A MONOGRAPH OF THE
FAMILY ATHEROSPERMATACEAE R.Br.

by

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Volume I —— TEXT

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I do not wish that my thesis,
"A Monograph of the family
Atherospermataceae R.Br.", be
made available for loan or
photocopying until after the
expiry of the two year period
following the award of my degree.

Richard Schodde
26 Sept., 1969

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Volume I

SUMMARY

A taxonomic study has been made of the genera and species placed by recent monographers in the tribe Laurelieae or subfamily Atherospermoideae of the family Monimiaceae (Angiospermae: Laurales); characteristics of gross morphology, supplemented by those of the secondary xylem, pollen form, and ecology, have been used. These characteristics in combination are here compared for all genera for the first time; many of the characteristics have not been described before, particularly in the genera Laureliopsis, Nemuaron, and Dryadodaphne.

It is concluded that the genera represent a group which is taxonomically closely knit and equivalent in its combined features to other families such as Calycanthaceae, Gomortegaceae, or Lauraceae within the Laurales, on grounds of their tree habit, secondary xylem vessel and ray form and pitting, decussate leaf arrangement, essentially monopodial-dichasial inflorescence, bisexual and unisexual flowers, choritepalous basically tetramerous perianth, biglandular stamens with valvular dehiscence, syncolpate pollen, solitary erect ovules on a basal placenta, and perigynous lignified fruiting hypanthium enclosing plumose long-styled nutlets. The group is distinguished as a family, Atherospermataceae R.Br. Its characters and affinities are discussed, in which connection the family is shown to be more closely related to the Gomortegaceae and through it to the Lauraceae than to the Monimiaceae.

Its two tribes, Atherospermateae and Laurelieae Pax are redefined according to the diameter and frequency of secondary xylem pores, hair form, arrangement of floral parts on the hypanthium rim, form of the stamen apex and staminal glands, and construction of the fruiting hypanthium. The size of the inflorescence and presence of flower-enveloping bracts, used by previous revisers for grouping the genera, are shown to have little taxonomic significance.

Seven genera and sixteen species are recognised: *Atherosperma* Labill. with one species, *Daphnandra* Benth. with six species, *Doryphora* Endl. with two species, *Dryadodaphne* S.Moore with three species, *Laurelia* Juss. with two species, *Laureliopsis* Schodde with one species, and *Nemuaron* Baill. with one species. One genus (*Laureliopsis*) and five species (*Daphnandra apatela*, *D. johnsonii*, *D. melasmena*, *Dryadodaphne pterandrica*, and *D. trachyphloia*) are described as new. *Daphnandra dielsii* Perk. and *Nemuaron humboldtii* Baill. are treated as taxonomic synonyms of *Daphnandra repandula* (F.Muell.)F.Muell. and *Nemuaron vieillardii* (Baill.)Baill. respectively; the various species proposed by Gandoger in *Atherosperma* are shown to be unfounded; and *Doryphora austro-caledonica* Seem. is excluded from the family. Infraspecific taxa are distinguished in *Atherosperma moschatum* Labill. (two subspecies), *Doryphora sassafras* Endl. (two varieties), and *Dryadodaphne novoguineensis* (Perk.)A.C.Smith (two subspecies, two varieties).

Fossil records of the family are reviewed and discussed in relation to present-day distribution and ecology. Assessments are made of the unspecialised and derived characters in the family, and of phylogenetic relationships between the genera. It is concluded that (1) *Laureliopsis*, confined to primary temperate rainforest, is the most primitive member of the family whereas *Daphnandra*, adapted to life in subtropical rainforest seres, is the most advanced, and (2) there are two arcs of distribution, one subantarctic for the Atherospermateae in south-east Australia and Chile, and the other tropical montane-subtropical for the Laurelieae, extending from New Guinea (*Dryadodaphne*) into eastern Australia on one side, and New Caledonia, New Zealand, and Chile on the other.

STATEMENT OF ORIGINAL WORK

The thesis contains no material which has been accepted for the award of any other degree or diploma in any University; nor does it include, to the best of my knowledge, any information previously published or written by any other person, except where due reference is made in the text.

Richard Schodde

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I. INTRODUCTION

The Atherospermataceae, a family of evergreen trees of lauralean affinities, are characterised by opposite exstipulate toothed leaves with ethereal often aromatic oil cells, an actinomorphic choritepalous perianth, an androecium comprising biglandular stamens with valvular dehiscence and staminodes, syn (= di) -colpate pollen, numerous free carpels with solitary erect basally-attached ovules, Polygonum-type embryo sac, small hairy long-styled nutlets with albuminous endosperm that are variously enclosed by a lignified perigynous fruiting hypanthium, and an unspecialised heteroxylous secondary xylem that apparently lacks wood parenchyma. They have a geographical and general ecological distribution pattern like that of *Nothofagus* and the Winteraceae, occurring at present in the cooler rainforests of montane New Guinea, New Caledonia, Australia, Tasmania, New Zealand, southern Chile, and western Patagonia. They are represented by the following seven* genera and sixteen* species: *Atherosperma* Labill. (monotypic in south-eastern Australia and Tasmania), *Daphnandra* Benth. (six species in eastern Australia), *Doryphora* Endl. (two species in eastern Australia), *Dryadodaphne* S.Moore (two species in New Guinea and one in north-eastern Queensland), *Laurelia* Juss. (one species in New Zealand and one in southern Chile), *Laureliopsis* Schodde (monotypic in southern Chile and

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* Including those described in the present study.

western Patagonia), and Nemuaron (monotypic in New Caledonia).

Since the description of the first two genera, Pavonia Ruiz (1794) (= Laurelia) and Atherosperma (1806), the group has been recognised taxonomically; it was first distinguished as a family by Robert Brown (1814). Yet, despite its peculiarities, it has usually been treated as an integral member of the pan-tropic family Monimiaceae, as was done for example by de Jussieu (1809) when first establishing that family.

The group has been accepted in the Monimiaceae, largely in response to prevailing taxonomic opinion, by Möller (1882), Hobein (1888), Welch (1929), and Garratt (1934) who examined anatomical features of the bark, stems, leaves, and secondary xylem of several genera and whose work is summarised in Solereder (1899) and Metcalfe and Chalk (1950), by Henry (1949) and various authors in Manske (and Holmes) (1954, 1960, 1967) who reviewed the alkaloids of several species and Bick and co-workers (see chapters VIII.1, XIII.1, XIV) in their investigations of the alkaloids of Australian species, by Petrie (1912), Scott (1912), Jones and Smith (1924a,b), and Penfold (1921) when assessing the essential oils of several Australian species, by Sastri (1963) and Sampson (1967) who studied micro-and mega-sporogenesis and embryological features in two species, and by Müller-Stoll and Mädel (1962) and Rüffle (1965) who reviewed wood and leaf fossils ascribed to it. Of the essentially taxonomic assessments promoting this opinion, the most important have been those of J. D. Hooker (1855), Tulasne (1855), Baillon (1868, 1869), Bentham (1870, 1880 in Bentham and Hooker), Hobein (l.c.), Perkins (1901 with Gilg, 1911, 1925), Garratt (l.c.), Money et al. (1950), Müller-Stoll and Mädel (l.c.), and Ehrendorfer et al. (1968). These authors invariably treated the Atherospermataceae as a tribe or subfamily of the Monimiaceae. Its genera, moreover, were often associated with the large central American genus Siparuna Aubl. and its several congeners. The particular characters common to the Atherospermataceae and Siparuna group on which this relationship has been based are the relatively narrow xylem rays, usually opposite leaves, valved anthers, urceolate or cupular fruiting receptacle, erect ovule, and similar chromosome base numbers.

The resulting arrangements of all these genera into various subfamilies and tribes according to what character or groups of characters were considered important by each reviser has made the taxonomic literature of the Monimiaceae rather bewildering. All too often they have been based on recombinations of characters used by earlier authors rather than on any found through new lines of morphological research, with the consequence that many of the early gaps in knowledge, misinformation, and inaccuracies about them have been perpetuated. It is little value to review here in detail the complexity of these taxonomic arrangements, especially as they are discussed in more detail in appropriate sections of the text and are rarely confirmed, even in part. Suffice to say that the detailed anatomical and morphological investigations of Garratt (l.c.) and Money et al. (l.c.) support the taxonomic unity of the Atherospermataceae as defined here while indicating that *Siparuna* and its congeners are not at all closely related.

Yet while previous revisers have been preoccupied with the relationships between the Atherospermataceae and the various taxa included within the Monimiaceae, they have largely overlooked the remarkable features of the monotypic Chilean family, Gomortegaceae, many of which resemble closely those of the Atherospermataceae. *Gomortega*, which is rare in herbaria (cf. Hutchinson 1959), has been allied conventionally with the Lauraceae. Only Baillon (1869) and Stern (1955) have stressed affinities between *Gomortega* and the Monimiaceae, and then only in a general way without particular reference to the Atherospermataceae.

The taxonomic history of the genera recognised in the Atherospermataceae has not been so involved. Following the description a third genus, *Doryphora* (1837), Hooker (l.c.) united all three under *Athero-*

sperma, in which he was followed by Baillon (1868) in respect of *Laurelia* but not *Doryphora*. Baillon (1873) also recognised a fourth genus, *Nemuaron*, from New Caledonia. Both Tulasne (l.c.) and Bentham (l.c.) again distinguished *Atherosperma*, *Laurelia*, and *Doryphora*, and Bentham, whose understanding of the generic limits in the family has proved well founded, accepted *Nemuaron* and established a fifth, *Daphnandra*. Perkins (l c.) and all later revisers have corroborated Bentham's treatment of the genera, concerning which A.C.Smith (1941) has commented that "these genera, although small, are well marked and will presumably seem quite acceptable to future monographers". This assessment of current taxonomic opinion is borne out by the present study. The characters and relationships of *Dryadodaphne*, the only other genus so far described in the family, have been discussed by A.C.Smith (l.c., 1942) and L.S.Smith (1958).

The general revisions of Tulasne (Monographia Monimiacearum 1855), Bentham (Flora Australiensis 1870), and Perkins (Pflanzenreich 1901 with Gilg, 1911) have provided the basis for the various systematic treatments of the species of the family in the literature. More recently, L.S.Smith (l.c.) has reviewed briefly species of *Doryphora* and *Dryadodaphne* in Australia and New Guinea. Nevertheless, apart from the few early described species such as *Atherosperma moschatum* Labill., *Doryphora sassafras* Endl., and *Laurelia novae-zelandiae* A Cunn., which often or only occur where there are no other members of the family, the majority of species have been poorly described and understood, and their characters and affinities much confused. Testifying to this are two species of *Daphnandra*, *D. micrantha* (Tul.)Benth. and *D. repandula* (F. Muell.)F. Muell., which at one time or another were placed under *Atherosperma*, despite closer similarities to *Doryphora* in vegetative and fruit characters; *Doryphora aromatica* (F.M. Bail.)L.S. Smith was regarded as a species of *Daphnandra*[*] until Smith (l.c.) recently recognized the incongruities in the flower and nutlets; and *Daphnandra tenuipes* Perk. and the distinctive *Laureliopsis philippiana* (Looser) Schodde have been united under *Daphnandra micrantha* and *Laurelia sempervirens* (Ruiz & Pav.)Tul. respectively. Although *Laureliopsis philippiana* has been known since 1857, it does not ever appear to have been recorded that its flowers are predominantly bisexual or that its staminodes elongate to surround the fruiting gynoecium as in *Atherosperma*.

The shortcomings in existing taxonomic treatments of the Atherospermataceae have resulted, in summary, from inadequate knowledge of the range and variation of the flower and fruit features of the family, and the use of few, often single, characters as critical taxonomic criteria. This, undoubtedly, has been largely the consequence of having very few and inadequately documented specimens available for study. Atherospermataceous plants occur in regions and environments that are remote and of difficult access, and it is not surprising that

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[*] Bailey (1886) even commented that the species might belong to *Atherosperma*!

they were particularly scarce in collections before the turn of the century; some genera, notably Laüreliopsis and Nemuaron, are poorly represented even today. The last general revisions were those of Perkins (l.c.). Much new material has been accumulated since then, particularly from the previously little explored regions of New Guinea and the Australian rainforested areas.

Based on presently available herbarium material and the observed ecological and geographical distribution of all genera and species occurring in New Guinea, New Caledonia, Australia, and New Zealand, in conjunction with a re-examination of the secondary xylem and pollen morphology of all genera and most species, a taxonomic revision of the Atherospermataceae is presented here.

The use of new names and new combinations in this thesis does not constitute valid publication.

II. MATERIALS, METHODS, and DEFINITIONS

1. Materials and Methods

(a) Herbarium

The study of herbarium material was begun in a preliminary way at the herbarium of the Division of Land Research, C.S.I.R.O., Canberra (CANB), and completed in detail at the State Herbarium of South Australia (AD).

Herbarium Collections

Relevant collections were examined and annotated from the following herbaria which are abbreviated according to Lanjouw and Stafleu (1964): A, AD, B, BAB, BM (p.p.), BO, BRI, CANB, CANTY, CBG, CHR, GH, K (p.p.), L, LAE, LIL, LY (p.p.), MA (p.p.), MEL, NSW, OXF (p.p.), P (p.p.)*, SGO (p.p.)*, SI, SING, UC, US, WELT. Specimens were also seen from the following institutions not listed by Lanjouw and Stafleu (l.c.): the herbarium, Atherton Office, Department of Forestry, Queensland (ATHERTON); the herbarium, Belangry State Forest Office, Forestry Commission of New South Wales (BELANGRY); the herbarium, Botany Dept., Canterbury University, Christchurch, New Zealand (CANU); the herbarium, Coffs Harbour Office, Forestry Commission of New South Wales (COFFS); the herbarium,

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* Owing to their late arrival, collections of Laurelia sempervirens and Laureliopsis philippiana from these herbaria are not included on distribution maps for these species.

