, 22.vi.1972. fr. (CANB,NSW,NT).- Gittins 1334, Borroloola-McArthur rd., vii.1967. m.fl.,bisex.fl./f.fl.,fr.

- (BRI,CANB,NSW).- Henry 698, 18ml SSE of Calvert Hills, H.S., 27.v.1973. fr. (CANB,NT,PERTH).- Hill 722, 5 mile bar MacArthur R., 19.i.1912. m.fl. (MEL).- Maconochie 2023, 5.5km W of Tin Hole Crossing, 11.vi.1974. st. (BRI).- Perry 1651, 50 ml NNE of Creswell Stn., 13.vii.1948. fr. (AD,BRI,CANB,NSW).- Robinson 52, 2ml E of Katherine, s.dat. m.fl. (BRI, NT).
- QUEENSLAND:- Bycroft 160, Burke distr., Mornington Is., vii.1976. fr. (BRI225859).- Bycroft & Memmott 160, Mornington Is., vii.1977. f.fl.,fr. (BRI241423).
- WESTERN AUSTRALIA:- Kenneally 4112, Pseudomys Hills, Drysdale R. N.P., Kimberley, 8.viii.1975. fr. (PERTH).

50. *Dodonaea adenophora* Miq. in *Linnaea* 18:95 (1844), in Lehm., Pl. Preiss. 2:235 (1848); Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 31.I:408 (1858); Bentham, Fl. Aust. 1:486 (1863), p.p. (excl. N.S.Wales and Queensland material - see *D. sinuolata*); Mueller, Cens. Aust. Pl. 1:25 (1882), p.p. (excl. 'N.S.W. Q. '), Sec. Cens. Aust. Pl. 1:43 (1889), p.p. (excl. 'N.S.W. Q. '); Maiden et Betche, Proc. Linn. Soc. N.S.Wales 24:641 (1899); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:349 (1904); Ewart, Proc. R. Soc. Vic. 19:39 (1907), p.p. (excl. var. *ovata*); Radlkofer, Pflanzenreich IV.165:1390 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:327 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).

Thouinia (?) *adenophora* Miq. in Lehm., Pl. Preiss 1:224 (1845); [Bentham, Fl. Aust. 1:486 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1390 (1933) pro syn.]

TYPE: "Swan river". Lectotype: L. Preiss 2442, in Nova Hollandia ora occid. in confragosis mont. continuorum Darling's range, s.dat. fr. (U179044). Isolectotype: MEL84076.

[*D. boroniaefolia* auct. non G. Don: Blackall & Grieve, W. Aust. Wildfls. 2:326 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970); Willis, Hdbk. Pl. Vic. 2:359 (1972), p.p. (as to "W.A." only).]

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:326 (1956).

DESCRIPTION (Fig. 7.55):

Dioecious shrub, 0.3-2(-2.5)m high, erect or spreading, multistemmed. Branches dense, spreading or sometimes divaricate; branchlets terete or slightly angular, dark red-brown, viscous, with brown, verruculose glands, puberulent, sometimes sparsely so. Leaves imparipinnate, 0.35-0.55(-0.8)cm

long (excluding petiole); petiole (1-)1.5-2.5(-3)mm long, sparsely puberulent; rhachis narrow-channelled above; leaflets (3-)5-7, opposite, rarely irregularly alternate, narrow-obovate to obovate, sometimes linear-obovate, rarely toothed at the apex, concave above, sometimes conduplicate, (1.5-)2-3.5(-5) x 0.8-1.2(-1.5)mm, coriaceous, thick, viscous, with brown, verruculose glands, puberulent, sometimes sparsely so, base narrow-cuneate, sessile, margin entire, apex obtuse, rarely toothed, usually recurved, midvein impressed above, visible below, lateral venation obscure. Flowers unisexual, monadic or sometimes diadic, axillary; pedicels 2-3.5mm long, reflexed, viscous, with verruculose glands, glabrous or sparsely puberulent. Sepals 4, ovate, 1-1.5(-1.8) x 0.8-1.2mm, acute, viscous, outer surface with verruculose glands, glabrous or sparsely pubescent, inner surface villous, caducous; at anthesis the sepals in male flowers are spreading to recurved, in females they are valvate & free at the apex only, surrounding the ovary. Stamens in male flowers (6-)7-8, exceeding the sepals, divergent; filaments 0.4-0.5mm long, glabrous; anther lobes broad-oblong, 1.1-1.6 x 0.5-0.7mm, glabrous; apical appendage absent, or a very small obtuse lobe less than 0.5mm long, glabrous; stamens in female flowers absent. Ovary in female flowers 4-carpellate, globose, angled, 1 x 0.9-1mm, viscous, pubescent; styles 4, connate for almost entire length, straight, 3-6.5(-8)mm long, glabrous, separating shortly at the apex into 4 broad lobes to 0.1mm long; in male flowers rudimentary ovary present. Capsule 4-winged, in lateral view transverse-elliptic, deeply contracted along the central axis, (6-)6.5-7.5 x 8-9 (-10)mm, membranous, viscous, with verruculose glands on the carpels, pubescent on the carpels and sometimes on wing margins, red, red-brown or purple-brown at maturity, base deeply cordate, with the wings overlapping, apex deeply obcordate, with the wings overlapping; carpel excluding wing transverse-ovate, with septa enclosing the ventral surface, inflated,

2.5-3(-3.5) x 2(-2.5)mm; wing (1.5-)2-2.5mm broad, extending from apex to base of carpel, usually broadest at the capsule apex, sometimes the same width from apex to base, broader than or approx. equal to the width of the valve, translucent; dehiscence septicidal. Seeds 2-4, lenticular-globose, 1.5-1.6 x 1.3-1.4mm, black, +shiny; aril absent. Seedling with verruculose glands, glabrous; hypocotyl ca.9mm long; cotyledons linear, 12-14 x 1.5-2mm, acute, glabrous; epicotyl ca.1mm long; the first 2-6 leaves imparipinnate, with (3-)5-7 leaflets, the leaflets usually toothed or lobed at the apex, otherwise as in mature leaves.

Chromosome number: not known.

TYPIFICATION:

Miquel based *D. adenophora* on Preiss collection no. 2442, of which I have seen two specimens (U179044, MEL84076). Both contain fruit and are very small and scrappy. Since Miquel's main herbarium is held at U, where he worked and the U specimen bears a label in his handwriting U179044 is here selected as the lectotype.

DISTRIBUTION (Fig. 7.55):

D. adenophora occurs in southern Western Australia. It is widespread from Pindar to east of Mt. Magnet in the north to Naremben and Norseman in the south, and as far east as Zanthus.

ECOLOGY:

D. adenophora is a shrub of semi-arid and arid mallee scrub and open woodland communities. It often grows in granitic sands and in red sandy loams. Associated species include *Eucalyptus wandoo*, *E. loxophleba*, *E. flocktoniana*, *E. gracilis*, *E. transcontinentalis* and *Melaleuca uncinata* and *Codonocarpus* sp.

The small amount of flowering material available for this species indicates it usually flowers in winter. Capsules are present from September to December.

PUTATIVE HYBRIDS:

1. *D. adenophora* x *D. inaequifolia*

Populations of *D. adenophora* and *D. inaequifolia* occur together in several areas of Western Australia. In some of these locations, e.g. north of Merredin (West 3172-3182) and near Campion (West 3357-3362), putative hybrids occur between these two species. The typical forms of the two taxa are distinct in habit, leaf size, leaflet shape and number, in indumentum, inflorescence structure and in capsule shape, size, number of carpels and dehiscence. The individuals showing intermediate morphology superficially resemble *D. adenophora* in their habit with its characteristic, red-brown, spreading branchlets and its general leaf morphology. The intermediate plants vary from the typical forms in being dense, rounded shrubs, ca. 1m high, with leaves 0.9-1.4cm long, petioles 4-6mm and leaflets 7-9(-11), linear-obovate, 2-5(-7) x 1-1.5mm and with verruculose glands. The capsules have several characters which are intermediate, e.g. they may be 3 or 4-winged, the carpel shape and wing shape, size, and texture are intermediate, and different fruits on the same plant dehisce either septically or septifragally. A very small number of seeds, collected from one putative hybrid plant in the Merredin population are similar to those of *D. inaequifolia*. Attempts to germinate two of these seeds failed.

When the collections were made in 1978 the plants were not in flower and so no information regarding floral characters or pollen fertility is available. From the individuals in fruit it appears as though the inflorescence structure is also intermediate between the two species.

Specimens:

WESTERN AUSTRALIA:- Maiden s.n., Southern Cross, xi.1909. fr. (G,NSW).-
West 3179 & 3180, 4.1km NW of Merredin on rd. to Nungarin, 30.xi.1978.
 fr. (AD).- West 3357 & 3362, 2.6km E of Campion, 7.1km W of Warralakin,
 10.xii.1978. fr. (AD).

2. *D. adenophora* x *D. lobulata*

Plants showing intermediate morphology between these two species have been found in one location near Broad Arrow (West 3429-3437), in which the two species occur together. These intermediate individuals have imparipinnate leaves with 7-9 opposite leaflets and they superficially and vegetatively resemble *D. adenophora*. The leaves (>0.9cm long) and leaflets however, are larger than in this species and are usually linear or narrow-oblong. The fruits of West 3434 resemble those of *D. adenophora*, but the inflorescence structure is that of *D. lobulata*. No flowers have been seen.

Specimens :

WESTERN AUSTRALIA:- West 3434 & 3435, 10.1km W of Broad Arrow on rd. to Ora Banda, 12.xii.1978. fr./st. (AD).

NOTES:

1. This species has been confused in the past with *D. boroniaefolia* G. Don and *D. microzyga* F. Muell. It is closely related to the latter species (see AFFINITIES), but its confusion with the former has resulted from a misapplication of the name *D. boroniaefolia* to W.A. material.

2. Bentham (1863) united *D. tenuifolia* Lindl. (= *D. sinuolata* West) with *D. adenophora*. However, the material he saw from eastern Australia (that relating to *D. sinuolata*) was not fruiting and so some of the major

differences between the two species were not evident to him. Bentham realised this problem and suggested they would be distinct species if the capsule dehiscence alone proved to be different. There are major differences in leaf shape, inflorescence structure and capsule characters between *D. adenophora* and *D. tenuifolia*.

AFFINITIES:

D. adenophora is closely related to *D. microzyga*. In sterile condition the two species are sometimes confused, but the fruits and flowers serve to distinguish them. *D. microzyga* has longer pedicels, larger sepals and shorter filaments. The larger, coriaceous capsules of *D. microzyga* dehisce septifragally and the seeds are twice the size of those of *D. adenophora*. Plants of the latter species with larger leaves resemble *D. microzyga* var. *acrolobata* in leaflet length, but usually var. *acrolobata* has a larger number of broader leaflets.

SPECIMENS EXAMINED: selection only (62 collections examined)

WESTERN AUSTRALIA:- Ashby 2612, Anketell, 13.ix.1968. fr. (AD,PERTH).-
Chinnock 3277, 6.9km E of rabbit proof fence on Hyden-Lake Cronin rd.,
 7.x.1976. fr. (AD).- Drummond 38, Swan R., s.dat. fr. (CGE,G,MEL,NSW).-
Keighery 1618, 3km W of Jackson mining camp, 4.v.1978. f.fl. (PERTH).-
Keighery 1645, North Ironcap, ENE of Hyden, 6.v.1978. f.fl./m.fl. (PERTH).-
de Rebeira 79, Cunderin Hill, Yandegin, 27.ii.1979. m.fl. (PERTH).-
West 3314-3318, 0.5km S of Pindar, 8.xii.1978. fr./st. (AD).- West 3358-3361, 2.6km E of Champion and 7.1km W of Warralakin, 10.xii.1978. fr./st. (AD).- Whibley 4587, 8km E of Norseman, 29.x.1974. fr. (AD).- Wilson & Herbert 125, Merredin, xi.1920. fr. (PERTH).

51. *Dodonaea microzyga* F. Muell., Ann. Rep. Govt. Bot. & Melb. Bot. Gdn. 1862-3 4:12 (1863), Fragm. 9:86 (1875); Brown, For. Fl. S. Aust. t.30 (1882); Diels in Diels et Pritzl, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:348, fig.43C (1904); Black, Fl. S. Aust. edn 1. 363 (1926); Radlkofer, Pflanzenreich IV.165:1387, fig.44C (1933); Black, Fl. S. Aust. edn 2. 542 (1952); Blackall & Grieve, W. Aust. Wildfls. 2:326 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970); Chippendale, Proc. Linn. Soc. N.S.Wales 96:246 (1972).
TYPE: "On the River Neales. J.M. Stuart." Holotype: J. Macd. Stuart s.n., Neales River, Central Australia, s.dat. fr. (MEL84115).