Forestry Research Institute, Canberra, Australia (FRI); the herbarium, Office de la Recherche Scientifique et Technique Outre-mer, Nouméa, New Caledonia (NOUMÉA). Requests seeking the loan of collections from the Naturhistorisches Museum, Wien, Austria (W), the herbarium of the University of Tasmania, Hobart (HO), and several South American herbaria were unsuccessful. All pre-war collections of Atherospermataceae in herb.W, like many in herb. B, appear to have been lost as a result of World War II (Prof. Dr.K.H. Rechinger, pers.comm.).

The types of all validly published names referred to genera of the Atherospermataceae have been seen except for those of Daphnandra dielsii Perk. and Theyga chilensis Mol. The type specimen of Daphnandra dielsii in herb. B has been destroyed and no duplicates have been traced; Molina's collections also appear to have been lost (see under Laurelia sempervirens). Photographs of type material of Atherosperma integrifolium A.Cunn., Doryphora sassafras Endl., Laurelia novae-zelandiae A.Cunn., Laurelia serrata R.Phil., and Pavonia sempervirens Ruiz & Pav. in herb. K, of Doryphora austro-caledonica Seem. in herb. BM, of Doryphora? vieillardii Baill. in herb. P, and of Laurelia serrata R.Phil. and Pavonia sempervirens Ruiz & Pav. in herb. US were also available to supplement the type collections loaned for study. In several cases, the photographs proved necessary for holo- and lecto-typification.

For purposes of comparison, herbarium material of critical taxa related to the Atherospermataceae was available from several herbaria, as follows: Chimonanthus (Calycanthaceae) - 1 collection, with fruit (AD); Glossocalyx (Siparuna group) - 1 collection, with flowers (SING);

Gomortega (Gomortegaceae) - 3 collections, 1 with flowers (US); *Hortonia* (Monimiaceae alliance) - 3 collections, 2 with flowers, 1 with fruit (BO); Lauraceae - many collections in flowers and fruit (AD, CANB); Monimiaceae - many collections in flowers and fruit (AD, BO, CANB, L, LAE, SING); *Peumus* (Monimiaceae alliance) - 3 collections, 2 with flowers, 1 with fruit (BM, SGO); *Siparuna* (*Siparuna* group) - 10 collections, all with flowers, 2 with fruit (BO, BRI, MEL, NSW, SI).

Details of the series of specimens examined are summarised under appropriate sections in the treatment of the species in the text and are enumerated in full in index I.

Unless it is stated otherwise, the descriptions of all taxa are drawn from herbarium material except that characters of the habit, bark, wood, and odour, and the colour of leaf, flower parts, and fruiting hypanthium are taken from life. Measurements of all flower parts are taken from flowers of dried herbarium specimens soaked in a mixture of water and household detergent. It was found that the organs of flowers soaked in this way almost regained the size of their counterparts in living flowers. The colours of dried leaves have been quoted only when they are rather constant on a species.

Secondary Xylem

Microscopic examination of the secondary xylem of all genera and most species of the Atherospermataceae, and of related taxa, *Endiandra* (Lauraceae), *Gomortega* (Gomortegaceae), *Hedycarya* (Monimiaceae), *Peumus* (Monimiaceae), Siparuna group, Trimenia (Trimeniaceae), and Wilkiea (Monimiaceae).

Wood for study was first boiled in water for about two hours to soften it and remove the air. It was subsequently sectioned on a sledge microtome, model 860, manufactured by the American Optical Company. Transverse sections were cut at 15-20μ thickness and radial and tangential longitudinal sections at 10-12 μ . Sections were stained with aqueous safranin, dehydrated in ethanol, and mounted in Canada balsam. They were examined with a light microscope at magnifications of 100x and 400x. Photo-micrographs of wood sections were taken with a Zeiss (Oberkochen) automatic photomicroscope.

An analysis of variance of the secondary xylem vessel diameters and vessel frequency per unit area of transection between and within all genera of the family was calculated on three collections of each species recorded in table II, using the inner tangential diameters of 50 randomly chosen vessels and the numbers of vessels (between 50 and 200) counted in four randomly chosen microscopic fields. The results are summarised in chapter IV.2.

Pollen Grains

Features of pollen grain morphology were investigated in all genera and compared with those in members of the related groups, Calycanthaceae (*Calycanthus*), Lauraceae (*Endiandra*), Monimiaceae (*Hedycarya*), *Siparuna* group (*Siparuna*), and Trimeniaceae (*Trimenia*). The material examined is held in the slide collection at the Department of Geography, Research School of Pacific Studies, Australian National University. Vouchers and other reference data for the pollen collections studied are given in index III.

Pollen for examination was prepared by acetolysis and mounted unstained in silicone oil (AK 2000). Descriptions are based on observations and measurements made using a Zeiss (Oberkochen) automatic photomicroscope with planapochromatic objectives 25/0.63 and 100/1.32 and anisol immersion fluid at magnifications of 400x and 1600x. Photomicrographs were taken with the same instrument. Examination of pollen tetrads was made on unacetolysed material from young anthers preserved in FAA.

All pollen grain dimensions for the genera of the Atherospermataceae cited in the text are taken from averaged measurements of not less than 10 grains.

Alkaloids

New information included in the text on the alkaloids of the species of Daphnandra is taken from analyses performed by Dr.I.R.C. Bick, Department of Chemistry, University of Tasmania, and collaborators on material of these species selected or collected by me for such investigation.

(b) Field

All species and infraspecific taxa were observed and collected in the field, except Dryadodaphne novoguineensis subsp. occidentalis in western New Guinea and Laurelia sempervirens and Laureliopsis philippiana in Chile. The species of Dryadodaphne in New Guinea (at the Lai-Lagaip Divide, Western Highlands District; Spreader Divide and Angabena Ridge, Morobe

District; Subitana, Central District), Nemuaron vieillardii in New Caledonia (at Table Unio), and Laurelia novae-zelandiae in New Zealand (at Kaitoke Water Reserve and Lake Ponui) were only seen locally on single occasions during visits to those islands.

The Australian species and forms have been examined over most of their geographic range at various times of the year. Areas in which field studies were carried out were the Mt. Lewis range and Atherton Tableland (north-east Queensland), Lamington plateau (south-east Queensland), Whian Whian State Forest (far north-east New South Wales), Coffs Harbour area - Dorrigo plateau (north-east New South Wales), Oakes State Forest (north-east New South Wales), Belangry, Dingo, Doyles River, and Mt Boss State Forests (lower north-east New South Wales), the Barrington Tops (east New South Wales), the remnant rainforests of the Illawarra district and Robertson plateau (south-east New South Wales), Clyde Mountain and Currowan State Forest (south-east New South Wales), Brown Mountain (south-east New South Wales), Donna Buang range (south-east Victoria), and Mt Barrow, Mt.Field National Park, and the Hastings Caves area (Tasmania).

As a result of such field studies, maps have been prepared showing the ecological occurrence of all species over much of their geographic range The density of the symbols for any species on the maps gives only an approximate indication of the frequency of that species in forest at the site of observation; no census of trees was taken.

Particular trees of Atherosperma moschatum at Brown Mountain and Doryphora sassafras in Currowan State Forest in south-east New South Wales were kept under regular monthly inspection, during the seasons 1963-4 and

1964-5 for the purpose of recording the flowering and fruiting cycles in these species.

A special effort was made to record features of the living plant, such as habit, bark and wood texture and colour, leaf colour, flower and fruit colours, and seedlings, for all species collected.

In addition to the collection of herbarium specimens, flowering and/or fruiting material of all species seen, except *Dryadodaphne trachyphloia*, was preserved in FAA. Wood samples were taken from *Daphnandra apatela*, *D. melasmena*, *D. micrantha*, *D. repandula*, *D. tenuipes*, *Doryphora aromatica*, *D. sassafras*, *Dryadodaphne novoguineensis* var. *novoguineensis*, *D. novoguineensis* var. *macra*, *D. pterandrica*, *D. trachyphloia*, and *Nemuaron vieillardii*. Bark and leaf material of *Daphnandra apatela*, *D. repandula*, *D. tenuipes*, *Doryphora aromatica*, *D. sassafras*, and *Dryadodaphne trachyphloia* was collected also for analysis of alkaloids.

The first set of herbarium collections and all FAA material is lodged in herb. CANB, and the first set of wood samples with the Division of Forest Products, C.S.I.R.O., Melbourne, Australia.

2. Definitions

Organs, Tissues, Distribution, and Ecology

The terminology used for habit and bark characters is adapted from Corner (1952). The term "bole" is used for that section of tree trunk devoid of limbs and therefore excludes the crown.

Terms used to describe characters of the secondary xylem and other anatomical features have been drawn from the texts of Metcalfe and Chalk

(1950), Money et al. (1950), and Eames and MacDaniels (1951). Those for xylem rays havebeen taken from Kribs (1935).

Leaf sizes are described generally in the text as microphyllous, notophyllous, and mesophyllous, according to the definitions by Webb (1959). Most leaves in the family fall within the microphyll and notophyll range. Notophyllous leaves, larger than microphylls, have a length range of $7\frac{1}{2}$-$12\frac{1}{2}$ cm (Webb l.c.). The terminology used for leaf shapes, and indeed all plane organ shapes in the family, follows the chart from the Systematics Association Committee (1962) and Lawrence (1951), except that the term "lanceate" is used in the sense advocated by Baranov (1965). The numbers of main nerves per leaf quoted in the descriptions represent the number on one side of the midrib only. The terms describing stormates are taken from Metcalfe and Chalk (1950).

The definitions of inflorescence type are taken from Lawrence (1951, f.3). The number of flowers quoted per inflorescence in the formal descriptions is the perfect number and does not admit the frequently fewer flowers found in practice that result from obvious damage or abortion of buds.

The term "pistilliferous" is used here to refer to functionally female flowers. It is used in preference to "pistillate" or "carpellate" because these flowers often bear functional stamens while staminate flowers, wherever they occur in the family, never show any vestiges of carpellary structures.

The term "hypanthium" has been used for the floral torus according to the definition given by Lawrence (1951) which assumes that the "appendicular units", perianth and androecium, have contributed significantly to its structure. That part of the hypanthium referred to as the "rim" in the formal descriptions and elsewhere bears specifically all perianth and androecium parts.

The paired staminal appendages on the functional stamens in all species of the family were called staminodes by Money et al. (1950). They are here designated "staminal glands", as was done by Sampson (1967), to avoid confusion with the other staminodes in the flowers of atherospermataceous plants. The new term "batilliform" (spade-shaped) has been introduced to describe the characteristic shape of the staminodes in species of several genera such as *Daphnandra*, *Laurelia*, and *Nemuaron*. It is intended to suggest the more acute shape of a spade as on playing cards, rather than the more square shape of the conventional digging implement.

For most pollen characters, the descriptive terms used are taken from Faegri and Iversen (1964); those describing tetrad arrangement, LO-analysis, and symmetry are taken from Erdtman (1943, 1952).

The terms used to define ovule orientation follow Bocquet and Bersier (1960). The term "achene" used by most previous authors for the small plumose monocarpellary uniovulate fruitlets of all members of the family is replaced here by "nutlet" (cf. Jackson 1928). "Achene" has been applied ambiguously in much of the botanical literature to both the one-seeded fruitlets of an apocarpous gynoecium (*Ranunculus*) and an inferior syncarpous ovary (Asteraceae).

Localities in the text are cited in the geographic order of north to south, west to east. Details given of distribution and dates of flowering and fruiting for each species are based mainly on localities and dates from all herbarium specimens seen and field observations and are not unduly influenced by previously published information. The terms subtropical rainforest, submontane rainforest, and temperate rainforest are used in the text in general accordance with the definitions given by Warming (1925), Schimper and v. Faber (1935), Baur (1957), Richards (1952), Cockayne (1958), and Webb (1959).

Taxa

In the text, the term "Monimiaceae alliance" is used collectively for all those taxa, Amborellaceae, Trimeniaceae, and Monimiaceae comprising *Hortonia*, *Peumus*, Monimiaceae (as Monimioideae), Atherospermataceae (as Atherospermoideae), and the *Siparuna* group (as Siparunoideae), treated by Money et al. (1950) in their classic review of the morphology and relationships of the Monimiaceae. The name Monimiaceae is reserved for those genera included in the subfamily Monimioideae by Money et al. (l.c.), excluding *Peumus*.

The term "lauralean" is used for those taxa incorporated within the order Laurales by Cronquist (1957), Hutchinson (1959), and Takhtajan (1959), and suborder Laurineae by Thorne (1968). The families included are Austrobaileyaceae, Calycanthaceae, Gomortegaceae, Hernandiaceae, Lauraceae, the Monimiaceae alliance, and several others.

The term "woody ranalean" is used as it was by Money et al. (1950) for those plant groups characterised by oil cells in their tissues, actinomorphic choritepalous flowers with parts in spiral or cyclic arrangement, apocarpous gynoecia, and unspecialised secondary xylem. They have been included in the orders Polycarpicae (Eichler 1878, Warming and Möbius 1929, Wettstein 1935, Skottsberg 1940, and Takhtajan 1959), Anonales-Ranales (Hallier 1912), Ranales (Bessey 1915, Rendle 1952, Pulle 1938, Benson 1957), Magnoliales (Gundersen 1950, Soó 1961, Buchheim 1964), and Annonales (Thorne 1968).

Species and genera of other families associated taxonomically, geographically, and floristically with members of the Atherospermataceae are usually cited in the text without authors because the accuracy of their names has not been checked.

Arrangement of Taxa

The tribes and genera of the Atherospermataceae are arranged in the text according to their relationships as outlined in chapter XVI. The arrangement of species follows the same sequence.

The complex and variable shape and arrangement of the bracts, bracteoles, perianth, and androecium in the family, and the inclusion of secondary xylem and pollen grain features have required lengthy descriptions for the family, genera, and species. In order to avoid unnecessary repetition in species descriptions, a section has been added to the descriptions of polytypic genera enumerating a number of general features common to their species. For practical purposes, diagnoses crystallising the diagnostic characters of the family and species have also been added.

Such procedures create a problem for the description of monotypic genera in which generic and species characters are more-or-less indistinguishable. In these cases, the generic description has been prepared so as to be comparable with those of the polytypic genera of the family; it also represents the diagnosis of the species. The data that would otherwise be included in the section of additional characters under the generic descriptions of the polytypic genera are incorporated in the detailed species description.

III. ATHEROSPERMATACEAE* R.Br.

Atherospermataceae* R.Br. in Flinders, Voy.Terr.Austral. (1814)533 "Atherospermeae"; [Juss., Dict.Sc.Nat. 32(1824)451 "Atherospermeae" pro syn. Monimiacearum] [n.v.]; Lindl., Intr.Nat. Syst.Bot. (1830)29 "Atherospermeae", ed.2,(1836)189 "Atherospermaceae" [n.v.]; A.Cunn., Ann.Nat.Hist. 1(1838)380 "Atherospermeae"; Meisn., Pl.vasc.gen. 1(1841)324, 2(1841)236 "Atherospermeae"; Raoul, Choix Pl.N.-Zél. (1846)42 "Atherospermeae"; Lindl., Veg.Kingd. ed.3,(1853)300 "Atherospermaceae"; Pichon, Bull. Mus.Hist.Nat.Par.II, 20(1948)384 p.p.; Lemée, Dict.gen.phan. (suppl.) 9(1951)15 p.p.; Bullock, Taxon 7(1958)7 "Atherospermaceae"; Buchheim, Willdenowia 3(1963)375 p.p.; Good, Geogr. Fl.Pl. ed 3,(1964)64 p.p. "Atherospermaceae"; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7,(1966)104 p.p.

TYPE GENUS: Atherosperma Labill.

Monimiaceae-Atherospermatoideae (R.Br.)Endl., Gen.Pl. (1837)314 "Atherospermeae"; id., Enchir.Bot. (1841)195; id., Gen.Pl.

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* Because the greek neuter noun "sperma" is not latinised as "spermum" in Atherosperma, and its stem is "spermat" (cf. Stearn 1966, p.82), the family name is spelt Atherospermataceae, in accordance with art. 18, I.C.B.N. 1966. The subfamily and tribe names are formed in the same way.

suppl.2,(1842)35 "Atherospermeae"; Hook.f., Fl.Tasm. 1(1855)11 "Atherospermeae"; Pax, Pflzfm. 3,2(1889)96,97,102,103,104 p.p. "Atherospermoideae"; Perk., Bot.Jb. 25(1898)547 p.p. "Atherospermoideae"; Perk. & Gilg, Pflzr. 4(1901)3,7,9,14,73 p.p. "Atherospermoideae"; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80 "Antherospermoideae"; Perk., Gattung.Monim. (1925) 4,5,9,15,47 p.p. "Atherospermoideae"; Lemée, Dict.gen.phan. 1(1929)447, 2(1930)501,726, 3(1931)970, 4(1932)673 p.p. "Athérospermoïdées"; Garratt, Trop.Woods 39(1934)22,23,27 et seq. p.p. "Atherospermoideae"; A.C.Smith, J.Arn.Arbor. 22(1941)251, 23(1942)442 p.p. "Atherospermoideae"; Money, Bailey, & Swamy, J.Arn.Arb. 31(1950)381 et seq. p.p., 400 "Atherospermoideae"; Lemée, Dict.gen.phan. (suppl.) 9(1951)107 "Athérospermoïdées; L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)49 "Atherospermoideae"; Müller-Stoll & Mädel, Trans.Geol.Soc.S.Africa 65(1962)96 "Atherospermoideae"; Buchheim in Melchior, Syllab.Pflzfm. ed.12,2(1964)122; Hutchinson, Gen.Fl.Pl. 1(1964)113,120 p.p. "Atherospermoideae"; Rüffle, Geol. Jahrg. 1(1965)98 "Atherospermoideae"; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342 "Atherospermoideae"; Thorne, Aliso 6(1968)59.

Monimiaceae-Atherospermateae (R.Br.)Juss., Dict.Sc.Nat. 32(1824)533 "Atherospermeae" [n.v.]; Schnizlein, Icon. 2(1849)n.105 "Atherospermeae"; Gay, Fl.chil. 5(1851 or 1852)353 "Aterospermeas"; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)277,294,414

"Atherospermeae"; C.Muell.in Walp., Ann.Bot. 4(1857)83,115 "Atherospermeae"; F.Muell., Pl.Vict. 1(1860)22,24 "Atherospermeae"; Seemann, Fl.Viti. (1867)205 "Atherospermeae"; A.DC., Prod. 16,2(1868)642,674 "Atherospermeae"; Baill., Adansonia 9(1869)133 "Athérospermées"; id., Hist.Pl. 1(1869)317,327, 330 "série dès Atherosperma, Athérospermées"; id., Adansonia 10(1873)350 "Athérospermées; id., Dict.Bot. 1(1877)310 "Athérospermées"; Benth. in B.& H., Gen.Pl. 3(1880)138,139 p.p. "Atherospermeae"; Baill., Dict.Bot. 2(1886)468 "Athérospermées"; Hobein, Bot.Jb. 10(1888)64,73 p.p. "Atherospermeae"; Baill., Dict.Bot. 3(1891)423 "Athérospermées"; Lesquereux, U.S.Geol. Surv.Monogr. 17(1892)108; Solereder, Syst.Anat.Dicot. (1899) [transl.Boodle, Fritsch, & Scott, 2(1908)699]; F.M.Bail., Queensl.Fl. 4(1901)1288 "Atherospermeae"; Stapf, Curtis Bot. Mag. 135(1909) t.8279 "Atherospermeae"; F.M.Bail., Compr.Cat. Queensl.Pl. (1913)419 "Atherospermeae"; Welch, J.Proc.Roy.Soc. N.S.Wales 62(1929)362,363 "Atherospermeae"; Metcalfe & Chalk, Anat.Dicot. 2(1950)1143 "Atherospermoideae".

Monimiaceae-Achaeniophoreae* Tul., Arch.Mus.Hist.Nat.Par. 8(1855) 294,414 "Achaeniophorae" [nom.illeg*.]; C.Muell in Walp., Ann. Bot. 4(1857)83,115 "Achaeniophorae"; [A.DC., Prod. 16,2(1868) 674 "Achaeniophorae" pro syn. Atherospermatearum].

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* Proposed as an alternative name for the tribe Atherospermateae, and superfluous; I.C.B.N. 1966, art. 63.

Monimiaceae-Laurelieae Pax emend. Perk. & Gilg, Pflzr. 4(1901)14,73 [nom.illeg.*]; Stapf, Curtis Bot.Mag. 135(1909) t.8279; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80; Perk., Gattung.Monim. (1925)15,47; Lemée, Dict.gen.phan. 1(1929)447, 2(1930)501,726 "Lauréliées"; Garratt, Trop.Woods 39(1934)23; A.C.Smith, J.Arn.Arbor. 22(1941)251; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)381 et seq., text-f.11; Lemée, Dict.gen.phan. (suppl.) 9(1951)107; "Lauréliées"; Croizat, Man.Phytogeogr. (1952)281.

Monimiaceae Juss., Ann.Mus.Hist.Nat.Par. 14(1809)133 p.p. "Monimieae"; J.B.Muell., Bot.Wörterb.(1841)285 p.p. "Monimieae"; Hook.f., Fl.N.Zel. 1(1853)218 p.p.; Hook.f. & Thoms., Fl.Indica 1(1855) 164 p.p.; Hook.f., Handb.N.Zeal.Fl. 1(1864)239 p.p.; Seemann, Fl.Viti. (1867)205 p.p.; Benth., Fl.Austral. 5(1870)282 p.p.; F.Muell., Nat.Pl.Vict. 1(1879)20 p.p. "Monimieae"; Woolls, Pl. Indig.Neighbour. Sydney (1880)9 p.p.; F.Phil., Cat.Pl.Vasc. Chil. (1881)264 p.p.; F.Muell., Syst.Cens.Austral.Pl. 1(1882)3 p.p. "Monimieae"; C.Moore, Cens.Pl.N.S.Wales (1884)58 p.p.; F.Muell., Key Syst.Vict.Pl. 2(1885)6, 1(1887-1888)3,25,124 p.p. "Monimieae"; Bancroft, Proc.Linn.Soc.N.S.Wales 4(1889)1061 p.p.; F.Muell., Sec.Syst.Cens.Austral.Pl. 1(1889)5 p.p.; O.Kuntze, Rev.Gen. 2(1891)568 p.p.; Moore & Betche, Handb.Fl.N.S.Wales (1893)14 p.p.; O.Kuntze, Rev.Gen. 3(1898)276 p.p.; Solereder, Syst.Anat.Dikot. (1899) [transl.Boodle, Fritsch, & Scott,

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* Superfluous name: I.C.B.N. 1966, art.63.

2(1908)699 et seq.] p.p.; Deane, Rec.Geol.Surv.Vict. 1(1902) 17,27 p.p.; Rodway, Tasm.Fl. (1903)164 p.p.; Cheesem., Man. N.Zeal.Fl. (1906)598 p.p.; Dixon, Pl.N.S.Wales (1906)14,31 p.p.; Maiden, For.Fl.N.S.Wales 4(1910)158 p.p.; Petrie, Proc. Linn.Soc.N.S.Wales 37(1912)139,151 p.p.; Cheesem., Man.N.Zeal Fl. ed.2,(1925)456 p.p.; Domin, Bibl.Bot. 89,2(1925)672 p.p.; Hutchinson, Fam.Fl.Pl. (1926)89 p.p.; McLuckie & Petrie, Proc. Linn.Soc.N.S.Wales 52(1927)161 p.p.; Berry, Proc.U.S.Nat.Mus. 73,22(1928)21 p.p.; Field Nat.Club Vict., Cens.Pl.Vict. (1928) 29 p.p.; Francis, Austral.Rain-For.Trees (1929)94 p.p.; Warming & Möbius, Syst.Bot. ed.4,(1929)334 p.p.; Welch, J.Proc Roy.Soc.N.S.Wales 62(1929)350 et seq. p.p.; Ewart, Fl.Vict. (1931)519 p.p.; Berry, Bot.Gaz. 96(1935)751 p.p.; Berry, Geol. Soc.Amer.spec pap. 12(1938)35,75 p.p.; Macbride, Field Mus.Bot. 13,2(1938)784 p.p.; Lemée, Dict.gen.phan. 7(1939)33,235 p.p.; Cranwell, Rec.Auckl.Inst.Mus. 2(1942)291,293 p.p.; Hurst, Poison Pl.N.S.Wales (1942)122 p.p.; Guillaum., Fl.Anal.Synopt. Nouv.-Calédonie (Phan.) (1948)122 p.p. "Monimiacées"; Henry, Pl.Alkaloids ed.4,(1949)319 p.p.; Gundersen, Fam.Dicot. (1950) 65 p.p.; Manske in Manske & Holmes, Alkaloids 1(1950)6 p.p.; Metcalfe & Chalk, Anat.Dicot. 2(1950)1138 p.p.; Francis, Austral. Rain-For.Trees ed.2,(1951)35,383 p.p.; Lawrence, Taxon.Vasc.Pl. (1951)510 p.p.; Erdtman, Pollen Morph. & Pl.Taxon. (1952)271 p.p.; Rendle, Class.Fl.Pl. 2 repr., 2(1952)133 p.p.; Botany

Dept., University of Melbourne, Fam.Gen.Vict.Pl. (1953)72 p.p.; Couper, N.Zeal.Geol.Surv.Paleont.Bull. 22(1953)40 p.p.; Manske in Manske & Holmes, Alkaloids 4(1954)120 p.p.; Core, Plant Taxon. (1955)318 p.p.; Stern, Amer.J.Bot. 42(1955)874,881 et seq. p.p.; Anderson, Trees N.S.Wales (1956)368 p.p.; Hutchinson, Fam.Fl.Pl. ed.2,(1959)136 p.p.; Muñoz-Pizarro, Sinops.fl. chil. (1959)154 p.p.; Takhtajan, Evol.Angios. (1959)182 p.p.; Couper, N.Zeal.Geol.Surv.Paleont.Bull. 32(1960)36,47 p.p.; Croizat, Principia Botanica 1A(1960)378 et seq. p.p.; Emberger in Chadefaud & Emberger, Traité Bot. 2(1960)919,921,944 p.p. "Monimiacées"; Godley, Proc.Roy.Soc.Lond. B,152(1960)459 p.p.; Willis, Dict.Fl.Pl.Ferns ed.6,(1931)429 p.p.; Allan, Fl.N.Zeal.1 (1961)L,117,138 p.p.; Eames, Morphol.Angios. (1961)12,97,99, 134,411,422,425,430,432 p.p.; Evans in Beadle, Evans, & Carolin, Handb.Vasc.Pl.Sydney & Blue Mts. (1963)129 p.p.; Curtis, Stud. Fl.Tasm. 1(1956)XXXIV, XLIV, XLVII p.p.; Poole & Adams, Trees & Shrubs N.Zeal. (1963)44 p.p.; Sastri, Ann.Bot. 27(1963)431 p.p.; Cavaco, Webbia 19(1965)587 p.p.; Curtis, Stud.Fl.Tasm. 3(1967) 593 p.p.

Diagnosis

Bisexual or monoecious and polygamous, often aromatic evergreen trees, with monopodial branching; secondary xylem heteroxylous, the vessels ± solitary, narrow, angular, with perforation plates and intervascular pitting scalariform, fibro ground mass predominantly tracheidal, rays narrow and heterogeneous type II, with or without oil cells, parenchyma ± indistinguishable; leaves decussate, blades ± notophyllous to microphyllous, with toothed to crenate or almost entire margins, stomates anomocytic, hairs unicellular, centrifixed or basifixed, sometimes tufted; inflorescences axillary, pendant, monopodial and determinate, single-flowered, a simple dichasium, or decussately thyrsiform, with small or large flower-enveloping bracts; flowers choritepalous, perigynous, bisexual, staminate or pistilliferous; hypanthium with or without subtending or ± tepaloid perianth-contiguous bracteoles; perianth of ± isomorphic sepaloid to petaloid tepals, basically 8-partite in two tetramerous whorls or 2-± 8(-12)-partite in cyclic to semi-spiral arrangement; androecium of stamens and staminodes arranged in successive whorls in bisexual flowers, of ± staminodes only in pistilliferous flowers, stamens differentiated into glanduliferous filaments and bisporangiate anthers with valvular dehiscence; pollen grain tetrads tetragonal, the grains syncolpate with equatorial colpi and (micro-) reticulate; gynoecium apocarpous, carpels uniovulate, styles elongate and terminated by glabrous stigmatic filaments cohering in a conical to stellately branched column; ovules erect, ± anatropous, with ± basal placentation; fruiting hypanthium woody, enclosing nutlets, either elongated cylindrical-urceolate to pyriform, or cupular with inner staminodes free, elongated, and lignified; nutlets variably silky hirsute, the bodies small, the styles elongate-subulate; endosperm albuminous.