? *D. adenophora* Miq. var. *ovata* Ewart, Proc. R. Soc. Vic. 19(2):39 (1907); Radlkofer, Pflanzenreich IV.165:1390 (1933).

TYPE: "Specimens were sent, in 1884, from Adelaide by J.H. Brown to von Mueller." Holotype: MEL.

FIGURES: Brown, For. Fl. S. Aust. t.30 (1882); Diels in Engler's Bot. Jahrb. 35:348, fig.43C (1904); published again in Radlkofer, Pflanzenreich IV.165:1388, fig.44C (1933); Blackall & Grieve, W. Aust. Wildfls. 2:326 (1956).

DESCRIPTION (Fig. 7.56 & 7.77):

Dioecious shrub, 0.5-1.5m high, spreading. Branches intricate, rigid; branchlets terete or slightly angular, dark red-brown, viscous, with brown verruculose glands, puberulent or glabrous. Leaves imparipinnate, (0.25-) 0.3-0.9(-1.1)cm long (excluding petiole); petiole 1.5-4.5(-5)mm long, puberulent; rachis narrow-channelled above; lateral leaflets 2-8(-10), opposite, oblanceolate to broad-obovate, usually obovate, rarely narrow-spathulate, concave above, (1.6-)2-7.5(-8) x 1-3mm, coriaceous, thick,

viscous, with verruculose or sessile glands, puberulent, base cuneate, sessile, margin entire, or irregularly sinuate, rarely toothed, apex obtuse or rounded, or obscurely toothed or notched, recurved, midvein impressed above, sometimes visible below, lateral venation obscure; the terminal leaflet shorter than laterals & lobe-like in var. *acrolobata*, similar to laterals in var. *microzyga*. Flowers unisexual, monadic or rarely diadic; pedicels 3.5-5mm long, reflexed, viscous, with verruculose glands, usually pubescent at the base. Sepals 4, ovate, (1.8-)2-2.6 x 1.3-1.8(-2)mm, obtuse, viscous, outer surface with verruculose glands, glabrous, inner surface villous to tomentose, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are valvate, free at the apex only & surrounding the ovary. Stamens in male flowers 8(-10), approx. equal in length to the sepals, spreading; filaments 0.1-0.2mm long, glabrous; anther lobes broad-oblong, 1.4-1.8 x 0.7-1.1mm, glabrous; apical appendage a broad, obtuse lobe to 0.2mm long, puberulent, or rarely glabrous; in female flowers rudimentary stamens or filaments only present. Ovary in female flowers 3(-4)-carpellate, broad-globose, angled, 1-1.2 x 1.2-1.4mm, viscous, pubescent; styles 3(-4), connate, sometimes twisted in upper half, 3.5-4.5mm long, glabrous, separating at the apex into short lobes up to 0.2mm long; in male flowers rudimentary ovary usually present. Capsule 3(-4)-winged, in lateral view broad- to transverse-elliptic, (10-)12.5-13.5 x (10-)15-17.5mm, coriaceous, viscous, sometimes with verruculose glands on the carpels, glabrous or rarely with a few hairs on the carpels, purple to red or red-brown at maturity, base deeply cordate to cordate, usually with the wings overlapping, apex deeply obcordate, with the wings overlapping; carpel excluding wing transverse-oblong, (5-)5.5-7 x 3-4mm; wing (2.5-)3.5-4.5(-5)mm broad, extending from apex to base of carpel, usually the same width from apex to

base, sometimes broader at the capsule apex, broader than or approx. equal to the width of the valve; dehiscence septifragal. Seeds 2-3, lenticular, 2.5-3.2 x 2.3-2.5mm, black, shiny; aril absent. Seedling puberulent on branches & petioles; hypocotyl 13-20mm long; cotyledons linear-lanceolate, 17-20 x 1.5-2mm, acute, glabrous; epicotyl 2-4mm long; first 2 leaves imparipinnate with 3 leaflets, the terminal one 3-lobed, otherwise as in mature leaves.

KEY TO VARIETIES OF *D. microzyga*

Leaves with 2-3 pairs of lateral leaflets with the terminal leaflet of similar shape and size, leaflets entire, usually less than 4mm long.

var. *microzyga*

Leaves with 3-4 pairs of lateral leaflets with the terminal leaflet less than half their length, lateral leaflets irregularly sinuate, usually greater than 4mm long.

var. *acrolobata*.

var. *microzyga*

Leaves (0.25-)0.3-0.65(-0.9)cm long, with 2-3 pairs of lateral leaflets; leaflets (1.6-)2-3.5(-5) x 1-2.2(-3)mm, entire, apex usually obtuse or rounded, rarely toothed or notched.

DISTRIBUTION (Fig. 7.56):

D. microzyga var. *microzyga* occurs in central Australia and in northern South Australia. It is widely distributed in arid South Australia (mainly north of latitude 33°S) and extends into southern Northern Territory, western Queensland and the far north-west of New South Wales. The single record for Queensland is separated from the

closest N.T. and S.A. collections by the Simpson Desert and associated sandplains. Further collecting on rocky ridges and hills in south-west Queensland would probably locate this species at other sites.

ECOLOGY:

D. microzyga grows in a variety of arid habitats, and it is most commonly found on stony rises, hills and ridges composed of laterite, ironstone, granite or quartzite. Associated species vary over its distributional range.

In central Australia var. *microzyga* is often a component of open woodland or shrublands associated with *Casuarina cristata* and *Acacia sowdenii*, *Eucalyptus socialis* and with shrubs such as *Acacia kempeana*, *A. tetragonophylla*, *Eremophila* spp. and chenopods.

D. microzyga flowers in autumn to early winter (May to July) and mature capsules are present from August to November.

SPECIMENS EXAMINED: selection only (167 collections examined)

NORTHERN TERRITORY:- Chinnock 443, 6.4km E of Wallera Ranch, 23.viii.1973. fr. (AD,NT).- Lazarides 6133, 32ml NNE of Angas Downs Stn., 5.x.1956. fr. (AD,BRI,CANB,NSW).

QUEENSLAND:- Purdie 1018, Gregory North distr., 6km ENE of "Verdun Valley", 8.ix.1977. fr. (BRI).

SOUTH AUSTRALIA:- W. Barker 3018, North West region, 19.5km by rd NW of Cheesman Junction, 30.viii.1978. fr. (AD).- Chinnock 2600, Gairdner-Torrens region, 10km from Mt. Eba on Mt. Eba-Millers Creek rd., 27.ix.1975. fr. (AD).- Crisp 70/11, Eastern region, Koonamore stn., 400 km N of Adelaide, 19.v.1970. f.fl. (AD).- Lothian 3832-3833, North West region, Tallaringa Well, 140km W of Coober Pedy, 28.v.1967. m.fl./f.fl., fr. (AD).- West 1790-1792, Flinders Ras. region, 18km W of Wirrealpa H.S. and 18 km E of Blinman, 27.xii.1976. st./fr. (AD).- Whibley 4069, Moro Gorge, 20km S of Balcanoona, 13.ix.1973. fr. (AD).- Wilson 1798, Nullarbor region, Ooldea siding, 20.ix.1960. fr. (AD).

var. *acrolobata* West, var. nov.

Foliola lateralia 3-4(-5)-jugata, *foliolum terminale plus quam duplo longicra*, (3.5-)4.5-6.5(-8)mm longa, *marginē inordinatim sinuolato*.

TYPE: Holotype: J.G. West 3512, Western Australia, 12.1km E of Fraser Ra., 74.8km W of Balladonia Hotel, 32°03'S 122°57'E, 15.xii.1978. f.fl., fr. (AD).

The variety name refers to the small lobe terminating the leaf.

Leaves (0.55-)0.65-0.9(-1.2)cm long, with 3-4(-5) pairs of lateral leaflets; the lateral leaflets (3.5-)4.5-6.5(-8) x (1.5-)2-3.2mm, margin irregularly sinuolate, rarely entire, apex usually irregularly toothed or notched, rarely rounded.

DISTRIBUTION (Fig. 7.56):

D. microzyga var. *acrolobata* occurs in Western Australia from Meekatharra in the north to Norseman and the Fraser Range area in the south. One collection (George 8425) indicates extension of its distribution into the Great Victoria Desert to the east. The apparent disjunction of this record from those further west is probably due to the paucity of collecting in the intervening area.

ECOLOGY:

var. *acrolobata* is usually found in open eucalypt woodlands or mallee shrublands, which may be dominated by *Eucalyptus torquata*, *E. dundasii*, *E. lesouffii* with *Melaleuca pauperiflora*, *Triodia irritans* and chenopod shrubs.

SPECIMENS EXAMINED: selection only (78 collections examined).

WESTERN AUSTRALIA:- Ashby 2606, Anketell, 13.ix.1968. fr. (AD, PERTH).-

George 8425, 14ml E of Neale Junction, Great Victoria Desert, 11.x.1966. fr. (PERTH).- Kuchel 1746, Coolgardie, 13.ix.1964. fr. (AD).- Royce 3487, 5ml N of Norseman, 8.viii.1951. fr. (PERTH).- Speck 1105, 2ml S of Gabanintha, 31.vii.1958. fr. (AD,CANB,PERTH).- West 3493-3499, 36.4km E of Norseman on Hwy. 1, 15.xii.1978. fr./st. (AD).- West 3507-3513, 12.1km E of Fraser Ra., 74.8km W of Balladonia Hotel, 15.xii.1978. st./fr. (AD).- Wilson 7614, 38km E of Chifley, E of Kalgoorlie, 2.ix.1968. fr. (PERTH).- Wrigley s.n., 47ml W of Balladonia Motel on Eyre Hwy., 12.xi.1968. fr. (CBG31382,BRI118044).

NOTES:

D. microzyga exhibits considerable variation in leaf morphology, especially in Western Australia. Capsule morphology and inflorescence structure are consistent throughout the species. Although a large number of herbarium specimens are available, very little flowering material has been collected, and so the apparent consistency in flower morphology is drawn from only a small representation of the species. However, given that other polymorphic species in the genus, e.g. *D. viscosa* and *D. pini-folia*, show variation mainly in leaf morphology it is likely that this is the case in *D. microzyga* too.

The majority of plants in Western Australia have larger leaves with longer, narrow-obovate, often sinuolate leaflets compared with those in Central and South Australia (fig.7.56). Often this western form, which is here recognised at the varietal level, has 4 pairs of opposite, lateral leaflets and a very small terminal leaflet, while the typical form (var. *microzyga*) has 2-3 pairs of leaflets with the terminal one of similar shape and size. The leaflet apex of var. *acrolobata* is often notched or slightly emarginate and some plants have narrow-spathulate leaflets.

It is this western variety of *D. microzyga* that shows intergradation and possible hybridism with *D. lobulata* (see PUTATIVE HYBRIDS), and although flowers and fruits are distinct, the range of leaf morphology slightly overlaps with that of *D. adenophora*. While the distinction between the western and central Australian varieties is clear in the majority of cases, it is not absolute. Some specimens from South Australia, especially from the Nullarbor and north-west regions, have leaflets tending towards the shape of var. *acrolobata* and show intermediate leaf morphology. For this reason the subspecific classification at the level of variety only is proposed. Despite the apparent leaf polymorphism in this species and the intergradation with other species the distinction between the two varieties within *D. microzyga* is consistent and reliable in approx. 90% of the material examined.

The present geographical disjunction of the two varieties, apparently maintained by the intervening sandy desert and Nullarbor Plain, may be the result of recent isolation, with the two forms now evolving under differing environmental influences. Given that the S.A. plants with leaves showing similarities to var. *acrolobata* occur on the western part of the distribution of var. *microzyga* it is possible that the leaf morphology varied along a geographical east-west gradient. Further intensive field work and analysis at the population level may reveal further structure within *D. microzyga*.

PUTATIVE HYBRIDS:

D. microzyga x *D. lobulata*

D. microzyga and *D. lobulata* (Sect. *Dodonaea*) overlap in their distribution in some areas of Western Australia and South Australia, with *D. lobulata* extending further east into New South Wales. In certain locations in W.A. in which these two species occur, putative hybrid plants

have been found. These intermediate plants have a habit somewhat between the erect *D. lobulata* and the spreading *D. microzyga* var. *acrolobata*, and they usually have leaves of 0.8-2.5cm long with 9-11(-13) linear to linear-obovate leaflets. The leaves are longer than those of *D. microzyga* and shorter than *D. lobulata*. Some populations have intermediate plants with leaves more closely resembling *D. microzyga* var. *acrolobata* (e.g. West 3405-3411), while the intermediates of other populations have leaves more similar to *D. lobulata* (e.g. West 939-950). Still other populations are composed of *D. lobulata* individuals and plants with leaves tending towards *D. microzyga*, but no typical *D. microzyga* plants were located. Since these intermediate plants resemble those found in populations where the two putative parents do occur they are also included here as putative hybrids between these two species.