Detailed Description

Bisexual or monoecious and polygamous evergreen trees; boles with or without buttresses; branching monopodial, sometimes seemingly sympodial, forming cylindrical or spreading corymbiform crowns. Bark of boles pulpy or cork-like, outer surface smooth or shallowly to coarsely fissured, inside cream-white to deep yellow, with or without a pronounced safrol- or citronella-like odour, with bitter taste. Secondary xylem rather soft, closely textured, without figure, sordid grey-white to cream-brown when dry, frequently with a yellowish hue; diffuse porous; vessel members solitary or up to 20% in radial multiples of 2-3(-5), usually angular, narrow, (0.9-)1.0-1.7 (-2.0) mm long x (30-)40-110(-155)μ inner tangential diameter, ± thin-walled, the perforation plates oblique, extensively overlapping, and scalariform, with > 20(-100) bars, the intervascular pitting with intergradations between imperforate and perforate bordered pits in scalariform arrangement, tyloses occasionally present; fibres abundant, diffuse, and hardly tending to radial arrangement, ca. 1.2-2.6 mm maximum length range x (14-)22-48(-84)μ outer tangential diameter, varying from fibre tracheids with thick distinctly to flat indistinctly bordered pits variably numerous on all or particularly radial walls to libriform wood fibres with occasional septae and simple pits; rays distributed diffusely, heterogeneous, uniseriate rays of 2-6(-10) cubical cells, multiseriate rays predominant, ± narrowly fusiform, short, 0.2-1.8 mm high × 2-5(-8) cells wide, heterocellular, interior cells distinctly procumbent, 5-59 μ in tangential diameter, uniseriate tips of 1-3 ± upright cells sometimes including solitary oil cells*, vessel-ray pitting scalariform with large horizontal simple, sometimes bordered apertures, acicular crystals present or absent; parenchyma absent or obscurely diffuse. Ultimate branchlet stems compressed, often tetragonous, hispid-strigose to glabrous; primary cortex not well developed, becoming sclerosed or not; pericyclic region a composite cylinder of sclerenchyma, comprising septate fibres and hippocrepiform sclereids in alternating strands confronting respectively the fascicular and interfascicular parts of the eustele**; secondary phloem with sieve tubes and companion cells, and rod cells in older parts***; oil cells in cortex, phloem, and pith****. Vegetative buds conical to obcordiform or ± compressed ovoid, comprising a pair of valvate bract-like leaves that envelop the meristem and ultimately develop into the leaves

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* *Dryadodaphne*, *Daphnandra*?, *Doryphora*?

** Solereder (1899), Money et al. (1950).

*** Möller (1882), Hobein (1888), Solereder (1899), Money et al. (1950).

**** Solereder (1899), Metcalfe and Chalk (1950, f.276 F), Money et al. (1950).

of the successive node: scales absent. Nodes unilacunar, the trace frequently comprising a single arc-shaped strand, sometimes several separate strands concrescent in the petiole, derived from two subnodal strands*. Leaves decussately arranged, exstipulate, petiolate; blades variously elliptic, lanceate, ovate, or obovate, notophyllous to microphyllous**, bifacial, variably coriaceous***, with mucronately toothed, serrate, crenate, to almost undulate or entire ± recurved margins, and camptodrome or sometimes apparently brochidodrome venation; stomates predominantly anomocytic, the anticlinal walls of epidermal cells straight****; hypodermal layers present or absent on upper face of blade, pallisade parenchyma clearly differentiated and confined, mesophyll loosely organised and extensive, sclerenchymatous sheaths

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* Money et al. (1950).

** Mesophyllous only in Daphnandra repandula.

*** Constantly chartaceous only in Daphnandra repandula.

**** Money et al. (1950). The anticlinal walls are strongly undulate in Doryphora according to Hobein (1888).

present around vascular bundles of larger nerves*, spherical, sometimes aromatic ethereal oil cells ubiquitous**; hairs unicellular, two-armed centrifixed or simple basifixed, sometimes tufted.

Inflorescences axillary, variably pendant, monopodial and determinate, single-flowered, a simple dichasium, or decussately thyrsiform and terminating in simple dichasia, bisexual, monoecious, or polygamous, rarely dioecious, developing from buds similar in shape to vegetative buds; **buds** ± stipitate, comprising an outer pair of valvate bracts that envelop the ultimate inflorescence axes primordia and flower buds, and expand early or enclose flower buds until late in inflorescence maturation; peduncle nodes bracteate, with small or large cymbiform, variably persistent bracts.

Flowers actinomorphic, choritepalous, perigynous, protandrous, pale green, whitish, and/or reddish. Floral hypanthium cupular-poculiform in bisexual and pistilliferous flowers, patelliform in staminate flowers (= receptacle), with or without subtending or ± tepaloid perianth-contiguous bracteoles. Perianth cyathiform or rotatiform, basically 8-partite in two alternate tetramerous whorls, or (2 or) 4 or 6 (or 8)-partite in cyclic arrangement, or 3- ± 8(-12)-partite in hemicyclic or

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* Hobein (1888), Solereder (1899), Metcalfe & Chalk (1950), Money et al (1950).

** Oil cells present also in the tepals, filaments, anther connectives, and staminodes of most if not all genera.

sub-spiral arrangement, of ± isomorphic* sepaloid to petaloid tepals with imbricate aestivation and pinnate to palmate-parallel venation. Androecium of (3-)4-8(-9) stamens and (3-)5-18(-22) staminodes in successive whorls in bisexual flowers, of (4-)6- ± 20 stamens in staminate flowers**, and of (10-)12- ± 30(- ± 46) staminodes or occasional fertile stamens in pistilliferous flowers, the arrangement of parts basically tetramerous in alternate series, or trimerous, or hemicyclic to spiral; stamens differentiated into filament and anther, variably dorsiventrally compressed, filaments bearing a pair of stamen-like to planate or peltate staminal glands, anthers basifixed, bisporangiate, dehiscing by valves; tapetum amoeboid*** or secretory****; cytokinesis by successive*** or simultaneous**** division; pollen grain tetrads ± tetragonal, grains of medium size, oblate-ellipsoidal to oblate-spheroidal, with ± bilateral symmetry, the colpi transversales equatorial with non-bordered ragged-edged colpi linked at opposite arcs by shallow, thin-walled, finely sculptured depressions, grain walls thin, $1\frac{1}{2}$-$2\frac{1}{2}$ μ thick,

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*The outer whorls of bract-like or sepaloid parts in the seemingly differentiated perianth of Daphnandra are bracteoles.

**Staminodes also present in staminate flowers of Laureliopsis.

***In Atherosperma (Sastri 1963).

****In Laurelia novae-zelandiae (Sampson 1967).

surface sculpture (micro-)reticulate with OL-pattern, with lumina ½-2½ µ long, often varying in shape, ektexine ± thicker than endexine and apparently semi-tectate in structure, the muri with apparently simple columellae; staminodes stamen-like, ± batilliform, scale-like, or caudate-subulate, with or without reduced staminal glands. Gynoecium apocarpous, of (3-)4- ± 40(- ± 50) uniovulate carpels arranged spirally and attached superficially* to hypanthium chamber; styles slenderly elongate, terminal or lateral, usually hispidulous**, terminated by glabrous stigmatic filaments cohering in a narrowly conical to hemispherical cone or stellately branched column that is caducous after anthesis; ovule ellipsoidal, rostrate or obtuse at the chalazal end, erect, anatropous or ± hemitropous, with basal to sub-marginal placentation, bitegmic, crassinucellate, the embryo sac monosporic, 8-nucleate, of the Polygonum-type***.

Fruiting hypanthium woody, enclosing nutlets, either elongated cylindrical-urceolate to globulose-pyriform, or cupular with inner staminodes free, elongated, and lignified, dehiscing longitudinally into 1-4 valves, or the lignified staminodes reflexing to disseminate nutlets.

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* Becoming shallowly embedded in *Dryadodaphne*.

** Glabrous in *Nemuaron*.

*** Data for *Laurelia novae-zelandiae* only, from Sampson (1967).

Nutlets silky hirsute*, the bodies small, thin- and dry-walled, with an adaxial costa, the styles elongate-subulate, hirsute**, variably persistent; endosperm albuminous, cellular from an early stage; embryo straight, with erect or slightly spreading cotyledons.

Taxa, Geographic Distribution, and Ecology

The family Atherospermataceae comprises sixteen species in seven genera, Atherosperma Labill., Daphnandra Benth., Doryphora Endl., Dryadodaphne S.Moore, Laurelia Juss., Laureliopsis Schodde, and Nemuaron Baill. As explained below, the genera are grouped in two tribes. The family is presently confined to lands bordering the southern Pacific Ocean between latitudes 1° - 47°S: New Guinea, eastern Australia and Tasmania, New Caledonia, New Zealand, and Chile (maps 1, 2). According to apparently authentic fossil material, its former range included South Africa, Egypt, and Seymour island in Antarctica.

Its members occur in subtropical and temperate rainforests, often in mountain regions. With the particular exception of the two tropical montane species of Dryadodaphne in New Guinea and Laureliopsis in Chile, they prefer or are confined locally to the heads, lower slopes, or semi-alluvial beds of sheltered everwet forest gullies with permanent or near-permanent water. Their restriction to such sites explains their relative scarcity and even locally disjunct distribution in cool southern

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* Bodies glabrous in Doryphora.

** Vestigial and glabrous in Nemuaron.

hemisphere rainforests today.

They are often associated in these forests with *Nothofagus*, *Drimys*, *Eucryphia*, *Podocarpus* and allied genera, and genera of the families Cunoniaceae, Escalloniaceae, and Elaeocarpaceae, all of which have similar patterns of distribution. These associations are discussed in more detail in chapters VI and IX.

Phenology

With the exception of species of *Daphnandra* and *Dryadodaphne*, flowering in all members of the family is strictly seasonal, and takes place once a year in austral winter and spring months. It may be related to seasonal climatic oscillations which are most marked in temperate latitudes. The periodicity in flowering of the tropical latitude species *Doryphora aromatica* and *Nemuaron vieillardii*, in environments without such distinct seasonal fluctuations, is remarkable. To suppose that it is the result of inherited photo-periodic responses retained from more temperate latitude progenitors is not inconsistent with the conclusions reached on the origin of the family in chapter XVI. Such responses may also explain why the *Atherosperma* and *Doryphora* in south-eastern Australia are the only or main rainforest trees flowering in winter and early spring months. In all of these genera, the time from inflorescence bud initiation to fruit maturation is more than 12 months; inflorescence buds of the ensuing season appear before the fruiting hypanthia dehisce.

Flowering and fruiting times in *Daphnandra* and *Dryadodaphne* show more marked adaptation to or modification by local environments. The various species of *Daphnandra* flower once a year but at different times, possibly in response to variations in rainy seasons (chapter XIV). The two tropical-latitude species of *Dryadodaphne* in New Guinea, under relatively uniform seasonal conditions of day length, rainfall, and temperature, flower apparently at any time throughout the year.

Family Characters - see chapter IV.

Affinities - see chapters IV, V.

Supragenerić Taxa

The family is divided into two tribes: Atherospermateae and Laurelieae. They are characterised in particular by differences in the size and frequency of the secondary xylem vessels, leaf hairs, the position of insertion of perianth and androecium on the rim of the floral hypanthium, the form of the stamens and staminal glands, and the presence and modification of inner staminodes in the fruit, rather than by the type of inflorescence and occurrence of flower-enveloping bracts as indicated by Bentham (1880), Pax (1889), and Hutchinson (1964).

Notwithstanding the premise that they should be placed on the taxonomic rank immediately below that of family, the subfamily, these taxa are treated as tribes because their differences, on morphological grounds, are nearer in order of magnitude to the differences between the genera within the family than to those between the Atherospermataceae and other Lauralean families.

Key to the Tribes of the Atherospermataceae

1a. Leaf hairs centrifixed, with unequal arms; staminal filaments ± longer than anthers, with stamen-like stipitate staminal glands attached at or near the base; hypanthium rim in bisexual and pistilliferous flowers poorly-defined, concave; inner staminodes elongated around gynoecium column in fruit; nutlet dissemination by reflexion of staminodes surrounding gynoecium, with or without splitting of fruiting hypanthium .... VI. Atherospermateae

1b. Leaf hairs simple, sometimes tufted; staminal filaments ± shorter than anthers, with peltate, variously flap-shaped, or wing-like sessile or shortly stipitate staminal glands attached from near the base to near the apex; hypanthium rim in bisexual and pistilliferous flowers ± distinct, flat, convex, or sub-erect; inner staminodes not enlarged in fruit; nutlet dissemination by dehiscence of fruiting hypanthium.
.... IX. Laurelieae Pax

IV. A COMPARISON OF THE CHARACTERS OF THE ATHEROSPERMATACEAE, ITS GENERA, AND ITS RELATED TAXA

Taxonomic relationships within the Atherospermataceae, particularly between the genera, have been poorly understood as both the range of variation of morphological characters and the homologies of organs have been insufficiently known. The various modifications of androecium structures have never been documented adequately. Moreover, the pair of flower-subtending bracts used by Pax (1889) and Hutchinson (1964) to relate Doryphora to Atherosperma and by A.C.Smith (1941) to associate Dryadodaphne with Atherosperma, are attached at different positions on the inflorescence axes and doubtfully homologous. These features and others characteristic of the family are evaluated below. Some of them, such as types of hair, number and arrangement of flower parts, venation of tepals, form of the stigmatic column, and patterns of hairs on the nutlets have not been recognised before as being of taxonomic significance.

1. Habit

All members of the Atherospermataceae are trees. Most are forest canopy species. Under optimal conditions, one, Doryphora sassafras, even emerges above the forest canopy, reaching a height of ca 45-50 m. Only species of the genus Daphnandra represent regularly subcanopy forms, Combining monopodial branching with decussate leaf arrangement, the crowns of atherospermataceous trees are distinctly slender cylindrical or conical to rather corymbiform. That the mode of branching is monopodial has been determined not only from the life form of mature trees but also by observation of saplings at various growth stages in all genera except Laureliopsis. It is more difficult to recognise in Dryadodaphne than in other genera because of the marked development of lateral branches in the spreading crowns of mature trees of D. novoguineensis and D. trachyphloia (f.16).

The crown shapes are generally characteristic of each genus. The spreading crowns in Dryadodaphne have been mentioned. Those in Atherosperma and Laurelia (L. novae-zelandiae) are narrow and impress in their similarity to the crowns of Agathis (Araucariaceae). The smallest and most compact crowns relative to tree size occur in the two species of Doryphora (f.17).

Nemuaron, with a short,rounded or rather corymbiform crown, is distinctive in the ± upright posture of leaves at branchlet ends; Dryadodaphne pterandrica is the only other member of the family with a crown of similar form. In other genera, particularly Atherosperma and Daphnandra, the leaves are oriented in a relatively horizontal plane along the branchlets through slight twisting of consecutive internodes and unequal curving of the petioles. In contrast to Atherosperma, however, the crown in Daphnandra is relatively short, spreading, and somewhat corymbiform.

Though they are woody (with the exception of *Cassytha*), other members of lauralean families vary much in their growth habit. In contrast to Atherospermataceae, the Monimiaceae, *Hortonia*, *Peumus*, and *Siparuna* group of the Monimiaceae alliance, and Calycanthaceae comprise shrubs and small subcanopy trees. Several genera of Monimiaceae are climbers. Like Atherospermataceae, *Gomortega* of the monotypic family Gomortegaceae and most Lauraceae are tall trees of forest canopies.

The mode of branching in *Gomortega*, *Siparuna*, and tree members of Monimiaceae has apparently not been recorded in detail or with accuracy. In species of the monimiaceous genera *Hedycarya*, *Levieria*, *Steganthera*, and *Tetrasyndra* observed in the field, it is consistently widespreading and superficially sympodial. Corner (1952) quotes a monopodial habit for all species of Lauraceae discussed in connection with crown form.

2. Secondary Xylem

Although the secondary xylem of the family as a whole has been compared in some detail with that in related taxa such as Monimiaceae, the *Siparuna* group, and Lauraceae (Hobein 1888, Garratt 1934, Money et al. 1950), its variation within the family, notably between the genera, has not received much attention. In a brief way, Welch (1929) has investigated its features in the genera *Atherosperma*, *Daphnandra*, and *Doryphora*.

Examination of two or more sections of the secondary xylem of species of all genera* has revealed that there is variation between the genera in the following features: the degree of association of vessels in radial multiples, the diameters of vessels, the frequency of vessels per unit transverse area, the thickness of fibre walls, the proportion of fibre tracheids and libriform (septate) fibres, the thickness of borders on bordered pits, the size and heterogeneity of the multiseriate rays, and the presence or absence of oil cells in the uniseriate tips of multiseriate rays.

Within and between the species of each genus there is little variation in these features, as seems to be the rule (cf. Brazier 1968). Some variation occurs in the diameter of pores between _Laurelia novae-zelandiae_ and _L. sempervirens_, in the presence of oil cells in the rays of _Dryadodaphne novoguineensis_, _Daphnandra apatela_, and _Doryphora sassafras_, and in the occasional replacement of the scalariform perforation plates and vessel-ray pitting with pitted areas and small irregular pits respectively in _Doryphora sassafras_ (Garratt 1934).

The constancy of the secondary xylem characters within a genus and their differences between genera can be assessed from the figures for tangential vessel diameter and frequency of vessels

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* In genera with more than one species, sections from all species of _Doryphora_, _Dryadodaphne_, and _Laurelia_, and three of _Daphnandra_ were studied —— see index II.

TABLE I

	mean vessel diameter (μ)	mean vessel number per sq. mm in transection
Laureliopsis	49	123
Atherosperma	44	130
- - - - - - - -	- - - - - - - -	- - - - - - - -
Dryadodaphne	89	49
Nemuaron	75	80
Laurelia	64	70
Doryphora	70	60
Daphnandra	61	80

TABLE II

	range of vessel diameters (μ)	mean vessel diameter (μ)	range of vessel numbers per sq.mm in transection	mean vessel number per sq. mm in transection
Laureliopsis philippiana	35 - 78	49	96 - 150	123
Atherosperma moschatum	26 - 71	44	104 - 160	130
Dryadodaphne pterandrica	35 - 114	81	47 - 55	52
Dryadodaphne novoguineensis	33 - 142	88	32 - 64	48
Dryadodaphne trachyphloia	59 - 139	98	43 - 51	47
Nemuaron vieillardii*	38 - 123	75	54 - 106	80
Laurelia sempervirens	38 - 85	56	69 - 96	80
Laurelia novae-zelandiae	47 - 118	72	53 - 78	62
Doryphora aromatica	40 - 147	76	54 - 75	63
Doryphora sassafras	31 - 107	64	40 - 76	58
Daphnandra repandula	40 - 114	65	65 - 94	78
Daphnandra tenuipes	35 - 95	58	60 - 101	77
Daphnandra apatela	28 - 90	59	76 - 92	85

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* Data from only two collections of wood.

per unit transverse area in table II. According to an analysis of variance carried out on these figures, the characters are relatively constant between the species within each genus but differ significantly between the genera, corroborating the delimitation of generic groupings according to floral and fruit morphology.

Frequency of Vessels in Radial Multiples

One of the characteristic features of the secondary xylem in the family is the usually solitary occurrence of the vessels. There may be only up to 5% in radial multiples of 2-3 in Atherosperma, Doryphora, Laurelia, and Laureliopsis, and up to 10% in multiples of 2-3(-4) in the tropical latitude genera, Dryadodaphne and Nemuaron. Daphnandra stands somewhat apart in having up to 20% of its vessels in radial multiples of 2-5. The aggregation of vessels in radial multiples is regarded as an advanced condition (Tippo 1946, cf. Money et al. 1950). Such a tendency in Daphnandra is consistent with the specialised attributes of that genus and complements the development of septate libriform fibres in its secondary sylem.

Vessel Size and Frequency

There is variation in vessel diameter and frequency in the family at two levels. On one, the vessels are as a rule larger and less frequent in the tropical-latitude genera, notably Dryadodaphne, and are smaller and more frequent in more temperate-latitude genera, such as *Daphnandra*, *Doryphora*, and *Laurelia*. This trend, which appears to reflect largely the influence of prevailing environments, is discussed in more detail in chapter IX.

On the other, the vessels are more markedly narrow and frequent in *Atherosperma* and *Laureliopsis* than in any other genus. Garratt (1934) has already alluded to their small size in *Atherosperma*. Both genera occur at the most temperate i.e. coolest and seasonally most variable latitudes in the family. As a result, their vessel diameters and frequencies appear as the end points in the above described trend from broader and few vessels in tropical latitudes to narrower and many vessels in temperate latitudes.

Yet, though they may reflect similar environmental influences, these characters in *Atherosperma* and *Laureliopsis* are of a different order of magnitude in comparison with the range of vessel diameters and frequencies found in other genera. They suggest an older more deep-seated difference between the two groups of genera. That the differences are constant and significant is shown by the vessels in wood of species of the genera *Atherosperma* and *Doryphora*, representing the two generic groups, where they meet geographically in south-eastern New South Wales: *Atherosperma moschatum* (sample 2410) from Glenbog has a mean vessel diameter of [illegible] μ and ca 124 vessels per sq. mm of wood in transection, and *Doryphora sassafras* (Schodde 5181) from Currowan State Forest has a mean vessel diameter of 60μ and ca 75 vessels per sq. mm.

Fibre Tracheid-Septate Fibre Transitions

The wood fibres are predominantly or exclusively fibre tracheids with conspicuously to indistinctly bordered pits, except in *Daphnandra* in which they are frequently libriform with septae (f.37B). Septate fibres in the family are thought to have developed from fibre tracheids of the type found in other genera such as *Doryphora* (f.37A). Their prevalence in *Daphnandra* is therefore viewed as the derived condition (cf. Money et al. 1950). That such a transition has in fact occurred is indicated by the present pattern of fibre tracheids in early wood and occasional septate fibres in late wood of the tropical-latitude genera, *Dryadodaphne* and *Nemuaron*.

Ray Form

The rays are heterogeneous, with a marked preponderance of heterocellular, ± narrowly fusiform multiseriates, conforming to heterogeneous type II of Kribs' (1935) classification. They are most markedly heterocellular in *Atherosperma*, *Laureliopsis*, and *Dryadodaphne*, in which the cells of the uniseriate tips are particularly large, and indicate that in this character these genera are unspecialised (cf. Kribs l.c.). The rays are least heterocellular in *Daphnandra*.

The multiseriate rays are shortest and narrowest in *Atherosperma*, *Laurelia*, and *Laureliopsis*, and highest and broadest in *Doryphora*, *Dryadodaphne*, and *Daphnandra*; in the latter genus extensive aggregate rays are sometimes formed. From this it might be construed that the rays of *Doryphora*, *Dryadodaphne*, and *Daphnandra* are more like those of Monimiaceae and represent the ancestral type in Atherospermataceae. Nevertheless, in the light of Kribs' comment (l.c.) that specialisation of rays is dependent upon the degree of heterogeneity rather than upon size, such resemblances appear to be the result of parallel evolution.

Oil Cells

Oil cells were only observed in the rays of two species of *Dryadodaphne*: in *D. novoguineensis* where they are irregular in occurrence, and in *D. trachyphloia* where they are apparently ubiquitous (f.27). They have also been reported from *Daphnandra apatela* (as *D. micrantha*) and *Doryphora sassafras* (Garratt 1934), although their occurrence in the wood of these species has not been verified. Elsewhere in the plant body, oil cells are found regularly in the cortex, phloem, and pith tissues of the stem, the leaves, the tepals, the staminal filaments and connectives, and the staminodes of apparently all genera.

The presence of oil cells in the rays of living members of the family is of interest insofar as their chequered occurrence in the secondary xylem of apparently authentic fossils of the family (Müller-Stoll and Mädel 1962 - see chapter XV) and in related living groups appears to throw some light on the relationships between the families of the Monimiaceae alliance (chapter V). As oil cells are abundant in the earliest known fossil wood (Protoatherospermoxylon of Cretaceous age - chapter XV) and rare or absent in later fossil wood and living forms, their presence in atherospermataceous wood would appear to represent an ancestral feature. Among related living groups, they are characteristically present in the rays and xylem parenchyma of Hortonia and the Lauraceae, and absent in all others.

Xylem Parenchyma

Xylem parenchyma is so diffuse and sporadic in occurrence in living members of the family that it is almost impossible to distinguish in wood sections under the microscope; it may in fact be absent in some genera. It is also obscure in the more recent fossil wood, Atherospermoxylon, of Middle Oligocene age, but in early woods of Upper Cretaceous age (Müller-Stoll and Mädel 1962), distinct aggregates of parenchyma cells occur in diffuse disposition. This sequence supports the view of Money et al. (1950) ~~who have contended~~ that the Atherospermataceae evolved from Hortonia-like "prototypes" by the reduction of wood parenchyma concomitantly with the development of septate fibres and reduction in the width of rays. Loss of parenchyma is regarded as a relatively specialised feature (Money et al., l.c.).

Summary and Relationships of Secondary Xylem Features

The secondary xylem of the Atherospermataceae is unspecialised (i.e. primitive) in its structure according to the xylary phylogenetic sequences put forward by Bailey and Tupper (1918), Tippo (1946), Kribs (1935, 1937), and Money et al. (1950). This assessment is based on its characteristic combination of usually solitary, long, narrow, angular vessel members having extensively overlapping end walls, essentially scalariform perforation plates, and ± large intervascular and vessel-ray pits in ± scalariform arrangement, with a ground mass of usually fibre tracheids with distinctly bordered pits, obscure or absent parenchyma, and rays that are heterogeneous, never very high or broad, and have occasional oil cells.

Of the taxa conventionally included with Atherospermataceae in the Monimiaceae alliance, the family Monimiaceae itself has very similar secondary xylem features. Its members differ significantly, nevertheless, in their range of vessel member forms which exhibit trends in shortening, and of reduction of the overlapping end walls, development of simple from scalariform perforations at the end plates, and aggregation in radial multiples. They are also extraordinarily distinct in having large and very high rays, often over 10 cells wide (f.41, 42). Other distinguishing features are their transitions from scalariform to alternating multiseriate intervascular pitting, a lack of oil cells, and usually septate fibres with vestigially bordered pits. *Hedycarya* and *Levieria*, however, show transitions from fibre tracheids to septate fibres.

Hortonia, as mentioned above and described by Money et al. (l.c.), combines characteristics which link the Atherospermataceae with the Monimiaceae. It approaches Atherospermataceae in its long, solitary vessels with extensively overlapping end walls and scalariform perforation plates, non-septate fibres with conspicuously bordered pits, and rather smaller rays, 1-10 cells wide, with oil cells. It remains distinct in having alternating, near circular multiseriate type intervascular pitting of the type found in Monimiaceae. It differs from members of both families in having abundant parenchyma in the diffuse-in-aggregates pattern.

Peumus, on the other hand, diverges further from Atherospermataceae in its secondary xylem than it does from any member of Monimiaceae (f.40). As pointed out by Dadswell and Record (1936), it is unique among its congeners in having vessels with exclusively simple perforations, fine spiral thickenings, and alternate pitting, in combination with nearly homogeneous rays, and fibres with simple pits.