Some of the intermediates have fruits showing intermediate wing size and shape and fruit shape, but the majority resemble the capsules of *D. lobulata*. The inflorescence of 1-3-flowered botryoids appears to be intermediate between the solitary flowers of *D. microzyga* and the 2-3(-4)-flowered botryoids of *D. lobulata*. Flowers have not been seen on these intermediate plants and so no information is available on pollen fertility.

Two S.A. specimens (Williams 9486 and Kraehenbuehl 2784) held at AD closely resemble the intermediates from the hybrid swarms studied in W.A. and may also be intermediates between *D. microzyga* and *D. lobulata*.

Specimens:

SOUTH AUSTRALIA:- Douglas, per Williams 9486, Maralinga airstrip, s.dat. fr. (AD).- Kraehenbuehl 2784, 10km S of Andamooka H.S., 2.ix.1977. fr. (AD).

WESTERN AUSTRALIA:- Barnes WA/7429, S of Widgiemooltha, 1960. fr. (PERTH).-

Phillips s.n., Widgiemooltha, 4.ix.1968. fr. (CBG25388).- Saffrey 1502, 2.5km N of Widgiemooltha, 29.x.1970. fr. (PERTH).- Webster s.n., Coolgardie, 26.viii.1901. fr. (PERTH).- West 930, Afghan Rocks, 5km E of Balladonia Hotel, 7.viii.1975. immat.fr. (AD).- West 942, 946 & 949, Newman Rocks, 51.8km W of Balladonia Hotel, 7.viii.1975. st. (AD). West 3386-3389, 3394, 1.3km E of Bullabulling on Gt. Eastern Hwy., 11.xii.1978. fr./st. (AD).- West 3400-3403, 4.9km NE of Coolgardie on Gt. Eastern Hwy., 12.xii.1978. fr./st. (AD).- West 3408-3411, 10km SW of Kalgoorlie on Gt. Eastern Hwy., 12.xii.1978. st. (AD).- West 3468-3470, 3473-3474, Widgiemooltha, 14.xii.1978. fr./st. (AD).- West 3515-3517, Newman Rocks, 51.8km W of Balladonia Hotel, 15.xii.1978. fr./st. (AD).- West 3528, Afghan Rocks, 5km E of Balladonia Hotel, 16.xii.1978. fr. (AD).

AFFINITIES:

D. microzyga most closely resembles *D. adenophora* of Western Australia. In sterile condition the two species can be confused, but the septical, smaller, centrally constricted capsules, and flowers on shorter pedicels with smaller sepals and shorter filaments of *D. adenophora* distinguish the taxa. In W.A. where the two species are sympatric the leaves of *D. microzyga* var. *acrolobata* are longer, and the leaflets broader and usually more numerous than those of *D. adenophora*.

In W.A. *D. microzyga* intergrades with *D. lobulata* (see PUTATIVE HYBRIDS), but the two species are usually very distinct with the latter having simple, lobed leaves.

52. *Dodonaea uncinata* West, sp. nov.

Species nova Sect. *Pinnatarum*, *D. boroniaefoliae* G. Don *capsulis similaribus et foliolorum forma affinis, sed differt ramulis puberulis, foliis glandes verruculosas ferentibus, dentibus ad apicem foliolorum acutis, inflorescentiis terminalibus, ovariis glabris, antherisque glabris.*

TYPE: Holotype: K.A. Williams 55, Queensland, North Kennedy distr., Ewan rd. Mt. Spec area, 17.6km from Paluma, 18.ix.1974. fr. (BRI241251).

The specific epithet refers to the hooked apex of the terminal leaflet.

DESCRIPTION (Fig. 7.57, 7.58 & 7.78):

Dioecious shrub, 0.5-1m high, spreading. Branches arching outwards; branchlets terete, puberulent. Leaves imparipinnate, (0.4-)0.65-0.8(-1)cm long (excluding petiole); petiole (3-)4-5.5mm long, viscous, with verruculose glands, glabrous; rhachis rarely slightly winged, channelled above; lateral leaflets (4-)6-8, opposite, obovate to angular-obovate, concave above, (2.6-)3-5(-7) x 1.5-2(-3)mm, olive-green, coriaceous, thick, viscous, with verruculose glands, glabrous, base cuneate, sessile, margin entire, apex 3(-6)-toothed, the teeth acute & the central one recurved, midvein prominent below, obscure above, lateral venation obscure; the terminal leaflet shorter, sometimes lobe-like, strongly recurved or hooked, otherwise similar to the lateral leaflets. Flowers unisexual, in compound inflorescences composed of monads, terminating short lateral branchlets; pedicels (3-)4-6.5mm long, viscous, glabrous. Sepals 4, lanceolate in female flowers, ovate in male flowers, (1.6-)2-2.5(-3) x 0.7-1(-1.4)mm, acute to acuminate, viscous, outer surface with sessile glands, glabrous, inner surface tomentose or shortly villous, sometimes glabrous towards the base, persistent; at anthesis the sepals in male flowers are spreading, in female flowers they are valvate, erect & closed around the ovary.

Stamens in male flowers 8, usually exceeding the sepals, rarely approx. same length as the sepals, spreading; filaments 0.3-0.4mm long, glabrous; anther lobes broad-oblong, 1.2-1.5(-1.8) x 0.7-0.8mm, glabrous; apical appendage a triangular lobe, obtuse & flattened, to 0.1mm long, glabrous, or rarely very sparsely puberulent; stamens in female flowers absent. Ovary in female flowers 4-carpellate, globose, angled, 1 x 0.7-1mm, viscous, glabrous; styles 4, connate, 4.5-6.5mm long, sparsely pubescent at the base, separating unequally near the apex, the free arms up to 1mm long, divergent; in male flowers rudimentary ovary present. Capsule 4-winged, in lateral view transverse-broad-obovate or -elliptic, (11-) 12.5-16 x (8.5-)11-13(-14)mm, membranous, viscous, glabrous, bright red to purple at maturity, base cordate, apex deeply obcordate, with the wings overlapping; carpel excluding wing transverse-oblong & navicular, 6-8 (-8.5) x (2-)2.5-3.5mm; wing (3-)3.5-4.5mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve; dehiscence septifragal. Seeds not seen. Seedling not seen.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.57):

D. uncinata is confined to the Mt. Spec area on the eastern side of the Great Dividing Range, north-west of Townsville in north-eastern Queensland.

ECOLOGY:

This species is a shrub of open forests usually on sandstone soils. Field work is necessary to establish habitat preferences and its status in the wild.

AFFINITIES:

D. uncinata is most closely related to *D. boroniaefolia*, from which it can be distinguished by the arched hairs on the branchlets, the sunken glands on the upper leaflet surface, the pubescent anthers and axillary inflorescences of *D. boroniaefolia*.

SPECIMENS EXAMINED:

QUEENSLAND:- Gittins 501, North Kennedy distr., W of Paluma, v & vi. 1962. m.fl./f.fl./fr. (BRI).- Hill, per West 3583, between Paluma and Mt. Spec, NW of Townsville, 1.v.1979. m.fl. (AD).- Vessey 209, Mt. Spec, 40ml WNW of Townsville, 15.ix.1963. fr. (BRI).- Webb & Tracey 3331, 3ml E of Running R. on Gregory Hwy., 10.viii.1957. fr. (BRI).

53. *Dodonaea subglandulifera* West, sp.nov.

[*D. tenuifolia* auct. non Lindl.: Radlkofer, Pflanzenreich IV.165:1387-1389 (1933), p.p. (as to South Australian material only); Black, Fl. S. Aust. edn 2. 542, fig.698 (1952), p.p. (excl. "New South Wales; Queensland".)]

FIGURES: Black, Fl. S. Aust. edn 2. 542, fig.698 (1952).

Species nova Sect. *Pinnatarum*, *D. sinuolatae* West ssp. *sinuolatae folioliis linearibus obtusis et inflorescentiis similaribus affinis, sed differt capsulis transverse ellipticis, foliis brevioribus compactioribus, petiolis brevioribus, folioliis brevioribus integris et glandes verruculosas ad paginam inferiorem limitatas ferentibus.*

TYPE: Holotype: E.F. Boehm s.n., South Australia, Murray mallee region, Peep Hill, Sutherlands, 145km NE of Adelaide, 13.xi.1936. fr. (AD96222231).

The specific epithet refers to the verruculose glands on the underside of the leaves.

DESCRIPTION (Fig. 7.59, 7.60 & 7.79):

Dioecious, or rarely polygamo-dioecious shrub, 1-2m high, erect. Branches dense, spreading; branchlets angular to slightly ribbed, viscous, with verrucose glands, glabrous. Leaves imparipinnate, (0.7-)0.9-1.45(-1.55)cm long (excluding petiole); petiole (1-)1.5-2.5(-3)mm long, viscous, with verruculose glands on lower surface, glabrous; rhachis narrowly winged, ca.1mm broad, channelled above; lateral leaflets (8-)10-14(-16), opposite, linear, (3-)3.5-5.5(-7.5) x (0.8-)1-1.2(-1.5)mm, bright green, coriaceous, thick, viscous, with verruculose glands on lower surface only, glabrous, base narrow-cuneate, sessile, margin entire, very rarely with 1-2 teeth near the apex, apex obtuse, midvein prominent below, impressed or sometimes obscure above, lateral venation obscure; the terminal leaflet shorter, otherwise similar to lateral leaflets. Flowers

unisexual, or rarely bisexual, (for female flowers mature only available), diadic or triadic, axillary; pedicels (3.5-)5-6(-6.5)mm long, viscous, with verruculose glands, glabrous. Sepals 3-4, ovate, 1.6-2.5 x 1.2-1.6mm, broad-acute to obtuse, viscous, outer surface with verruculose glands & glabrous, inner surface villous, caducous; flowers at anthesis not available. Stamens in male flowers 6-8, approx. equal in length to the sepals, divergent; filaments 0.3-0.5(-0.6)mm long, glabrous; anther lobes oblong, 2-2.5 x 0.8-0.9mm, glabrous; apical appendage broad-triangular, obtuse, to 0.2mm long, pubescent; stamens in female flowers absent. Ovary in female flowers 3-4-carpellate, globose, angled, 1 x 1-1.2mm, viscous, with thin resin layer, sparsely pubescent; styles not seen; in male flowers rudimentary ovary usually present. Capsule 3-4-winged, in lateral view transverse-elliptic, 6.5-7 x (10-)13-15mm, coriaceous, viscous, with sessile to verruculose glands on carpels, carpels usually sparsely pubescent, pink to red-brown at maturity, base cordate, apex emarginate to obcordate; carpel excluding wing navicular & depressed-ovate, 4-5 x 3.5-4mm; wing 3-4mm broad, extending from apex to base of carpel, broadest at the capsule apex, usually broader than the valve, coriaceous to membranous, dehiscence septifragal. Seeds (immature only available), lenticular, 2.5 x 2.1mm, black, shiny; aril absent. Seedling not seen.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.59):

D. subglandulifera is known from a small number of collections in south-eastern South Australia. It occurs in isolated localities on northern Yorke Peninsula, near Port Wakefield north of St. Vincent's Gulf,

on the eastern side of the Mt. Lofty Ranges, near Peterborough in the northern Mt. Lofty Ranges and in the mallee area north-west of Renmark.

ECOLOGY:

All collections of *D. subglandulifera* are from semi-arid areas, but no specific information is available on the habitats from which this species has been collected. One plant observed south of Port Wakefield on the roadside appears to have germinated from among rubble used to build the road. Attempts to trace the origin of the filling for the road were unsuccessful.

NOTES:

No bisexual flowers have been observed for this species, but the presence of a very small number of fruit on predominantly male plants indicates that it is rarely polygamo-dioecious.

AFFINITIES:

D. subglandulifera is most closely related to *D. sinuolata* ssp. *sinuolata*. The two species can be distinguished by the latter's longer leaves, petioles and leaflets, which are irregularly sinuolate to lenticulate and rarely entire. The presence of verruculose glands on the lower surface of the leaf only is a characteristic unique to *D. subglandulifera*.

SPECIMENS EXAMINED: Herb. J.M. Black s.n., Sedan, 75km NE of Adelaide, x.1926. immat.fr. (AD96235107).- Copley 2883, Upper Yorke Pen., 5km N of Wallaroo, 1.xi.1969. immat.fr. (AD).- Hussey s.n., estuary of the Murray R., 1894. immat.fr. (P).- Ising s.n., Peterborough, 220 km N of Adelaide, 26.v.1925. st. (AD97648249).- Ising s.n., loc. cit., 3.iv.1932. mature f.fl. (AD966020511).- Ising s.n., loc. cit., 3.iv.1932.

mature f.fl. (AD966120192).- Ising s.n., Murray mallee region, Canegrass Stn., 60km NNE of Morgan, 20.ix.1937. m.fl. (AD96938308).- Jackson 367, Murray mallee region, W of Sutherlands, 30.ix.1961. fr. (AD,NSW).- Rothe 1360, Sedan, 1887. m.fl. (MEL84153).- Schomburgk s.n., Australia, s.dat. immat.fr. (AD96235116).- West 1620, Northern Lofty region, 9.6km S of Port Wakefield on Princes Hwy., 12.viii.1976. immat.fr. (AD).

54. *Dodonaea stenozyga* F. Muell., *Fragm.* 1:98 (1859), Pl. indig. Col. Vic. 1:88 (1862); Bentham, *Fl. Aust.* 1:486-487 (1863); Mueller, *Fragm.* 9:87 (1875), *Native Pl. Vic.* 1:123 (1879); Moore, *Fl. N.S.Wales* 95 (1893); Diels in Diels et Pritzel, *Fragm. Phytogr. Aust. occid.* in Engler's *Bot. Jahrb.* 35:349 (1904); Black, *Fl. S. Aust.* edn 1. 363-364 (1926); Ewart, *Fl. Vic.* 739 (1931); Radlkofer, *Pflanzenreich IV.*165:1389-1390 (1933); Black, *Fl. S. Aust.* edn 2. 543, fig.699 (1952); Blackall & Grieve, *W. Aust. Wildfls.* 2:327 (1956); Beard, *W. Aust. Pl.* edn 1. 61 (1965), edn 2. 81 (1970); Willis, *Hdbk. Pl. Vic.* 2:359 (1972).

TYPE: "In virgultis eremi ad flumina Darling et Murray legit J. Dallachy".

Holotype: Dallachy & Goodwin s.n., Darling R., s.dat. mature f.fl., fragmented fr. (MEL84138). Isotypes: MEL84139, BM.

FIGURES: Black, *Fl. S. Aust.* edn 2. 542, fig.699 (1952); Blackall & Grieve, *W. Aust. Wildfls.* 2:327 (1956).

DESCRIPTION (Fig. 7.61):

Dioecious shrub, 0.5-1.5m high, erect, rounded & compact. Branches dense, erect; branchlets angular, often 4-angled, glabrous. Leaves paripinnate, sometimes terminated by a very small tooth or lobe, including the petiole (0.9-)1.5-3(-3.8)cm long, often with only 2 opposite, terminal leaflets with the petiole taking the place of the rachis; petiole (9.5-)12.5-20(-24)mm long, terete, glabrous, with sessile glands, usually viscous; rachis terete, with very narrow groove above; leaflets 2-6(-10), opposite or irregularly alternate, + terete, concave or channelled above, often falcate, or some + flat and straight, (8-)9-13.5(-25) x 0.5-1(-2)mm, bright green, coriaceous, thick, viscous, with sessile glands, glabrous, base sessile, margin entire, apex obtuse, often recurved, midvein visible above, obscure below, lateral venation obscure. Flowers unisexual, usually diadic or triadic, rarely monadic, axillary; pedicels (4-)6-7.5(-8.5)mm

long, viscous, glabrous. Sepals 4, oblong-lanceolate in female flowers, ovate in male flowers, (1.5-)2-3(-3.2) x 1-1.3(-1.8)mm, usually smaller in females, acute to acuminate, viscous, outer surface with sessile glands, glabrous, inner surface villous, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are valvate, free & slightly recurved at the apex only, surrounding the ovary. Stamens in male flowers 7-8, shorter than the sepals, divergent; filaments 0.2-0.4(-0.5)mm long, glabrous; anther lobes oblong to broad-oblong, 1.8-2(-2.5) x 0.7-1mm, glabrous; apical appendage triangular-acute, sometimes obtuse & lobe-like, incurved, to 0.2mm long, glabrous; in female flowers rudimentary stamens sometimes present. Ovary in female flowers 4-carpellate, oblong-obovoid, angled, 1-1.2 x 0.9-1.1mm, glabrous, viscous, often with resin layer; styles 4, connate, slightly twisted above the middle, 3-4(-5) mm long, glabrous, separating into 4 short lobes at the apex, each lobe to 0.2mm long, straight; in male flowers rudimentary ovary usually present. Capsule 4-winged, in lateral view transverse-broad-elliptic or broad-obovate, (8.5-)10.5-13.5(-14.5) x (10-)11.5-14(-17)mm, coriaceous, viscous, with sessile glands on the carpels, glabrous, purple-brown or red to black at maturity, base cordate, apex obcordate, with wings often overlapping; carpel excluding wing navicular, depressed-ovate, (4-)5-7(-9) x 2-2.5mm; wing (3-)3.5-6(-6.5)mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve; dehiscence septifragal. Seeds 2-4, lenticular, 1.7-2 x 1.6-1.8mm, black, shiny; aril absent. Seedling glabrous, or rarely very sparsely puberulent; hypocotyl 6-10mm long; cotyledons linear, (7.5-)9-12.5 x 1.5(-2)mm, acute, glabrous; epicotyl 0.5-1mm long; the first 2-6 leaves imparipinnate with 3-5 oblong-oblong leaflets, otherwise as in mature leaves.

Chromosome number: $n = 14$. (West 1967, West 2681)

TYPIIFICATION:

The isotype of *D. stenozyga* held at MEL (i.e. MEL84139) bears a label which was used for display purposes (R.A. Smith, MEL, pers. comm. 1978). The specimen is very similar to the holotype material and was probably separated from it for the displays. The BM isotype is a very small sterile specimen.

DISTRIBUTION (Fig. 7.61):

D. stenozyga is widespread in southern Australia from southern Western Australia to western Victoria. In W.A. it occurs from Cowcowing to Pingrup in the west through to the S.A. border. Its distribution extends across the Nullarbor Plain into S.A. to northern and central Eyre Peninsula, central Yorke Peninsula, the Murray Mallee and into north-western Victoria.

ECOLOGY:

D. stenozyga is a shrub of semi-arid mallee scrub or open eucalypt woodland. Over its distributional range it grows on a variety of soil types and with a number of different dominant species. In the eastern part of its distribution (e.g. western Victoria) it occurs with *Heterodendrum oleaefolium*, *Cassia sturtii*, *Scaevola spinescens* and with mallee eucalypts. In South Australia *D. stenozyga* grows in red sands or sandy loams in mallee scrub often associated with *Eucalyptus oleosa*, *E. foecunda*, *E. gracilis*, *E. dumosa*, *Melaleuca pauperiflora*, *M. uncinata* and chenopod shrubs.

On the Nullarbor Plain it is found on limestone or sand overlying limestone with *Eucalyptus oleosa*, *E. socialis*, *E. aff. dumosa*, *E. yalatensis*

and with shrubs such as *Eremophila weldii*, *Westringia rigida*, *Melaleuca* sp., *Atriplex* spp. and *Maireana* spp.

On the western limits of its distribution (e.g. Pingrup area) *D. stenozyga* occurs in mallee scrub in sand with *Eucalyptus flocktoniana*, and *E. annulata*, while in the W.A. goldfields areas (e.g. near Kalgoorlie and Norseman) it associates with *E. clelandii*, *E. gracilis*, *E. lesouffii*, *E. dundasii* and *Melaleuca pauperiflora* in arid open woodlands or mallee shrubland.

D. stenozyga flowers in spring to early summer (September to December) and mature capsules are usually present at the same time.

NOTES:

On the Nullarbor Plain the majority of plants exhibit a slightly different leaflet form from that of *D. stenozyga* in other areas. These individuals differ in having a larger number of slightly broader leaflets which are almost flat. In all other features they are typical of *D. stenozyga*. Although the majority of plants show this variation, not all do and some show slightly intermediate forms. Given this inconsistency it is felt inappropriate to recognise this form at any formal subspecific level.

AFFINITIES:

D. stenozyga is closely related to *D. concinna*, which is the only other species with +terete leaflets. The two species can be distinguished by the puberulent indumentum of the branchlets, pedicels and stamen apical appendages of *D. concinna*, which also has shorter leaves with a larger number (never as few as 2) of shorter, straight leaflets and petioles less than 6mm long.

SPECIMENS EXAMINED: selection only (268 collections examined).

SOUTH AUSTRALIA:- Blaylock 1541, Yorke Pen., between Ardrossan & Pine Point, 2km N of Pine Point, 23.viii.1970. fr. (AD,W).- H. Turner s.n., Nullarbor region. South Mt. Beadell, nr. Maralinga, 4.ix.1960. f.fl.,fr. (AD97603373).- West 2132-2133, Eyre Pen., 44km ESE of Ceduna, 43km NW of Wirrulla on Eyre Hwy., 29.viii.1977. m.fl./f.fl. (AD).- West 2681-2686, on W.A./S.A. border, 4km S of Eyre Hwy., on track to Wilson's Bluff, 21.xi.1978. m.fl./f.fl.,fr. (AD).- Whibley 2671, Murray Mallee, between Brinkley and Hartley, 6.x.1968. m.fl. (AD).- Whibley 3672, Murray Mallee, 15km N of Overland Corner, 29.ix.1971. f.fl.,fr. (AD).

VICTORIA:- Henshall s.n., 50ml W of Red Cliffs, and 2ml S of Yarrara, 21.xi.1964. fr. (BRI,CANB,MEL,NSW).

WESTERN AUSTRALIA:- Chinnock 4968, 3.5km S of Hatter's Hill, 9.x.1979. fr. (AD).- George 7409, N of Pine Hill, 14ml NW of Mt. Ragged, 18.i.1966. f.fl./m.fl. (PERTH).- Jefferies 641008, 99ml E of Merredin, x.1964. fr. (PERTH).- West 3081-3084, 24.2km S of Pingrup (by rd.) on Ongerup-Pingrup rd, 27.xi.1978. m.fl./f.fl.,fr. (AD).- Wilson 7707, nr. Point Dover, Great Australian Bight, 4.ix.1968. fr. (PERTH).

55. *Dodonaea concinna* Benth., Fl. Aust. 1:487 (1863); Mueller, Fragm. 9:87 (1875), p.p. (excl. var. *plurifoliolata* - see *D. inaequifolia*); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:349 (1904); Radlkofer, Pflanzenreich IV.165:1389 (1933); Blackall & Grieve, W. Aust. Wildfls. 2:327 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).

TYPE: "In the south-west. Herb. F. Mueller." Holotype: F. Mueller s.n., S.W. Australia, s.dat. fr. (MEL84090).

[*D. adenophora* auct. non Miq.: Mueller, Fragm. 1:98 (1859).]

FIGURES: Blackall & Grieve, W. Aust. Wildfls. 2:327 (1956).

DESCRIPTION (Fig. 7.62):

Dioecious shrub, 0.5-1.5m high, erect, rounded & compact. Branches slender, spreading; branchlets angular, sometimes slightly ribbed, puberulent. Leaves imparipinnate, (0.4-)0.55-0.75(-0.8)cm long (excluding petiole); petiole (2.5-)3-6mm long, usually puberulent, sometimes glabrous; rhachis terete, with very narrow groove above; lateral leaflets 4-10(-12), opposite or alternate, linear, concave or channelled above, (4.5-)5-8.5(-9) x 0.7-1mm, olive-green, coriaceous, thick, viscous, with sessile glands, puberulent or sometimes glabrous, base narrow-cuneate, sessile, margin entire, apex acute or obtuse, midvein usually visible below, obscure above, lateral venation obscure; the terminal leaflet much shorter, lobe-like, otherwise similar to lateral leaflets. Flowers unisexual, (female flowers at anthesis not available), monadic, or diadic to triadic, axillary; pedicels (male flowers only) (3.6-)4-5.5mm long, viscous, puberulent near the base. Sepals 4, ovate, 2-2.4 x (1-)1.2-1.6mm, acute, viscous, outer surface with sessile glands, glabrous, inner surface villous to tomentose, becoming glabrous towards

the base, caducous; at anthesis the sepals in male flowers are spreading. Stamens in male flowers 8, approx. equal in length to the sepals, spreading or erect; filaments 0.3-0.4mm long, thick, glabrous; anther lobes oblong, 1.6-1.8(-2) x 0.7-0.8mm, glabrous; apical appendage triangular-obtuse, lobe-like, to 0.15mm long, puberulent. Ovary in female flowers not seen; in male flowers rudimentary ovary usually present. Capsule (3-)4-winged, in lateral view broad-elliptic, 9-10.5(-11) x (8.5-)9-12 (-12.5)mm, coriaceous, viscous, with sessile glands on carpels, dark red or purple to black at maturity, venation often visible on carpels, base cordate, apex obcordate, with wings sometimes overlapping; carpel excluding wing navicular & lunate, 5-6.5(-7) x (1.5-)2-2.5mm, thickened; wing (2.5-)3.5-4mm broad, extending from apex to base of carpel, broadest at the capsule apex, broader than the valve; dehiscence septifragal. Seeds 2-4, lenticular, 2.1-2.2 x 1.7-1.8mm, black, shiny; aril absent. Seedling not seen.