The Siparuna group is equally distinct in its more specialised vessels. These are arranged in radial multiples of varying extension, and are larger, more rounded in circumference, with rather truncated end walls and simple perforation plates. Intervascular pitting is of the alternating multiseriate type, and the rays, though narrow, are very high as in Monimiaceae. Fibres have vestigially bordered or usually simple pits, but resemble those in Atherospermataceae in the rarity of septae.

A characteristic feature is the general abundance of parenchyma, arranged frequently in apotracheal bands (f.43).

Among the other lauralean families, Lauraceae and monotypic Gomortegaceae have been singled out by recent investigators as having xylem characters resembling those of the Atherospermataceae (Garratt 1934, Money et al. l.c., Metcalfe and Chalk 1950, Stern 1954, 1955). Members of the Lauraceae, nevertheless, are particularly distinct in their vessels which occur usually in radial multiples and are rounded, of large diameter, and have simple perforation plates (f.39). Intervascular pitting is alternate and typically large; libriform fibres with or without septae predominate. Though resembling Atherospermataceae rather than Monimiaceae in the form of their rays and presence of oil cells, they differ again from both in having variably abundant parenchyma that is often paratracheal in disposition.

The resemblance between Gomortega and members of the Atherospermataceae in all secondary xylem characters is striking, as can be seen from f.38. The vessels in Gomortega are angular, thin-walled, narrow, and of similar diameter to those in the tribe Atherospermateae; their end walls overlap extensively and end plates are similarly scalariform with numerous bars; their intervascular and vessel-ray pitting is scalariform in arrangement; and they are ± solitary and diffusely distributed. The fibres, which comprise the xylem ground mass, are entirely tracheidal with distinctly bordered pits. The rays are small and narrow (1-3(-4) cells wide) like those of the Atherospermateae, but perhaps even more heterocellular; oil cells are apparently absent (cf. Stern 1955). Parenchyma, however, is rather abundant and diffuse (Stern l.c.).

In common with Atherospermataceae, Lauraceae, and Monimiaceae, Gomortega has oil cells in the primary cortex, phloem, and pith of stems, and in the mesophyll and hypoderm of leaves, and hippocrepiform sclereids in the pericycle of the young stem (Solereder 1899, Metcalfe and Chalk l.c.).

It is remarkable that the similarities between the secondary xylem of Gomortega and Atherospermataceae have not been recognised before. Garratt (l.c.) was the first to point out resemblances but declined a serious comparison because of lack of information about Gomortega. Stern (1955) virtually overlooked them. For this reason, the characteristics of the secondary xylem of Gomortega are reiterated above in some detail.

The Calycanthaceae have very few anatomical features in common with the Atherospermataceae (Garratt l.c.), despite their close affinity on other morphological and perhaps phytochemical grounds. The points of distinction, summarised in table III, are sufficiently outstanding to indicate that the relationship between the two families is rather remote. Only through the Siparuna group and Peumus is there sufficient similarity to suggest possible, if indefinite, affinity (Garratt l.c.),

3. Buds

Vegetative Buds

Vegetative buds comprise a pair of bracts which meet valvately to enclose the shoot meristem and eventually enlarge into the leaves of the consecutive node. In some lateral vegetative shoots, they even remain bract-like or small throughout life, as in *Laurelia sempervirens*. Terminal stem nodes in most genera have normally a single terminal bud flanked by a pair of smaller lateral buds. *Daphnandra* is exceptional in that this node in leader stems becomes markedly flattened and bears numerous accessory buds in serial arrangement. The reasons for such a development are discussed in chapter XIV.

The absence of bud scales in *Laurelia novae-zelandiae* to protect the growing points has been commented on by Sampson (1967). Bud scales are absent in all genera of the family and their protective function is obviously assumed by the unenlarged bract leaves and vestures of hairs. The relation of hairs to bud protection is described in the following section 4.

Buds in the Monimiaceae, *Hortonia*, *Peumus*, and *Siparuna* group are similar in form and lack bud scales. Sampson (l.c.) has pointed out that in the Lauraceae, bud scales are present in north temperate latitude genera *Laurus* and *Umbellularia*, but absent in the New Zealand species of *Beilschmiedia*. As he suggests, the absence of bud scales may simply reflect the milder oceanic climates in the southern hemisphere. The buds of *Gomortega* are similar in the above respects to those of Atherospermataceae.

Inflorescence Buds

Inflorescence buds resemble vegetative buds in that they comprise initially a pair of bracts that meet valvately to enclose the subsequent inflorescence growing points and flower buds.

The form of the buds differs between the genera of the family. In all genera except *Laurelia* they are stipitate, and vary from ovoid (*Atherosperma*) to variably compressed obcordiform (*Doryphora*, *Nemuaron*). In those genera with stipitate buds, gross bud ontogeny follows the ensuing sequence. When it first appears, the bud is sessile and somewhat compressed obcordiform in the leaf axil. After initial enlargement, an intercalary meristem is formed at its base and initiates the growth of a stipe (= base internode of the primary peduncle). The stipitate bud later expands further and from it develop the ultimate inflorescence axes and flower buds. The buds of *Laurelia* differ in remaining more-or-less sessile* with the bracts expanding at an early stage to reveal the tips of consecutive bracts and flower buds in a ± hairy globose mass. In other genera which ultimately develop relatively elaborate inflorescences, e.g. *Daphnandra*, *Dryadodaphne*, *Laureliopsis*, and *Nemuaron*, the bracts are hardly **enlarged and early caducous. In those genera with contracted inflorescences,** such as *Atherosperma* and *Doryphora*, they are variably persistent and enlarge to enclose the flower buds until the latter are ready to burst.

Cellular changes in the ontogeny of vegetative and inflorescence buds

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* The basal bracts may be ultimately situated several millimetres above the leaf axil in mature inflorescences because of intercalary growth at the base of the primary peduncle.

have been described for *Laurelia novae-zelandiae* (Sampson 1967) but no other species.

4. Hairs

There is good evidence that the hairs in members of the Atherospermataceae serve the particular function of protecting and insulating the relatively fragile growing points and floral structures from the environment. They are, for example, concentrated and sometimes confined to the buds and inflorescences, as in *Doryphora*. They are also generally densest and most ubiquitous in those genera, *Atherosperma* and *Laureliopsis*, which occur at the highest temperate latitudes in the family where seasonal variations in climate have the widest amplitude and coolest average temperatures; they are scarcest or virtually absent in *Dryadodaphne* which is confined to the lowest tropical latitudes in the family. Genera at intermediate latitudes, such as *Doryphora*, *Nemuaron*, and *Laurelia*, are intermediate in hairiness. The pattern of hairiness in *Daphnandra* is more variable, and possibly related to the adaptation of the genus to disturbed or secondary rather than primary rainforest habitat.

Hairs on the stems are characteristically simple and tufted. On the leaves they are either simple or centrifixed and unequally two-armed in different genera; their form is characteristic of the two tribes Atherospermateae and Laurelieae.

Stellate hairs and scales, which occur in most, if not all, genera of Monimiaceae, and are prevailingly to exclusively present in *Hortonia* and the *Siparuna* group, are lacking in Atherospermataceae. The hairs in other related families, Lauraceae, Gomortegaceae, and Calycanthaceae, are generally simple and unicellular.

5. Leaves

Within the Atherospermataceae, crown leaf sizes are mainly in the notophyll range of $7\frac{1}{2}$-$12\frac{1}{2}$ cm length, They reflect the subtropical, often montane rainforest formations and general environment in which most members of the family occur (cf. Webb 1959). They extend on the one hand to the mesophyll range in *Daphnandra repandula* which enters near-tropical rainforest in north-east Queensland. On the other, they are microphyllous in *Atherosperma moschatum*, *Doryphora sassafras* var. *microphylla*, and *Nemuaron vieillardii* where these species occur in temperate or ± montane subtropical forest. The notophyllous leaves of *Laureliopsis* would seem to be anomalous, considering the temperate environment in which the genus is found.

Exstipulate toothed leaves in decussate arrangement have long been used to characterise the Monimiaceae alliance among woody ranalean plants. Though these features are found together in all genera of the Atherospermataceae, they are not universal in allied taxa. The leaves are entire in *Hortonia* and some species of *Siparuna*, and alternate in *Glossocalyx* (*Siparuna* group) or sometimes sub-opposite in *Siparuna*. Exstipulate, decussately arranged, though entire leaves also occur in the related families Gomortegaceae and Calycanthaceae In Lauraceae, the leaves are exstipulate and entire, and decussate (*Cinnamomum*) to usually alternate in arrangement.

There are differences between the leaves of Atherospermataceae and other lauralean plants in the. stomates and in the vascular traces at the unilacunar leaf nodes. The stomates in the former are predominantly anomocytic (Metcalfe and Chalk 1950) whereas they vary between anomocytic and paracytic in Monimiaceae. In Hortonia, Peumus, and the Siparuna group, they are predominantly paracytic, as are those in Gomortega and the Lauraceae.

The nodal traces of atherospermataceous plants differ from those in Monimiaceae, Hortonia, and Peumus in that they tend to be single and arc-shaped at the nodal level rather than divided into three or more strands (Money et al. 1950). Though Siparuna has an apparently similar arc-shaped trace (Money et al. l.c.), it is Gomortega that bears the closest resemblance to the Atherospermataceae in nodal anatomy. The form of the trace is virtually identical in both, being derived from two groups of subnodal strands which concresce at the nodal level (cf.Stern 1955), and extend in a shallow arc through the petiole and midrib of the leaf. The trace at the leaf nodes in Lauraceae and Calycanthaceae is also usually single and arc-shaped.

6. Inflorescences

Structure

Irrespective of whatever terms* are used to define them, the

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* Both Rickett (1955) and Eames (1961) have drawn attention to the inaccuracy and inadequacy of conventional terms such as raceme and cyme to define inflorescences on developmental and comparative bases.

inflorescences of the Atherospermataceae comprise basically a determinate monopodial axis, with a varying number of nodes bearing in decussate arrangement solitary flowers or secondary axes, and terminating in a simple dichasium. The dichasial nature of the terminal flower group is clearly indicated by the invariably more advanced development and protanthesis of the central flower relative to its flanking flowers. No attempt has been made to interpret the inflorescences according to the concepts of Troll (1964).

Even without corroborative evidence from a comparative study of vascular traces, the inflorescences are clearly homologous with a lateral vegetative branch. This is revealed by their universally axillary position and their bracts which may be interpreted as the homologues of leaves*. The decussate arrangement of the bracts with the base pair situated in the transverse plane to the subtending leaf, their position at each node of the axis, and their occasional foliose form, as in _Daphnandra_, point to such a homology. Sampson (1967) has drawn attention to homologies between the terminal meristems of the vegetative stem and inflorescence in _Laurelia novae-zelandiae_. The two differ only in that the inflorescence meristem is determinate whereas the vegetative one is not.

The ontogeny of the inflorescence has been described in detail for

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* Cf. Section 3 above.

Laurelia novae-zelandiae by Sampson (l.c.), and its gross mode of development in other genera has been compared briefly in section 3 above.

Modifications of inflorescence structure characterise the genera of the family (f.l.). The form described above is regarded as the archetype from which other forms have been derived. Inflorescences with this structure are found in *Dryadodaphne*, *Nemuaron*, *Laurelia*, and, to an extent, *Laureliopsis*. In *Doryphora*, they are contracted to a simple though false* dichasium, and in *Atherosperma* to a single flower. *Daphnandra*, on the other hand, has a relatively elaborate inflorescence with accessory axillary flowers.

Modifications of the basic structure have apparently occurred both by processes of reduction, as in *Atherosperma* and *Doryphora*, and of elaboration, as in *Daphnandra*.

Evidence indicating that the inflorescence of *Daphnandra* has developed by augmentation is of three kinds: (1) the frequent presence of axillary accessory flowers or sometimes simple dichasia in the same position, (2) the occurrence of two or more whorls of bracteoles as the outer "sepaloid" parts of the perianth, and (3) the association of the most elaborate inflorescences with the smallest flowers in the family in a genus occurring uniquely in disturbed habitats. It may be that the combination of small flowers in elaborate inflorescences, in contrast to large flowers in contracted inflorescences (*Atherosperma*, *Doryphora*), is of advantage in

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* See chapter XIII.

disturbed and secondary rainforest seres.

Patterns of vascularisation in the peduncles of Atherosperma and Doryphora, which might be expected to show whether or how the inflorescences in these genera have become reduced, have never been studied in detail. Seemingly clear indications of what has happened are found in the ontogeny and gross morphology of the inflorescences in all genera. The stipitate unexpanded inflorescence buds of Daphnandra, Dryadodaphne, Nemuaron, and Laureliopsis are very like those of Atherosperma and Doryphora*. Their form suggests that the base internode of the primary peduncle (= inflorescence bud stipe) and base node bracts are homologous in all genera. The form of the base internode of mature primary peduncles in being different in dimensions, compression, and density of pubescence from that of successive internodes in those genera with elaborate inflorescences, and bearing often larger and more persistent bracts, is consistent with this interpretation. It indicates the base node as the site of inflorescence elaboration or reduction in the family. Accordingly, the inflorescence in Atherosperma and Doryphora may be visualised as having been arrested in its development, with its flowers confined to this node.

That the inflorescences of these genera are reduced through cessation of proliferation at the base node is particularly well shown in the two species of Doryphora, as described in chapter XIII. In Atherosperma,

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* As described in section 3 above.

the presence of stipes under pistilliferous and particularly staminate flowers in the axil of the subtending bracts, which themselves have a leaf-like rather than transitional tepal-like venation pattern, suggests that the main flower stalk is a peduncle (cf. Sampson 1967).

Bracts

The form, persistence, and position of the bracts and bracteoles in the inflorescences of the family varies strikingly between the genera. These characters have been used by most previous revisers* as principal taxonomic criteria for defining the genera and, in some cases, supra-generic taxa. Such an emphasis is not justified. As shown below, bract form and persistence vary in direct response to environmental pressures and can therefore not be regarded as reliable indicators of affinity, at least not above the rank of genus.

It has been mentioned that peduncular bracts are small and usually caducous well before flower-opening in those genera, *Daphnandra*, *Dryadodaphne*, *Laurelia*, and *Nemuaron*, which have relatively elaborate inflorescences of small to medium-sized flowers. They are most insignificant and earliest caducous in *Dryadodaphne* and *Nemuaron* which are confined to the lowest altitudes under the most uniform climates in the

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* Tulasne (1855), Bentham (1880), Pax (1889), Perkins and Gilg (1901), Perkins (1925), A.C.Smith (1941), L.S.Smith (1958), Hutchinson (1964).

family. The base node bracts at least are larger, more persistent, and often lignified in *Laurelia*. They are largest and most persistent in those genera, *Atherosperma*, *Doryphora*, and *Laureliopsis*, with reduced inflorescences of medium-sized to large flowers. These genera, with *Laurelia*, occur at the highest latitudes in the family where seasonal fluctuations of climate are most marked.

The correlation here between bract form and persistence with climate suggests that contracted inflorescences and large rather persistent flower enveloping bracts have evolved concomitantly to protect the developing inflorescence from the vicissitudes of the environment. Such a trend parallels the development of hairs on the vegetative shoots and inflorescences discussed in section 4 above, and short globose inflorescence buds in *Laurelia* (chapter XII). It also implies that the similarity between the bracts of *Atherosperma* and *Doryphora* may be just as likely the result of parallel evolution as of common ancestry. The former interpretation is consistent with the many differences between the two genera.

The structure and occurrence of bracteoles in several genera of the family have been found to be of hitherto unsuspected taxonomic significance. The regularity of perianth arrangement and number of tepals in *Atherosperma* and *Doryphora* indicates that they are lacking in these genera. Their absence may again be related to the reduced inflorescences in these genera and enlarged peduncular bracts that might be expected to assume their function. [It has been inferred above that the bracts in Atherosperma are peduncular, not pedicellar, in origin. Similarly in Doryphora, both pairs of bracts are borne on peduncule nodes, not pedicels, as described in chapter XIII.]

Bracteoles are present at the apices of the pedicels, sides of the floral hypanthium, or are quite contiguous with the perianth in all other genera of the family. They exhibit two trends concomitantly: (1) a progression up the hypanthium to a position contiguous with the perianth, and (2) the acquiring of a tepal-like form. What is regarded as the most unspecialised arrangement is found in Dryadodaphne and Laureliopsis. In these genera, a single pair of bracteoles are confined regularly (Dryadodaphne) or irregularly (Laureliopsis) to the apex of the pedicel and subtend the hypanthium.

Successive stages in the attachment of a single pair of bracteoles up the hypanthium towards the perianth are shown most clearly in Nemuaron and Laurelia. In Nemuaron, the bracteoles may be attached at the base of the hypanthium, where they are bract-like and caducous before anthesis like peduncular bracts, or towards the apex of the hypanthium subjacent to the perianth, where they are sepaloid and persistent with the perianth. Occasionally the bases of perianth-contiguous bracteoles are broadly decurrent on the hypanthium in the flower bud and would appear to indicate their concrescence with the hypanthium.

The bract-like structure of the bracteoles is almost completely lost in Laurelia. The bracteoles are almost indistinguishable from tepals as the outer pair of perianth parts in staminate flowers of both species of the genus and in pistilliferous flowers of *Laurelia novae-zelandiae*. Their bracteolar nature is nevertheless revealed by several characteristics described in chapter XII. Sampson (1967) has averred that there appears to be a gradation between "bracts" and perianth parts in *Laurelia novae-zelandiae* with transitional structures being inserted on the "receptacle" external to the perianth segments. This trend is well demonstrated by the bracteoles in the pistilliferous flowers of *Laurelia sempervirens* which are subjacent to the perianth, of more herbaceous texture, and markedly mucronate acute at the apices (f.8A).

The occurrence of bracteoles in *Daphnandra* is more complex. On grounds of structure and usually decussate arrangement, they are identified as the several outer pairs of herbaceous parts in the perianth (chapter XIV). Their position ± contiguous with the perianth, progressively tepal-like form, and number of more than one pair are regarded as specialised developments that have perhaps been initiated concomitantly with inflorescence augmentation in this genus.

Relationships of Inflorescence Structure

It seems established (cf. Sampson 1967) that the basic inflorescence structure in the families of the Monimiaceae alliance comprises a monopodial axis of varying elaboration, with decussate phyllotaxy, terminated by a simple dichasium. This form is adhered to strictly in Atherospermataceae and in *Hortonia*, which has small bracts resembling those of some members of the Atherospermataceae (*Daphnandra*, *Dryadodaphne*).

It is also found in many members of Monimiaceae, for example in *Hedycarya arborea* and *Wilkiea huegeliana*. In most genera of this family, however, there is a noticeable trend towards unequal elimination or elaboration of one or other opposite flower groups at the nodes of the primary inflorescence axis. As a result, the inflorescences often approach a sympodial*, clustered**, or monopodial structure with seemingly spirally arranged flowers***. Such modifications are even more marked in the *Siparuna* group in which, as in Monimiaceae, the bracts remain insignificant, and are very early caducous.

Among other lauralean families, the only inflorescence closely resembling that of the Atherospermataceae in structure is found in Gomortegaceae. It also comprises a monopodial axis bearing opposite flowers in decussate arrangement and terminates in a simple dichasium. All nodes are bracteate with small ± early caducous bracts. The pair of "bracteoles" subtending the flowers would seem to be analogous, if not homologous, with the bracteoles in *Dryadodaphne*. One anomalous feature is the occasionally terminal inflorescence.

The inflorescences of Lauraceae differ in being divaricately branched or clustered in the same way as those in Monimiaceae. Those in Calycanth-

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* *Tetrasynandra*, tropical species of *Hedycarya*.

** *Wilkiea* spp.

*** *Palmeria*.

aceae are largely single-flowered with a multi-bracteate rhachis.

7. Sexes of Flowers and Inflorescences

Vagaries in the sex of the flowers and inflorescences characterise the Monimiaceae alliance. Members of the Atherospermataceae are no exception to this rule.

The flowers of *Daphnandra*, *Doryphora*, *Dryadodaphne*, and *Nemuaron* are regularly bisexual. In *Laurelia*, the other genus of the tribe Laurelieae, flowers may be either staminate without vestiges of carpels, or pistilliferous and functionally unisexual with an androecium comprising more-or-less entirely sterile members. Stages of abortion of the analogues of the outer fertile androecium whorls of bisexual flowers are exhibited in the pistilliferous flowers of *L. novae-zelandiae*, in which several of the outer staminodes often retain apparently functional pollen sacs. Rarely dioecious or polygamous, the inflorescences themselves are usually monoecious with staminate flowers occupying terminal and basal nodes of the primary peduncle and any secondary peduncles, and pistilliferous flowers the intermediate nodes (f. IE, 8). Staminate flowers predominate in numbers. Where pistilliferous flowers occur in the terminal dichasium of the primary peduncle, they are almost invariably one or both of the flowers flanking a central staminate flower. No explanation has been offered for this peculiar yet consistent disposition of unisexual flowers.

The two genera of the tribe Atherospermateae also have peculiar patterns of sex distribution. The flowers of *Laureliopsis* are mostly bisexual, but the central flower in the terminal dichasium of the inflorescence is often or usually staminate. Bisexual flowers at nodes below are also occasionally functionally female with partial to complete abortion of the anthers. The single flowered inflorescences of *Atherosperma* are unisexual; flowers at ultimate branchlet nodes are staminate, and those below are pistilliferous with staminodes. This arrangement resembles that in *Laurelia* and *Laureliopsis* except that here the position concerns inflorescences on a stem, not flowers in an inflorescence. As both the flowers of *Laurelia* and *Laureliopsis* and the inflorescences of *Atherosperma* occur at the ends of "branchlets", the factors governing sex expression might well be the same in each of these genera.

Transitions as described above between bisexual and unisexual flowers in *Laureliopsis* and in pistilliferous flowers of *Laurelia novae-zelandiae*, together with the presence of staminodes in all pistilliferous flowers, indicates that unisexuality is a derived condition. It is probably the result of independent attempts in the family to promote cross pollination. The polygamous inflorescences in *Laureliopsis* appear to represent early, even incipient, stages in the evolution of unisexual flowers, a feature consistent with the generally unspecialised characteristics of this genus.

Because flower parts are initiated in acropetal succession (Sampson 1967), it is easy to understand why there are no vestiges of carpels in staminate flowers; they are simply not cut off. Accordingly, the retention of staminodes successive to stamens in the staminate flowers of *Laureliopsis* may be regarded as transitional to the development of flowers with stamens only, as occur in *Atherosperma* and *Laurelia*. The development of the atherospermataceous pistilliferous flower is more complex if one assumes that the staminal structures (staminodes) are formed so that carpels can be initiated subsequently. The consequent sterilisation of staminal parts in this flower requires further physiological steps. Testifying to the more complicated processes involved in the development of these flowers is the incomplete suppression of apparently functional stamens in *Laurelia* and *Laureliopsis*.

Many taxa within the Monimiaceae alliance have unisexual flowers, notably the Monimiaceae, *Peumus*, and the *Siparuna* group. In contrast to monoecious Atherospermataceae, they are predominantly dioecious. Moreover, the pistillate flowers of Monimiaceae have lost, if they ever had them, all vestiges of the staminodal structures so characteristic of both bisexual and pistilliferous flowers of the Atherospermataceae, and to an extent *Hortonia*. *Hortonia*, like most genera of the Atherospermataceae, has unmodified bisexual flowers.

Bisexual flowers occur almost invariably in the related lauralean families Lauraceae, Gomortegaceae, and Calycanthaceae.

8. Pollination

Pollination in the Atherospermataceae is effected by insects, evidence for which comes from three sources. First, Sampson (1967) recorded insects, including the blowfly Calliphora, visiting the flowers of Laurelia novae-zelandiae.

Second, showy white flowers occur in Atherosperma and Doryphora, and areas of red pigmentation are developed in the flowers of species in most other genera, as described in the following section. Whether the red pigmentation serves to attract insects is uncertain because insects are not in general sensitive to the higher wave-lengths of the spectrum which include red. The very pattern of such pigmentation on and adjacent to stamens suggests, however, that it specifically leads insects to the nectariferous staminal glands. Moreover, some red-coloured flowers have been shown to attract bees by virtue of the amount of ultra-violet light which they reflect (Wigglesworth 1964). The blowfly Calliphora, which visits the flowers of Laurelia novae-zelandiae, is sensitive to red light (Sampson l.c.).

Third, the paired glands on the stamens are nectariferous in all members of the family, or at least in those of the tribe Laurelieae. That these glands function to promote pollen distribution by insects is obvious from their form and orientation to the direction of dehiscence of the stamens, aspects of which are described in chapter IX. Sampson (l.c.) has shown furthermore that the glands in Laurelia novae-zelandiae secrete sucrose with perhaps traces of raffinose, a nectar characteristic of some ranalean groups. ~~(cf. Percival 1961).~~

Protandry in all genera may promote cross fertilisation; but this can hardly be very effective because in those genera with bisexual flowers, flowers open at different times on one inflorescence while in genera with unisexual flowers, flowers of both sexes always occur in the one tree* or on the one inflorescence. As sampson (l.c.) has pointed out, self fertilisation can be expected to be of much more common occurrence than cross fertilisation, unless some form of self-incompatibility mechanism were operating. It is not known whether such a mechanism occurs in Atherospermataceae.

9. Flower Pigmentation

The colour of the flowers in most members of the family is pale green, or whitish green, or slightly yellowish on the upper face of the perianth and the androecium parts (most species of Daphnandra, one, sometimes two species of Dryadodaphne, Laurelia, Laureliopsis, and apparently Nemuaron). The large flowers of the two remaining genera, Atherosperma and Doryphora, are generally white.

The consistent occurrence of a pale marone to purple-red pigment in the flowers of some species of at least five genera, Atherosperma, Daphnandra, Dryadodaphne, Laurelia, and Laureliopsis, is a characteristic feature of the family. Flowers may be entirely reddish, as in species

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* Dioecism has never been verified in any genus of the family.

of *Dryadodaphne* and one of *Daphnandra*, or only the androecium may be coloured as in *Laureliopsis*, and in part *Atherosperma* and *Laurelia*. In *Atherosperma*, the red pigmentation is largely confined to the staminate flowers; in *Laurelia*, it is confined to the anther valves which stand out conspicuously in otherwise pale green flowers.

Because of entomophily, it is likely that green colours represent the unspecialised condition and patterns of red pigmentation the derived in atherospermataceous flowers. White colour may well be correlated with the development of large size in the showy flowers of *Atherosperma* and *Doryphora*.

10. Flower Morphology

Atherospermataceous flowers differ from those in other families of the Moniniaceae alliance in their perigynous hypanthia, choritepalous imbricate perianths, and androecium comprising in bisexual flowers and some unisexual forms both stamens and staminodes arranged respectively in acropetal sequence. These features of flower structure are discussed in more detail below. The ontogeny of floral parts has been recorded in detail in *Laurelia novae-zelandiae* by Sampson (1967), but in no other species.

Floral hypanthium

Compelling evidence that the cupular to poculiform hypanthium in all genera of the Atherospermataceae has been formed by concrescence of the basal parts of the perianth and androecium is furnished by the gross form of the mature fruiting hypanthium in *Laureliopsis*, *Doryphora*, and *Laurelia sempervirens*, as described in section 16. Eames (1961) has emphasised that the perigynous receptacles of most angiosperms are constructed in this way.

The various positions occupied by the perianth and androecium parts on the hypanthium in all genera of the Atherospermataceae also provide a clue to its construction. They are characteristic of the two tribes of the family. In one, comprising *Atherosperma* and *Laureliopsis*, the hypanthium is shallowly cupular, and tepals and androecium parts are attached successively down its inner face towards the carpels. In the other, exemplified by *Dryadodaphne*, *Laurelia*, and *Nemuaron*, the tepals and androecium parts are confined to a rather flat or convex rim well above the carpels, or attached down the outer face of the hypanthium. The type of arrangement in the former tribe is thought to be less specialised because the parts are less concrescent. The shallower hypanthium may, in fact, represent a transitional stage in the evolution of a deeply poculiform hypanthium with a confined and well-defined rim. Such an interpretation is consistent with the generally unspecialised characteristics of the two genera of the Atherospermateae.