Chromosome number: $n = 14$. (West 2954)

DISTRIBUTION (Fig. 7.62):

D. concinna is confined to a small area in the south-west of Western Australia. Its distribution extends from the Pingrup-Borden area to the Oldfield River region east of Ravensthorpe.

ECOLOGY:

D. concinna is a shrub of mallee scrub associated with *Eucalyptus anceps*, *E. spathulata*, *E. transcontinentalis*, *E. flocktoniana* and shrubs such as *Daviesia* spp. It usually grows in loamy soil and often with ironstone pebbles at the surface.

Capsules are present from August to November or December and are often accompanied by buds. The fruits appear to take approx. 12 months to reach maturation.

AFFINITIES:

D. concinna is closely related to *D. stenozyga*, from which it can be distinguished by the glabrous branchlets, pedicels and stamen apical appendages of *D. stenozyga*, as well as several characters of the leaves. *D. stenozyga* has longer leaves with glabrous petioles greater than 9mm long and with a smaller number of longer leaflets (often 2 only), which are often falcate and recurved at the apex.

SPECIMENS EXAMINED: selection only (29 collections examined).

WESTERN AUSTRALIA:- Chinnock 4382, 5.9km SW of Ravensthorpe, 13.xi.1978. fr.,f.buds. (AD).- Eichler 20250, 52km NNW of coast at Stokes Inlet, 15.x.1968. fr. (AD).- George 7057, W of Ravensthorpe, 30.x.1965. fr. (PERTH).- Newbey 1343, 10ml S of Jerramungup, 16.viii.1964. fr. (PERTH).- Simmons, per Copley 5015, Chillingup rd., 28.ix.1976. fr. (AD).- Tindale 3894, 7.5ml NNW of Ongerup, 31.viii.1973. fr. (AD,NSW).- West 1033-1037, 152km NE of Albany, and 30km N of Borden, 10.viii.1975. immat.fr./st. (AD).- West 2954-2960, 12.6km E of Ravensthorpe on Eyre Highway, 24.xi.1978. m.fl./m.buds./fr. (AD).- Wilson 8012, 1km W of Burlabup Creek, 33km E of Ravensthorpe, 27.ix.1968. fr. (PERTH).

VI. Sect. *Plagiopterae* (Radlk.) West, stat. nov.

Ser. *Pinnatae* Benth., Fl. Aust. 1:483 (1863), p.p.

Ser. *Platypterae* subser. *Plagiopterae* Radlk., Pflanzenreich IV.165:1356 (1933), basionym.

TYPE SPECIES: Lectotype (here designated): *D. inaequifolia* Turcz.

DIAGNOSIS:

Leaves imparipinnate, petiolate, leaflet margin entire, apex acute to obtuse, terminal leaflet long & similar to laterals; capsule transverse-oblong or -obovate in lateral view, carpel crustaceous, wing membranous or coriaceous, oblique, longer than broad, usually extending to apex & base of carpel; seed exarillate.

TYPIFICATION:

The three species included in this section are equally available for lectotypification. *D. inaequifolia* is selected since it agrees most closely with Radlkofer's protologue.

DISTRIBUTION:

Two species of Section *Plagiopterae* occur in south-eastern Queensland and eastern New South Wales, and the third, *D. inaequifolia* is confined to south-west Western Australia.

D. inaequifolia Turcz.

D. megazyga F. Muell. ex Benth.

D. tenuifolia Lindl.

KEY TO SPECIES OF SECTION *PLAGIOPTERAE*

- 1a. Leaflets \geq 4mm broad, lanceolate, oblique; rhachis winged, 1.5-3mm broad, not channelled above. 56. *D. megazygga*
- 1b. Leaflets \leq 2mm broad, linear, not oblique; rhachis not winged, 1-1.5mm broad, channelled above 2
- 2a. Pedicels glabrous; capsule 3-4-winged, carpel crustaceous but not thickened; leaves (excluding petiole) usually $<$ 4.5cm long, usually sparsely pubescent, rarely glabrous 57. *D. inaequifolia*
- 2b. Pedicels sparsely puberulent; capsule 4-winged, carpel crustaceous & thickened; leaves (excluding petiole) usually $>$ 4.5cm long, glabrous 58. *D. tenuifolia*

56. *Dodonaea megazyga* F. Muell. ex Benth., Fl. Aust. 1:483-484 (1863), p.p. (excl. "Dogwood Creek, Leichhardt" - see *D. macrozyga*); Mueller, Fragm. 9:86 (1875); Moore, Fl. N.S.Wales 94 (1893); Bailey, Fl. Qld. 1:316-317 (1899); Radlkofer, Pflanzenreich IV.165:1395-1396 (1933); Beadle et al., Fl. Syd. Reg. 387 (1972).

D. viscosa Jacq. var. *megazyga* F. Muell., Pl. indig. Col. Vic. 1:86 (1862), basionym.

TYPE: "Hastings River, Herb. Lindley, Beckler; Dogwood Creek, Leichhardt; Parramatta, Woolls." Lectotype (here designated):

Dr. Beckler s.n., Hastings River, s.dat. fr. (MEL84112). Isolectotypes: L908.269-879, MEL84113, MEL84114, U91876, U91877. Syntypes: Dr. Woolls s.n., Parramatta, s.dat. mature f.fl. (NSW140534, MEL).

DESCRIPTION (Fig. 7.63):

Dioecious shrub or small tree, 2-5m high, erect. Branches dense, slender; branchlets acutely angled, puberulent. Leaves imparipinnate, (7.2-)8.5-14.5(-20.5)cm long; petiole (18.5-)24-30(-47.5)mm long, puberulent; rhachis winged, 1.5-3mm broad; leaflets (13-)19-29(-31), usually irregularly alternate, sometimes opposite, lanceolate, usually oblique, (17-)19-24.5(-42) x 4-6(-7.5)mm, dark green above, paler below, coriaceous, viscous, with sessile glands, very shortly puberulent, base cuneate, margin entire, revolute, apex acute, midvein prominent & raised below, impressed above, lateral venation obscure. Flowers unisexual, in axillary panicles composed of monads to botryoids; pedicels (2.2-)4-5.3(-7)mm long, viscous, sparsely puberulent. Sepals 3 in female flowers, 4 in male flowers, lanceolate to broad-ovate or broad-oblong, (1.8-)2-2.5(-2.7) x 1-1.4(-1.6)mm, obtuse or rarely acute, viscous, outer surface glabrous, inner surface tomentose, caducous; at anthesis the sepals in male flowers

are spreading, in female flowers they are erect, free and recurved at the apex, valvate near the base, surrounding the ovary. Stamens in male flowers 8, just exceeding the sepals, divergent; filaments 0.4-0.6mm long, glabrous; anther lobes oblong, 1.6-2(-2.3) x 0.7-1.1mm, glabrous; apical appendage acuminate, broad, incurved, 0.3mm long, pubescent with stiff hairs; stamens in female flowers absent. Ovary in female flowers 3-carpellate, obovoid, angled, 0.8-0.9 x 0.8mm, viscous, with sessile glands, sparsely pubescent; styles 3, connate, 2-3.5mm long, glabrous, separating at the apex into 3 short lobes up to 0.2mm long; in male flowers rudimentary ovary usually present. Capsule 3-winged (7.5-)8.5-10.5 x (13.5-)16-21(-22.5)mm, viscous, glabrous, red-brown at maturity, base truncate to cordate, apex emarginate; carpel excluding wing navicular-globose, 3.5-4 x 2.5-3mm, thickened, crustaceous; wing (4.5-)6.5-8mm long, usually extending to apex & base of carpel, broadest at the capsule apex, broader than the valve, membranous; dehiscence septifragal. Mature seeds not seen. Seedling not seen.

Chromosome number: not known

TYPIFICATION:

Eight sheets of the type collections (L,MEL(4 sheets),NSW,U(2 sheets)) have been examined. It is necessary to select a lectotype for the name *D. megazyga* as Bentham did not nominate any one of these sheets as the type. The three MEL specimens collected by Beckler all bear Mueller's handwriting and a 'B' indicating that Bentham saw them. The two sheets at U and one at L are also of the Beckler, Hastings River collection but, there is no indication that the author actually used them when drawing up the description for this species. Since MEL84112, of the three MEL sheets, agrees best with the protologue and contains the best material, it is here selected as the lectotype.

DISTRIBUTION (Fig. 7.63):

Dodonaea megazyga occurs in north-eastern New South Wales and south-eastern Queensland. Its distribution extends from the Sydney area northwards along the eastern side of the Great Dividing Range to just north of the Queensland/N.S.W. border.

ECOLOGY:

D. megazyga is a tall shrub or small tree found in dry sclerophyll forests or on the margins of rainforests, usually growing on sandstone.

The capsules of this species appear to require 10-12 months to mature and plants often bear flowers and fruits simultaneously, usually during spring and summer (September to March).

AFFINITIES:

D. megazyga is a distinct species showing little resemblance to any other species. The capsules are similar to those of other species in *Platypterae*, but the compound, puberulent leaves, with oblique, lanceolate leaflets are very characteristic.

SELECTED SPECIMENS: selection only (31 collections examined)

NEW SOUTH WALES:- Boorman s.n., Coolpi Mts., Upper Hastings R., x.1909. immat.fr. (NSW108380).- P. Burgess 127, French's Ck., Bulga S.F., 6.iii. 1962. f.fl.,fr. (NSW).- Coveny 14, 30ml SW of Gloucester, 30.ix.1967. m.fl. (NSW).- McReaddie s.n., Washpool S.F., 12.x.1967. fr. (NSW108377).- Maiden s.n., Cooiloongoobook Forest, x.1907. m.fl. (NSW131461).- Rodway s.n., Upper Williams R., 18.viii.1935. st. (NSW108379).- Salasoo 2421, Lagoon Pinch, Barrington Tops, 29.ix.1962. fr. (NSW).- Schodde 3202, by Williams R., nr. Barrington Guest House, 40ml N of Singleton, 2.ii.1963. f.fl./fr. (AD,CANB).

QUEENSLAND:- Schneider s.n., Nerang Creek, s.dat. m.fl./fr. (BRI74175).-
White 11877, Lamington N.P., 28.xi.1942. m.fl. (BRI).

57. *Dodonaea inaequifolia* Turcz., Bull. Soc. Imp. Naturalistes Moscou 31,I:408 (1858): Bentham, Fl. Aust. 1:486 (1863); Mueller, Fragm. 9:87 (1875); Diels in Diels et Pritzel, Fragm. Phytogr. Aust. occid. in Engler's Bot. Jahrb. 35:348, fig.43D (1904); Radlkofer, Pflanzenreich IV.165:1394-1395, fig.44D (1933); Blackall & Grieve, W. Aust. Wildfls. 2:326 (1956); Beard, W. Aust. Pl. edn 1. 60 (1965), edn 2. 81 (1970).
 TYPE: "Nova-Hollandia, Drum. IV. n. 258." Syntypes: J. Drummond 258, Swan R., W.A., s.dat. fr. (BM,CGE,G,MEL84102,W92009).

D. leptozyga F. Muell., Fragm. 1:219-220 (1859); [Bentham, Fl. Aust. 1:486 (1863) pro syn.; Radlkofer, Pflanzenreich IV.165:1394 (1933) pro syn.]
 TYPE: "In rupibus calcariis ad flumen Murchison. A. Oldfield." Lectotype (here designated): Oldfield s.n., Murchison River, s.dat. fr. (MEL).
 Isolectotypes: MEL,W.

[*D. concinna* auct. non Benth.: Mueller, Fragm. 9:87 (1875), p.p. - var. *plurifoliolata* (coll. C. Gray, Greenough Flat).]

FIGURES: Diels in Diels et Pritzel in Engler's Bot. Jahrb. 35:348, fig.43D (1904); published again in Radlkofer, Pflanzenreich IV.165:1388, fig.44D (1933); Blackall & Grieve, W. Aust. Wildfls. 2:326 (1956).

DESCRIPTION (Fig.7.64):

Dioecious shrub, 1-3(-5)m high, erect. Branches slender, spreading; branchlets angular, with sessile glands, glabrous. Leaves imparipinnate, (1.5-)2-4.3(-5.2)cm long (excluding petiole); petiole (7-)10-17.5(-25)mm long, viscous, with sessile glands, usually sparsely pubescent; rhachis channelled above, 1-1.5mm broad; leaflets (17-)19-23, opposite or irregularly alternate, linear, channelled above, convex below, (2-)4.5-

13(-23.5) x (0.5-)1-1.5mm, coriaceous, thick, viscous, with sessile glands, usually with sparse adpressed hairs, rarely glabrous, base narrow-cuneate, sessile, margin entire, thickened, apex obtuse, rarely tri-dentate, midvein impressed above, prominent below, lateral venation obscure.

Flowers unisexual, in 2-6-flowered botryoids & metabotryoids, axillary; pedicels (3-)4.5-8.5mm long, glabrous, with sessile glands. Sepals 3(4) in female flowers, 4(3) in male flowers, ovate, (1.5-)1.8-2.8(-3.5) x (1.3-)1.4-2(-2.3)mm, acute, viscous, outer surface with sessile glands, glabrous, inner surface tomentose, caducous; at anthesis the sepals in male flowers are spreading, in female flowers they are free and spreading to form a cup-shaped structure. Stamens in male flowers 6(-8), slightly shorter than the sepals, divergent; filaments 0.4-0.5mm long, glabrous; anther lobes oblong, (1.6-)2.1-2.5 x 0.8-1mm, glabrous; apical appendage broad-triangular & lobe-like, 0.1-0.2mm long, shortly pubescent; stamens in female flowers usually absent, filaments only sometimes present. Ovary in female flowers 3(-4)-carpellate, globose to obovoid, angled, 0.9-1 x 1-1.2mm, viscous, with sessile glands, glabrous, sometimes sparsely pubescent near the apex; styles 3(-4), connate, sometimes twisted, 2.5-3.5mm long, glabrous, separating shortly at the apex, each free arm 0.2-0.3mm long; in male flowers rudimentary ovary usually present. Capsule 3(-4)-winged, (4.5-)5.5-7(-7.5) x (9-)12-14(-16)mm, glabrous, with sessile glands on carpel when immature, dark red to red-brown at maturity, base cordate, apex emarginate; carpel excluding wing navicular, transverse-ovate, 3.5-4.5(-5) x 3-3.5(-4)mm, crustaceous; wing (2-)3.5-5mm long, rounded or sometimes pointed, extending from apex to base of carpel, longest near the capsule apex, usually larger than the valve, membranous; dehiscence septifragal. Seeds 2-3, lenticular, 1.9-2.4 x 2-2.1mm, black, dull; aril absent. Seedling not seen.

Chromosome number: $n = 14$ (West 3282)

TYPIFICATION:

Five sheets of the type collection of *D. inaequifolia*, Drummond no. 258, have been examined (BM,CGE,G,MEL84102 and W92009). Turczaninow's main herbarium is housed at KW and it has not been possible to this time to find out whether there is another Drummond 258 specimen at KW. The typification of this species will be clarified upon receiving information or material from KW.

It was necessary to select a lectotype for the synonymous name *D. leptozyga* as three sheets of the type collection have been seen (MEL (2 sheets),W), and Mueller did not nominate any one as the type. The MEL specimen, here chosen as the lectotype, bears Mueller's handwriting and label information as in the type citation, it agrees with the protologue and contains the better material.

DISTRIBUTION (Fig. 7.64):

D. inaequifolia is confined to south-west Western Australia. It occurs in a north-west/south-east arc extending from Dirk Hartog Island and Shark Bay area to the Merredin and Southern Cross regions.

ECOLOGY:

This species occurs in semi-arid areas usually in rocky granite or laterite soils. It is most often a shrub of mallee heath, mallee scrub, or open woodland dominated by *Eucalyptus loxophleba*, *E. salmonophloie* and *E. wandoo*.

D. inaequifolia flowers in autumn and early winter (April to June) and mature capsules are present from August to November.

PUTATIVE HYBRIDS:

D. adenophora x *D. inaequifolia*, see *D. adenophora*.

AFFINITIES:

D. inaequifolia resembles *D. tenuifolia* of south-eastern Queensland in leaf and fruit morphology. The two species can be distinguished by the longer, glabrous leaflets, puberulent pedicels, smaller sepals, and the capsules with 4 usually pointed wings and thickened carpels of *D. tenuifolia*.

SPECIMENS EXAMINED: selection only (125 collections examined).

WESTERN AUSTRALIA:- Allan 45, Mollerin, N of Tammin, 23.vii.1969. f.fl. (PERTH).- Beard 6773, between Denham and Monkey Mia, 9.x.1973. fr. (PERTH).- Brooker 1801, NE of Westonia, 4.vi.1969. m.fl. (PERTH).- Burns 17, Z bend, Murchison R., Kalbarri N.P., 21.vi.1969. f.fl. (PERTH).- Filson 8560, 7 ml N of Murchison R. bridge, NW Coastal Hwy., 6.ix.1966. fr. (MEL,PERTH).- George 11530, East Fisherman Paddock, Dirk Hartog Is., 4.ix.1972. fr. (Perth).- Long 20, 80ml E of Geraldton, 1.iv.1960. m.fl. (PERTH).- West 3172-3182, 4.1km NW of Merredin on rd. to Nungarin, 30.xi.1978. fr./st. (AD).- West 3223-3224, Pithara, 0.5km E of township, 1.xii.1978. fr./st. (AD).- West 3287-3289, 11.3km NW of Three Springs on Geraldton Hwy., 6.xii.1978 fr./st. (AD).

58. *Dodonaea tenuifolia* Lindl. in Mitchell, Journ. Exped. Trop. Aust. 248 (1848); [Bentham, Fl. Aust. 1:486 (1863) pro syn. sub *D. adenophora*]; Mueller, Fragm. 9:85-86 (1875), p.p. (excl. material pertaining to *D. sinuolata* West); Bailey, Fl. Qld. 1:318 (1899), (Condamine River, Darling Downs specimens n.v.); Radlkofer, Pflanzenreich IV.165:1387-1389 (1933), p.p. (Mitchell, Belyando R. only, excl. material pertaining to *D. sinuolata* West); Black, Fl. S. Aust. edn 2. 542, fig.698 (1952), p.p. (excl. material pertaining to *D. subglandulifera* West).
- TYPE: leg. Mitchell, Belyando River, 25.vii.1846. Holotype: Lieut.-Col. Sir T.L. Mitchell 209, Sub-tropical New Holland, 25.vii.1846. m.buds. (CGE). Isotype: NSW142638.

- D. macrozyga* F. Muell. Fragm. 4:135 (1864); Mueller, Fragm. 9:86 (1875); Bailey, Fl. Qld. 1:317 (1899); Radlkofer, Pflanzenreich IV.165:1395 (1933); [Bentham, Fl. Aust. 1:484 (1863), p.p. (sub *D. megazyga* - "Dogwood Creek, Leichhardt" only)] - syn. nov.
- TYPE: "In tractu arenoso-rupestri juxta originem fluvii Cape River. E. Bowman." Holotype: Bowman 175, sources of the Cape R., s.dat. f.fl., fr. (MEL84111). Probable isotypes: MEL, NSW108371.

DESCRIPTION (Fig. 7.65):

Dioecious shrub, 1-3m high, spreading. Branches dense; branchlets flattened, sharply angled, glabrous. Leaves imparipinnate, 4.5-8.5(-9.5)cm long (excluding petiole); petiole (8.5-)10-15(-18)mm long, broad at the base, viscous, glabrous; rhachis winged, 1-1.5mm broad, channelled above, keeled below; leaflets (9-)13-23(-25), upper ones opposite, the lower alternate, linear, usually shallowly channelled above, (9-)12-22(-30) x 1-1.5(-2)mm, coriaceous, thick, viscous, glabrous, base narrow-cuneate, sessile, margin entire, apex broad-acute to obtuse, midvein prominent,

lateral venation inconspicuous. Flowers unisexual, (male flowers not available), in 6-10-flowered botryoids & metabotryoids, axillary; pedicels 6.5-9mm long, viscous, sparsely puberulent. Sepals 4, ovate, 1.5-1.6 x 1-1.3mm, acute, viscous, outer surface glabrous, inner surface villous, caducous; at anthesis the sepals in female flowers are erect, free & recurved at the apex, valvate below, surrounding the ovary. Stamens not seen. Ovary in female flowers 4-carpellate, broad-obovoid, angled, 1 x 1-1.2mm, with resin layer, glabrous; styles 4, connate, twisted, 3-5.6mm long, glabrous, scarcely separating at apex into 4 short lobes less than 0.1mm long. Capsule 4-winged, in lateral view transverse-oblong, 4.5-5 (-9) x (10.5-)11-16(-20)mm, viscous, glabrous, dark brown-purple or red at maturity, base truncate to cordate, apex truncate to emarginate; carpel excluding wing lunate & navicular-globose, 3-4.5 x 2-3.5(-4)mm, thickened, crustaceous; wing (2.5-)3-5(-9)mm long, oblique, pointed, rarely rounded, sometimes extending to base and apex of carpel, longest near the capsule apex & usually larger than the valve, coriaceous; dehiscence septifragal. Seeds 1-2, lenticular, 2.3-2.4 x 2.1-2.2mm, black, +dull, with hyaline membrane lifting over entire seed; aril absent. Seedling not seen.

Chromosome number: not known.

TYPIFICATION:

Two specimens of the type collection of *D. macrozyga*, MEL s.n. and NSW108371 (ex MEL), are regarded as probable isotypes because, although they are both from the same locality as the holotype and both contain female flowers and appear to be from the same collection, neither sheet includes any information about the collector.

DISTRIBUTION (Fig. 7.65):

D. tenuifolia is known from a relatively small number of widely dispersed populations in south-eastern Queensland. Its distribution extends from the Cape River in the north to south of Roma, and as far inland as Enniskillen.

ECOLOGY:

This species appears to grow on rocky hillsides and in mountain ranges, often associated with open eucalypt forests on sandstone.

D. tenuifolia flowers in March or April and mature capsules are present from August until November or December.

NOTES:

Examination of the types of *D. macrozyga* F. Muell. and *D. tenuifolia* Lindl. indicates that these two taxa are conspecific. *D. macrozyga* F. Muell. is therefore regarded as a synonym of the earlier published *D. tenuifolia* Lindl. (Stafleu et al., 1978, Art. 11). Most material (other than the type), attributed to *D. tenuifolia* has been incorrectly classified and actually belongs to the new species *D. sinuolata*.

One collection (White 12392) from Enniskillen differs from most other specimens in having larger wings on the capsules. In all other characters it agrees closely with the typical form of *D. tenuifolia*.

AFFINITIES:

D. tenuifolia shows most resemblance to *D. sinuolata* in general leaf morphology, but the two species can be readily distinguished on the smaller number of shorter, sinuate to denticulate leaflets of *D. sinuolata* as well as the different capsules.

D. inaequifolia resembles *D. tenuifolia* in fruit and leaf morphology. The shorter, sparsely pubescent leaflets, glabrous pedicels, larger sepals and usually 3-carpellate capsules with rounded wings of *D. inaequifolia* distinguish the species.

SPECIMENS EXAMINED:

QUEENSLAND:- Bancroft s.n., Burnett distr., Eidsvold, s.dat. fr. (BRI72255,NSW142637).- Blake 6995, Leichhardt distr., Lexington, N of Springsure, 23.vii.1934. fr. (BRI,CANB).- Gittins 2747, 7ml N of "Yoothappinna", Injune distr., 4.ix.1974. fr. (BRI,NSW).- Gordon 44, Leichhardt distr., Carnarvon Gorge, viii.1948. fr. (BRI).- Gordon 45, Maranoa distr., Thomby Ra., 6.viii.1948. fr. (BRI).- Leichhardt s.n., Dogwood Creek, 8.vii.1847. (MEL).- O'Shanesy 1285, Table Mt., 17.iii.1871. m.fl./f.fl. (MEL).- O'Shanesy 1308, nr Rockhampton, s.dat. m.fl. (MEL).- Webb s.n., 35ml (by rd.) S of Rolleston on Rewan rd., 23.viii.1967. fr. (BRI75072).- White 12392, Mitchell distr., Enniskillen, 12.xi.1943. fr. (BRI).

VII. Sect. *Inappendiculatae* (Radlk.) West, stat.nov.

Ser. *Pinnatae* Benth., Fl. Aust. 1:483 (1863), p.p. (as to *D. humilis*).

Ser. *Aphanopterae* subser. *Inappendiculatae* Radlk., Pflanzenreich IV.165:1357 (1933), p.p., basionym.

TYPE SPECIES: Lectotype (here designated): *D. humilis* Endl.

DIAGNOSIS:

Leaves imparipinnate, petiolate, leaflet margin entire, apex usually toothed or lobed, terminal leaflet usually smaller than laterals; capsule lobed, crustaceous, hirsute or pubescent, often with glandular hairs, appendage absent; seed exarillate, with hyaline membrane lifting over entire seed or at margin only.

TYPIIFICATION:

A lectotype must be selected from the only two species, *D. humilis* and *D. macrossanii*, which are common to both Radlkofer's subseries *Inappendiculatae* and the section proposed here. *D. humilis* is chosen as the lectotype since Radlkofer saw more of this species and it is more widespread than *D. macrossanii*.

DISTRIBUTION:

The three species of this section have restricted distributions in different parts of Australia. *D. macrossanii* is confined to south-east Queensland and north-east New South Wales, *D. humilis* occurs in southern South Australia and *D. glandulosa* is known from only two populations in south-west Western Australia.

D. glandulosa West

D. humilis Endl.

D. macrossanii F. Muell. et Scortechini

KEY TO SPECIES OF SECTION *INAPPENDICULATAE*

- 1a. Capsule 2- or 4-lobed, > 4mm long, with glandular hairs &/or pubescent; stamen filaments > 1mm long; leaves (excluding petiole) > 0.5cm long (rarely 0.5cm long), leaflet apex obtuse or shallowly 3-5(-7)-toothed or -lobed above the middle, either glabrous, rarely with sparse hairs on midvein below, or pubescent & with glandular hairs 2
- 1b. Capsule 3(-4)-lobed, < 4mm long, hirsute or pubescent, never with glandular hairs; stamen filaments 0.2mm long; leaves (excluding petiole) < 0.5cm long, leaflet apex deeply 2-3-toothed sometimes to $\frac{1}{2}$ length of leaf, hirsute 59. *D. macrossanii*
- 2a. Vegetative parts with glandular hairs; leaflets < 2mm long, apex obtuse, recurved; flowers axillary; capsule 2-valved 60. *D. glandulosa*
- 2b. Vegetative parts lacking glandular hairs; leaflets > 2mm long, apex lobed or toothed; flowers terminal; capsule 4-lobed 61. *D. humilis*

59. *Dodonaea macrossanii* F. Muell. et Scortechini, Chem. & Drugg. Australas. Suppl. 4:69 (1882); Bailey, Fl. Qld. 1:318 (1899); Radlkofer, Pflanzenreich IV.165:1403-1404 (1933).

TYPE: "Near Miles, in South-western Queensland. Rev. B. Scortechini." Lectotype (here designated): Scortechini s.n., Miles, SW Queensland, xii.1881. fr. (MEL84109). Isolectotype: Scortechini s.n., SW Queensland, s.dat. fr. (MEL84110). Possible isoelectotype: Scortechini s.n., Myles, s.dat. st. (BRI72341).

DESCRIPTION (Fig. 7.66):

Dioecious shrub, 0.2-0.3m high, spreading. Branches prostrate; branchlets terete or angled, pilose. Leaves imparipinnate, (0.15-)0.2-0.28(-0.56)cm long (excluding petiole); petiole 0.8-1.4(-2.5)mm long, hirsute; rhachis ±winged, 0.6-1mm broad, channelled above; lateral leaflets (2-)4(-6), opposite, obtriangular, angular-obovate or obovate, 2-3-toothed at the apex, sometimes divided to half the length of the leaflet, (1.8-)2-3(-4) x 1-1.8(-3.2)mm, coriaceous, thick, viscous, hirsute, sometimes near the apex only, base cuneate to broad-cuneate, margin entire, apex recurved, obtuse or 2-3-toothed, the teeth obtuse, midvein sometimes prominent below, usually obscure, lateral venation obscure; the terminal leaflet usually elliptic or obovate, usually entire, rarely toothed or divided, 1-2 x 0.7-0.9mm, otherwise similar to lateral leaflets. Flowers unisexual, monadic, axillary; pedicels 0.7-0.8mm long, reflexed, viscous, hirsute. Sepals 3, ovate, (1.5-)1.7-2 x 1-1.4(-1.8)mm, acute to acuminate, viscous, outer surface hirsute, inner surface villous at the apex, persistent; at anthesis the sepals in male flowers are spreading, in female flowers they are free, erect & surrounding the ovary. Stamens in male flowers 6, exceeding the sepals, erect; filaments 0.2mm long, glabrous; anther lobes oblong, twisted at anthesis, 1.5-1.6 x 0.5-

0.7mm, glabrous; apical appendage +absent or a broad lobe ca.1mm long, pubescent; stamens in female flowers absent. Ovary in female flowers 3(-4)-carpellate, globose, 3-lobed, 0.7-0.8 x 0.7-0.8mm, viscous, pubescent; styles 3, connate for entire length, sometimes twisted, 5-6.5mm long, glabrous; in male flowers rudimentary ovary present. Capsule 3(-4)-lobed, in lateral view transverse-elliptic, 2-3.5 x 4-6mm, crustaceous, viscous, hirsute, sometimes sparsely so or pubescent, red-brown at maturity, base truncate, apex truncate to emarginate, style base persistent; carpel depressed-ovate to globose, 2-3.5 x 2-3mm; appendage absent; dehiscence septifragal. Seeds 1-2, lenticular, 1.9-2 x 1.6-2mm, black, with hyaline membrane lifting over entire seed; aril absent. Seedling not seen.

Chromosome number: not known.

TYPIFICATION:

Lectotypification was necessary for this species as there are two specimens of the type collection at MEL and the authors did not nominate one of them as the type. Both MEL specimens contain fruit and appear to be from the same collection. MEL84109 bears a label which is probably Scortechini's field label and another in Mueller's handwriting with date and locality, as well as a note by Mueller about the similarities and differences of this new species and other *Dodonaea* species. This specimen is here designated as the lectotype. The other sheet held at Melbourne (MEL84110) does not have Mueller's writing on it, although he most probably saw it, it is undated and has only a small fruiting specimen. BRI holds a collection of several specimens by Scortechini from Miles (BRI72341) which is sterile and undated. This is regarded as a

possible isolectotype because it is possible that these specimens, which have few leaves did bear fruit when they were collected, and may be part of the type collection.

DISTRIBUTION (Fig. 7.66):

D. macrossanii occurs in the Darling Downs region of south-eastern Queensland and just over the border in north-eastern New South Wales on the western slopes of the Great Dividing Range.

ECOLOGY:

This species occurs in sandy soils usually in *Callitris* and *Eucalyptus* woodland associations. It grows with such species as *Eucalyptus viridis*, *E. bakeri* and *Casuarina luehmannii*. In some situations it is a prostrate shrub associated with *Callitris columellaris* - bloodwood - ironbark forest, with shrubs such as *Acacia doratoxylon* var. *angustifolia*, *A. conferta*, *Westringia* sp. and *Hakea purpurea*.

D. macrossanii flowers in winter from May to August, and mature fruit are present from September to November.

AFFINITIES:

D. macrossanii shows most affinity to *D. humilis* of South Australia in leaf shape and fruit characters. The two species are easily distinguished on the larger, usually glabrous leaves, the larger stamens, 3-6-flowered terminal inflorescences and the glandular hairs on the capsule of *D. humilis*.

SPECIMENS EXAMINED:

NEW SOUTH WALES:- Lane s.n., 10.4km W of Yetman, x.1971. fr. (NSW108359).

QUEENSLAND:- Alden s.n., Millmerran, ix.1933. f.fl. (BRI72338).-

Althofer s.n., Kogan-Tara rd., 1952. fr. (NSW108370).- Boorman s.n.,
Inglewood. ix.1910. fr. (NSW108369,W5287,W15665).- Cameron s.n., Barakula,
1959. m.fl. (BRI24213).- Carroll 878-879 & Telford, Barakula, N of
Chinchilla, 20.v.1967. m.fl./f.fl. (CBG).- Coveny 6814 & Hind, Auburn to
Chinchilla rd., 40.7km (by rd.) N of Chinchilla, 29.viii.1975. immat.fr.
(NSW,BRI201141).- Doggrell 159, Whetstone, vii.1929. m.fl./fr. (BRI).-
Gordon 52, Yuelba and Kogan, 21.x.1947. fr. (BRI).- Everist 3506, 6ml
W of Kogan, 12.x.1948. fr. (BRI,CANB).- Hockings & Cockburn s.n., Cecil
Plains, ix.1901. fr. (BRI30188).- McDonald 1167, 4.2km S of Inglewood on
Texas rd., 3.ix.1975. fr. (BRI).- Phillips s.n., 61ml E of St. George
on Moonie Hwy., 25.viii.1961. immat.fr. (CBG20449).- Ross s.n., 5km
from Miles on rd. to Wandoan, 22.viii.1977. f.fl. (BRI238934).-
Shoobridge s.n., 8ml W of Kogan along Condamine Hwy., 29.ix.1964. fr.
(CBG51418).- Simmons, per Copley 5078, Chinchilla, 19.x.1977. m.fl. (AD).-
Ward 177, Miles, 15.viii.1962. m.fl. (MEL).

60. *Dodonaea glandulosa* West, sp. nov.

Species nova Sect. *Inappendiculatarum*, *D. humili* Endl. capsulis similibus pilos glandulosos ferentibus, pilo glanduloso solitario in apicibus staminum affinis, sed differt indumento glanduloso eglandulosoque in foliis, capsulis bivalvatis inappendiculatis, foliolis valde recurvis et filamentis longioribus.

TYPE: Holotype: J.G. West 3154, Western Australia, 2.3km NW of Kulin on rd. to Corrigin, 32°40'S 118°09'E, 29.xi.1978. fr. (AD98008412). Isotypes: to be distributed.

The specific epithet refers to the indumentum of glandular hairs.

DESCRIPTION (Fig. 7.67, 7.68 & 7.80)

Dioecious or rarely polygamo-dioecious shrub 0.2-0.6m high, erect, multistemmed. Branches erect; branchlets angular or ribbed, pilose or pubescent, with glandular hairs. Leaves imparipinnate, (0.5-)0.8-1.2 (-1.8)cm long, (excluding petiole); petiole 0.5-1mm long, pubescent & with glandular hairs; rhachis winged, ca.0.5mm broad; leaflets (9-) 11-19, subopposite or irregularly alternate, oblong to transverse-oblong, sometimes broad-obovate, (0.8-)1-1.8 x (0.8-)1-1.5(-1.8)mm, dark green above, paler below, coriaceous, thick, viscous, pubescent, rarely sparsely so, with glandular hairs, base cuneate, sessile, margin entire, revolute, apex obtuse, strongly recurved, sometimes giving emarginate appearance from above, midvein prominent below, obscure above, lateral venation obscure. Flowers unisexual, rarely bisexual, monadic or rarely diadic, axillary; pedicels 0.5-1mm long, viscous, pubescent. Sepals 4, ovate to ovate-lanceolate, usually fused at the base for approx. 1/3 their length, upper free parts (1-)1.5-2.5 x (0.7-)1-1.5(-1.8)mm, acute, viscous, outer surface pubescent & with glandular hairs, inner surface sparsely pubescent, persistent; at anthesis the sepals in male, female & bisexual flowers are

free, imbricate & erect. Stamens in male & bisexual flowers 5-6(-8), far exceeding the sepals, divergent; filaments (1.7-)2-3.2(-3.5)mm long, glabrous; anther lobes oblong, 1.5-1.9 x 0.6-0.8mm, glabrous; apical appendage a single glandular hair to 0.2mm long; stamens in female flowers absent. Ovary in female & bisexual flowers 2-carpellate, obovoid, rounded, 1-1.3 x 0.9-1.2mm, viscous, with short glandular hairs, usually pubescent, sometimes glabrous; styles 2, connate, 6-8mm long, glabrous, separating at the apex, each free arm 0.2-0.8mm long, curved; in male flowers rudimentary ovary usually present. Capsule 2-valved, obovoid, rarely ellipsoid, 6-8 x 4-5.5mm, crustaceous & thickened, with glandular hairs, usually pubescent, sometimes with glandular hairs only, reddish-brown at maturity, base cuneate, apex rounded; carpel broad-lunate, 6-8 x 2-2.5mm; appendage absent; dehiscence septifragal. Seeds 1-2, lenticular, 1.8-1.9 x 1.7-2, black, shiny, with hyaline membrane lifting over the entire seed. Seedling pubescent, & with glandular hairs; hypocotyl 8-10mm long; cotyledons linear to linear-lanceolate, 11-14 x 1.5mm, acute, glabrous; epicotyl ca.1mm long; the first 4 leaves imparipinnate with 5-9 leaflets, otherwise as in mature leaves.

Chromosome number: not known.

DISTRIBUTION (Fig. 7.67):

D. glandulosa is known from two localities in south-west Western Australia only, i.e. near Kulin and south of Hatter Hill (east of Lake King).

ECOLOGY:

At Kulin *D. glandulosa* is a small shrub of a semi-arid mixed mallee scrub community with *Eucalyptus anceps*, *E. flocktoniana*, *E. calycogona*,

E. eremophila, *E. sheathiana*, *E. erythronema*, mallee form of *E. wandoo*, *Dodonaea bursariifolia*, *Eutaxia* sp., *Daviesia obtusifolia* var. *parvifolia* and *Acacia* aff. *inamabilis*. It grows in red-brown loamy clay with laterite and quartz nodules near the surface.

It appears that *D. glandulosa* flowers in August or September. Mature fruit has been collected in November and December.

AFFINITIES:

D. glandulosa is most closely related to *D. humilis* of South Australia, with which it shares similar thickened, crustaceous capsules bearing glandular hairs, and the stamen apical appendage of a single glandular hair. The two species are easily separated, since *D. glandulosa* has several characters unique in the genus. For instance, it is the only species with glandular hairs on the vegetative parts, with 2-valved, inappendiculate capsules, with strongly recurved, very small oblong leaflets, and it has longer filaments than most species.

SPECIMENS EXAMINED:

WESTERN AUSTRALIA:- Chinnock 4964, 10.6km S of Hatter's Hill, 9.x.1979. fr. (AD).- Chinnock 4965-4966, 9.6km S of Hatter's Hill, 9.x.1979. m.fl./f.fl., immat.fr. (AD).- Newbey s.n., N of Kulin, viii.1970. immat.fr. (PERTH).- Newbey 3427, 1.5ml N of Kulin, 12.ix.1971. mature m.fl. (PERTH).- Newbey 3470, 4ml S of Hatter's Hill, 6.i.1972. fr. (PERTH).- West 3144-3154, 2.3km NW of Kulin on rd. to Corrigin, 29.xi.1978. fr./mature m.fl. (AD).- Wittwer 1454, 40ml W of 90 mile Tank (Daniels-L. King), 17.x.1974. fr./m.fl. (PERTH).

61. *Dodonaea humilis* Endl., Atakta bot. t.31 (1835), Nov. stirp. dec. IV:26 (1839); Miq., Linnaea 18:95 (1844); Mueller, Pl. indig. Col. Vic. 1:89 (1862), p.p. (excl. reference to South-Western Australia); Bentham, Fl. Aust. 1:485 (1863); Mueller, Fragm. 9:86 (1875); Black, Fl. S. Aust. edn 1. 363 (1926); Ewart, Fl. Vic. 740 (1931); Radlkofer, Pflanzenreich IV.165:1403 (1933); Black, Fl. S. Aust. edn 2. 543 (1952); Willis, Hdbk. Pl. Vic. 2:359 (1972).

TYPE: Holotype: F. Bauer's illustration in Endlicher, Atakta bot. t.31 (1835). Probable isotypes: R. Brown 5442, Memory Cove (Bay IX), 22.ii.1802. m.fl./f.fl./fr. (BM,MEL84101).

[*D. boroniaefolia* auct. non G. Don: Tepper, Trans. R. Soc. S. Aust. 3:37 (1880); Mueller, Cens. Aust. Pl. 1:25 (1882), p.p. (as to "S.A." only), Sec. Cens. Aust. Pl. 1:43 (1889), p.p. (as to "S.A." only); Tate, Trans. R. Soc. S. Aust. 12:75 (1889), Hdbk. Fl. Extratrop. S. Aust. 28 (1890); Domin, Biblioth. Bot. 22(89^h):912 (1927), p.p. (as to "South Australia" only); Ewart, Fl. Vic. 739 (1931), p.p. (as to "South Australia" only); Radlkofer, Pflanzenreich IV.165:1387 (1933), p.p. (as to South Australia occurrence only).]

FIGURES: Endlicher, Atakta bot. t.31 (1835)

DESCRIPTION (Fig. 7.69):

Dioecious shrub, 0.1-1m high, spreading. Branches dense, procumbent; branchlets terete or angular, puberulent, usually with some longer hairs as well. Leaves imparipinnate, (0.9-)1.1-2.6(-4.5)cm long (excluding petiole); petiole 1-3(-4)mm long, usually pubescent, rarely glabrous; rhachis winged, 1.5-2.5mm broad, channelled above; lateral leaflets (2-)4-12(14), opposite, obtriangular, obovate to broad-obovate, rarely oblanceolate, concave above, 3-5(-7)-toothed or -lobed at the apex,

(3-)4-7(-8) x (2-)3.5-5(-7)mm, dark green above, paler below, coriaceous, thick, mostly glabrous, sometimes with sparse simple hairs on midvein below, base attenuate to broad-cuneate, margin entire, apex 3-5(-7)-toothed, the teeth acute to obtuse, midvein prominent below, sometimes conspicuous above, lateral venation usually obscure; the terminal leaflet usually elliptic or obovate, usually entire, rarely toothed or divided, 2.5-4 x 2-3mm, otherwise similar to lateral leaflets. Flowers unisexual, in terminal compound inflorescences composed of monads to 3-5-flowered botryoids; pedicels (1.5-)2.5-3.5(-4)mm long, erect, pubescent. Sepals 4, lanceolate-ovate, (1.8-)2-2.8 x 1-1.6(-1.8)mm, acute or obtuse, viscous, sparsely pubescent, often with glandular hairs on the margin, persistent; at anthesis the sepals in male flowers are recurved, in female flowers they are free, erect, imbricate & surrounding the ovary. Stamens in male flowers 8, exceeding the sepals, divergent; filaments 1.2-1.8(-2.3)mm long, glabrous; anther lobes oblong, (2.3-)2.5-2.9 x 0.8-1.2mm, glabrous, with a single sessile gland at the apex of each lobe; apical appendage a single glandular hair to 0.6mm long; stamens in female flowers absent. Ovary in female flowers 4-carpellate, globose to broad-oblong, angled, 0.8-1 x 0.8-1mm, viscous, with sessile glands, often with resin layer; styles 4, connate for almost entire length, usually straight, 6.5-15mm long, separating at the apex into 4 short lobes, the lobes 0.1mm long; in male flowers rudimentary ovary usually present. Capsule 4-lobed, in lateral view oblong, 4.5-6(-7) x (4.5-)5-6mm, crustaceous & thickened, viscous, with dense glandular hairs, red-brown at maturity, base truncate to cordate, apex truncate or emarginate, style base persistent; carpel lunate, transverse-oblong, 4.5-6(-7) x 2-2.5mm; appendage absent; dehiscence septifragal. Seeds 3-5, lenticular, 2-2.4 x 1.7-2mm, black, shiny, with hyaline membrane lifting at the margin; aril absent. Seedling

with puberulent stem & branches, leaves glabrous; hypocotyl 11-15mm long; cotyledons linear, 11-18(-25) x 1.4-1.8mm, acute, glabrous; epicotyl 1-5mm long; the first 2(-4) leaves simple, alternate, sessile, obovate, irregularly toothed at the apex, the teeth acute to obtuse, base attenuate, sparsely pubescent on midrib, the later leaves imparipinnate and as in mature foliage.

Chromosome number: $n = 14$ (West 1291, West 1320, West 1346, West 2016)

TYPIFICATION:

The illustration by Bauer in Endlicher (1835) is the nomenclatural type of *D. humilis* Endl. (no text was published to plate 31 (Stearn, 1947)). However, there is some doubt as to whether the illustration is a holotype or a lectotype. It is not known whether Endlicher based the species on specimen(s) collected by Bauer or on his illustration. There are no Bauer specimens of *D. humilis* at W, in which his herbarium is housed (Riedl, W. pers. comm. 1979), and so until such time as any Bauer collections are located, the illustration is regarded as the holotype. Bauer accompanied Robert Brown on the Flinders Expedition (1801-1805) and his illustrations were mostly based on material collected by or in the care of Robert Brown (BM) (Stafleu and Cowan, 1976). Thus, the specimens collected by Brown now held at BM and MEL, which contain flowers and fruits as in Bauer's illustration, are probably isotypes.

DISTRIBUTION (Fig. 7.69):

D. humilis is endemic to southern South Australia. It occurs on Eyre, Yorke and Fleurieu Peninsulas, in the Upper South East and on Kangaroo Island.

ECOLOGY:

This is a shrub of mallee scrub and often grows on limestone or calcareous soils or sand over limestone. In coastal situations *D. humilis* is found in *Eucalyptus diversifolia* scrub with associated species such as *Eucalyptus rugosa*, *Melaleuca lanceolata*, *Pomaderris* sp., *Correa pulchella*, *Templetonia retusa*, *Beyeria leschenaultii*, *Lepidosperma carphoides*. It also occurs on dune systems (overlying limestones) with *Triodia irritans*, *Senecio glossanthus*, *Rhagodia crassifolia* and *Geijera linearifolia*. In inland mallee scrub communities *D. humilis* grows with *Eucalyptus calycogona*, *E. socialis*, *E. ?oleosa*, *E. brachycalyx* and *Acacia notabilis*.

D. humilis flowers in summer (November to March) and mature fruit are present from August to December.

PUTATIVE HYBRIDS:

D. hexandra x *D. humilis*, see *D. hexandra*.

AFFINITIES:

D. humilis shows most affinities to *D. macrossanii* of Queensland. The two species are similar in leaf shape and capsule characteristics, but can be distinguished on the smaller, hirsute leaves, smaller stamens, solitary, axillary flowers and hirsute capsules of *D. macrossanii*.

D. glandulosa from Western Australia is the only other species in the genus with glandular hairs. This species shows other similarities with *D. humilis* in capsules and leaflet shape.

SPECIMENS EXAMINED: selection only (153 collections examined)

SOUTH AUSTRALIA:- Blaylock 31, Yorke Peninsula, Pondalowie Bay, 10km NW of Stenhouse Bay, 10.x.1965. fr. (AD,MEL).- Cooper s.n., Kangaroo Is., Muston, Pelican Lagoon, xii.1963. fr. (AD).- Copley 4984, Yorke

Pen., southern boundary rd. of Hd. of Carribie, 90km SW of Maitland,
27.viii.1976. f.fl. (AD).- Fagg 479, Eyre Pen., 20ml N of Cummins,
25.xi.1967. m.fl. (AD).- Schodde 556-557, Kangaroo Is., at mouth of
Harriet R., Vivonne Bay, 30.xii.1957. m.fl./f.fl., fr. (AD,CANB).-
Sharrad 335 & 341, Upper South East, 6km W of Malinong, 3.xi.1959. fr.
(AD).- West 1314-1319, Kangaroo Is., Flinders Chase N.P., 0.5km N of
Rocky R. mouth, 29.xii.1975. m.fl./f.fl., fr. (AD).- West 1348-1350,
Murray mallee region, nr. Monarto, 0.5km S of "Mallee View" H.S.,
27.ii.1976. m.fl./f.fl.,fr. (AD).- West 1555-1561, Yorke Pen., Innes
N.P., 5km NNE of Pondalowie Bay, 1.5km E of Royston Head, 9.viii.1976.
mature m.fl./immat.fr. (AD).- Wheeler 488, Eyre Pen., 7km NW of Bascombe
Well H.S., 1.x.1967. fr. (AD,NSW).- Wilson 987 & 995, Murray Region,
Chauncey's Line, 15km SW of Murray Bridge, 2.xii.1958. m.fl./fr. (AD).

EXCLUDED SPECIES

Dodonaea discolor Desf., Catal. pl. Hort. Paris edn 3. 457 (1829),
nom. nud. = *Beyeria viscosa* Miq., Ann. Sci. Nat. Bot. Ser. 3. 1:350,
t.15 (1844).

Dodonaea hispidula Endl., Atakta bot. t.30 (1835) = *Distichostemon*
hispidulum (Endl.) Baill., Hist. Pl. 5:411 (1874).

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