Whether or not the perianth and androecium are the sole contributors to the hypanthium is not known. The attachment of the carpels and nutlets to the (lower) sides of the hypanthium chamber, particularly in the fruit of *Nemuaron*, the retention of elongated staminodes free from the hypanthium wall in both *Atherosperma* and *Laureliopsis*, and the frequent thickening of the pedicel below the bracteole scars in the fruiting hypanthium of *Dryadodaphne*, suggests that at least some axial tissue has been incorporated in the base of the hypanthium.

Trends from hypogyny to perigyny and even epigyny occur throughout lauralean plants. Elsewhere within the Monimiaceae alliance, hypanthia are developed consistently only in the *Siparuna* group. There, however, more-or-less extensive cohesion and adnation of perianth parts has led to the formation of a velum (Money et al. 1950), quite unlike anything found in the Atherospermataceae. The receptacle in flowers of both sexes in Monimiaceae, and in *Hortonia* and *Peumus*, is patelliform to rather cupular.

Among other related families, the floral hypanthium of the Calycanthaceae bears a striking resemblance to that in the Atherospermataceae. From its scars, it appears to have been formed in a similar way from coalescence of bracteoles and/or perianth parts (cf. Baillon 1869). In the Lauraceae, a family usually characterised by small hypogynous to slightly perigynous patelliform receptacles, thin-walled hypanthia also occur in several genera. These are apparently derived from perianth parts (Core 1955, Lawrence 1951), and enlarge into a cupule partly or completely enveloping the drupe.

The "receptacle" in Gomortegaceae shows perhaps as close similarities to the hypanthium of the Atherospermataceae as any. Apparently a hypanthium, it is also thick with a well-defined rim. It differs, however, in being adnate to the carpels. Such differences need not be of fundamental taxonomic significance as trends from perigyny to epigyny are exhibited in the related *Siparuna* group, and are known to occur also within a number of angiosperm families, such as Ericaceae, Myrtaceae, and Rosaceae.

Arrangement of Flower Parts

The perianth of *Atherosperma*, *Dryadodaphne*, and *Laureliopsis*, and their androecium in bisexual flowers, are arranged in a definite number of tetramerous whorls on a decussate plan. The perianth in each of these genera is consistently 8-partite in two often slightly dimorphic whorls. In *Doryphora aromatica*, the tepals are arranged in a single ± tetramerous whorl; the androecium is not so consistently quadripartite in arrangement, often comprising 5 stamens in an outer main whorl and two inner whorls of ± 3-6 staminodes each.

In *Doryphora sassafras* and *Nemuaron* , the arrangement of parts is still cyclic but varies between tetra- and tri-mery. Excluding bracteoles, *Nemuaron* has 4 or 6 tepals in decussately arranged pairs, usually 6 stamens in one main whorl, and ± two whorls of 3-4 staminodes each. The flowers of *Doryphora sassafras* are more markedly trimerous, comprising a regularly 6-partite perianth in two obscure whorls, usually 6 stamens and 6 stamen-like staminodes in consecutive whorls, and (4-)8-12(-14) small staminodes in one or two inner whorls.

In the remaining two genera, *Daphnandra* and *Laurelia*, the number of flower parts is less regular and their arrangement often sub-spiral.

The number and disposition of the tepals is also difficult to determine because of the presence of perianth bracteoles in both these genera. As well as the single pair of bracteoles in all flowers, *Laurelia* has(2-)3-6(-10) tepals in staminate flowers and (2-)3-8(-12) tepals in pistilliferous flowers, all in one to three obscure whorls. Similarly in *Daphnandra*, the perianth comprises two (or three) outer whorls of (4-)5(-6) bracteoles and one or two inner whorls of (4-)6-8(-10) tepals. Its androecium, of (3-)4-7(-9) stamens and (3-)5-10(-13) staminodes, is arranged in three to five obscure whorls or a compressed spiral. In both these genera, the androecium parts approach a spiral arrangement more closely than do the tepals which in turn are less strictly decussate in arrangement than the outer pairs of bracteoles.

The androecium in the staminate flowers of *Atherosperma* and *Laurelia* comprises (10-)12- ± 20 and (4-)6-11(-12)stamens respectively distributed in spiral arrangement over the patelliform receptacles, as in genera of the Monimiaceae and *Peumus*. In the staminate flowers of *Laureliopsis*, both stamens and staminodes are disposed in successive tetramerous whorls. The greatest number of staminodes occur in the pistilliferous flowers of *Atherosperma* and *Laurelia*, numbering 24-30(-40) in the former and (10-)12-32(-46) in the latter, in an irregular number of whorls.

In summary, a cyclic arrangement of flower parts in tetramerous whorls is the most common in the family. It is found exclusively in the two genera *Dryadodaphne* and *Laureliopsis* which, in other characters, are regarded as the least specialised in the family. A trend away from this plan towards irregularity in number and spiral arrangement of parts is most marked in *Daphnandra* and *Laurelia*. Only rarely do the number of tepals and stamens present in bisexual flowers exceed 8 in species of these genera. Variation in the number of flower parts is greatest in staminodes, less in stamens, and least in tepals.

The number of carpels present appears to be unrelated to the number and arrangement of perianth and androecium parts. It varies from (3-) 4-8(-10) carpels in several species of *Daphnandra* and *Nemuaron* to up to 30-40(-50) in species of *Atherosperma* and *Laurelia*. Like the staminodes, carpels ~~they~~ are greatest in number in those genera with functionally unisexual flowers. That they are spirally arranged is confirmed by Sampson's (1967) observations of carpel ontogeny in *Laurelia novae-zelandiae*.

Although a flower form of a variable number of parts in spiral arrangement is generally postulated as the primitive condition in angiosperms (Zimmermann 1959, Thorne 1963, Hutchinson 1964), the tetramerous flower with whorled parts is regarded as the less specialised, indeed basic form in the Atherospermataceae. Money et al. (1950) have already pointed out that the arrangement of the perianth in all members of the Monimiaceae alliance is fundamentally decussate with transitions to cyclic. Moreover, if the androecium parts in the atherspermataceous flower have developed from tepal-like structures, and the tepals in turn from bracts, as appears likely from evidence presented in the following sections, then the flower formed from these organs may be expected to exhibit a basically tetramerous cyclic, rather than spiral plan, because of the decussate phyllotaxy of the atherospermataceous inflorescence.

The flower with an irregular number of parts disposed in an apparent spiral, of the type found in Daphnandra and Laurelia, is therefore regarded as derived. A clue to its development may be provided by the partly or frequently trimerous flowers in Doryphora and Nemuaron. The suppression of single members in originally tetramerous whorls of parts would give rise to this arrangement. More extensive suppression of members in successive whorls in a multiseriate tetramerous flower would lead ultimately to a spiral arrangement of parts. The fact that more than 8 true tepals occasionally occur in the flowers of Laurelia and Daphnandra does not necessarily contradict this supposition as processes of elaboration may accompany those of suppression; it has already been suggested (section 6) that the inflorescence of Daphnandra is augmented.

As mentioned above, all members of the Monimiaceae alliance have a basically decussate arrangement of flower parts. Even the distinctively calyptrate and variably concrescent perianths of most genera in the Monimiaceae and Siparuna group show traces of a tetramerous plan. They are accompanied by a trend to valvate aestivation. Their stamens, moreover, are more variable in number, and parallel the condition in the staminate flowers of Atherosperma and Laurelia. Those less specialised members of the Monimiaceae with free tepals, such as Hedycaria, differ from both Atherospermataceae and other Monimiaceae in their rather irregular number of parts. Peumus, like Hedycaria, has ca 10-12 free tepals on flowers of both sexes, and numerous stamens in staminate flowers.

In view of its suggested unspecialised form (Money et al. l.c.), Hortonia has a flower that is unexpectedly irregular in its number of parts, bearing little apparent relation to a decussate or tetramerous plan. The perianth, with imbricate aestivation, resembles the derived arrangement in Daphnandra to a remarkable degree in comprising two outer decussate pairs of fleshy tepals (≡ bracteoles), and numerous (15-20) petaloid tetals in several whorls. The androecium comprises 7-9 stamens with or without inner whorls of staminodes.

The plan of the flower of Lauraceae is fundamentally different in being ± trimerous (Sastri 1963), with often antipetalous stamens. Staminodes are inconsistent in occurrence. In Calycanthaceae, the flowers are generally multiseriate with series of tepals, stamens, and stamen-like staminodes arranged in ± spiral succession (cf. Baillon 1869).

The arrangement of flower parts in Gomortega exhibits perhaps the closest similarities to that in Atherospermataceae. Accounts of the plan of the Gomortega flower are conflicting. Baillon (1869) implies that it is tetramerous and related to that of the Monimiaceae alliance, whereas Stern (1955) suggests that it is trimerous and associated with the condition in Lauraceae. As Stern (l.c.) has pointed out, the basic structural plan of the Gomortega flower is rather obscured by the variation in numbers of floral parts, resulting partly from "frequent transitions between the members of the perianth and androecium".

In the single collection with flowers examined by me (Rossovsky 2:US), the perianth, in comprising seven parts in three whorls of 2+2+3, shows transitions from a decussate to trimerous arrangement. Its androecium, moreover, comprises ± 8 stamens and 2-3 staminodes in heteromorphic di-, tri, or tetra-merous whorls or ± sub-spiral disposition. This arrangement of parts is somewhat intermediate between the conditions prevailing in Atherospermataceae and Lauraceae. The aestivation of the perianth in all three families is imbricate.

Perianth Structure

The choritepalous perianth of the atherospermataceous flower is, like that in many other groups of woody ranalean plants, hardly differentiated into outer sepaloid and inner petaloid parts. These parts are variously coloured (section 9), and of a variably thick petaloid nature. In species of Atherosperma, Doryphora, Dryadodaphne, and Laureliopsis, the inner series of tepals may differ slightly from the outer in dimensions, more petaloid texture, and sparser hairiness, and suggests an incipient stage of differentiation. As has been mentioned, the perianth structure in Daphnandra, Laurelia, and Nemuaron is complicated by the addition of one or more pairs of bracteoles.

The size of the perianth, reflecting in turn the size of the flower, differs between rather than within the genera of the family. Being

There are also differences between the genera in the texture of the tepals, which, irrespective of tepal size, is thickest in *Dryadodaphne* and *Nemuaron*, and thinnest in *Daphnandra* and *Doryphora*.

That the perianth has been formed from bract structures is indicated by (1) the gross transitions of herbaceous bracteoles to tepal-like structures contiguous with the perianth in *Daphnandra*, *Laurelia*, and *Nemuaron*, (2) the tepal-like bracts and bracteoles, and bract-like tepals in *Laureliopsis*, and (3) the patterns of venation in the bracts and tepals. The way in which bracteoles ascend the hypanthium wall to a position subjacent to the perianth while assuming a tepal-like form in *Nemuaron* and *Laurelia* has been described in section 6. In *Daphnandra*, moreover, the inner bracteoles closest to the tepals are larger and more obtuse than the outer, and have broad petaloid margins transitional in form between those of bracteoles and tepals. The inner pairs of bracts in the inflorescence of *Doryphora* are also remarkably similar to the tepals in their texture and venation pattern.

Venation patterns in the bracts and tepals of *Atherosperma*, *Doryphora*, and *Laurelia* have been studied by Sampson (1967). He has inferred, on the basis of similarities in these patterns, that the tepals in the three genera have been derived from bracts, consistent with Hiepko's (1965a,b) conclusion that the perianths of woody ranalean plants are bracteoid in nature. The venation patterns of the bracts in these genera are leaf-like and pinnate in arrangement. The presence of a single mid-nerve, as occurs in *Atherosperma* and *Doryphora*, is considered to represent the primitive condition.

On the assumption that the most primitive type of tepal venation is that which most clearly resembles the pattern in bracts and leaves, the pinnate venation pattern found in all perianth parts of *Doryphora* and *Laureliopsis* is unspecialised. Accordingly the palmate-parallel system of 3 or 5 main vascular strands in the tepals of *Atherosperma*, *Daphnandra*, and, to an extent, *Laurelia*, may be regarded as derived. The pattern of venation in the thick tepals of *Dryadodaphne* and *Nemuaron* is difficult to discern and has not been examined closely; it appears to be transitional between pinnate and palmate-parallel.

The distinctive nature of the variably coalesced perianth of Monimiaceae and the *Siparuna* group has been stressed above; only the components of the choritepalous perianths of *Hedycaria* and allied genera, *Peumus*, and *Hortonia* bear any resemblance to those in the Atherospermataceae. The venation pattern in the tepals of *Hortonia* is of the pinnate type, with obscure nerves. In *Peumus*, it approaches the palmate-parallel form.

The perianths of Lauraceae, Gomortegaceae, and Calycanthaceae have not been studied in detail but are similarly choritepalous, and, like those in the Atherospermataceae, comprise tepals scarcely or not at all differentiated into outer sepaloid and inner petaloid whorls. The tepals are particularly thick, herbaceous, and obscurely nerved in *Gomortega*.

11. Androecium

The androecium in the Atherospermataceae, with its biglandular bisporangiate valvular dehiscing stamens and staminodes arranged in bisexual flowers in acropetally successive whorls, is unlike that of any other member of the Monimiaceae alliance. Features of the ontogeny of its component parts have been studied in detail in *Laurelia novae-zelandiae* by Sampson (1967), but not in any other species. The general characteristics and form relationships of the stamens, staminal glands, and staminodes are discussed below.

Stamen Form

The form of the stamens (and their direction of dehiscence) differs between but hardly within the genera. Together with the form of staminal glands, it is perhaps the most reliable taxonomic character for distinguishing the genera; it is also characteristic for the two tribes within the family.

In several genera, the stamens are elongated into slenderly aristate (*Doryphora*) or variously expanded (*Dryadodaphne*) tips. In others, they are truncate, ± slenderly so in *Atherosperma* and *Laureliopsis*, and broadly in *Daphnandra*. Variation in the form of the stamen apex between species of a genus occurs only in *Dryadodaphne*, and there it is shortest and apiculate in the least specialised species, *D. pterandrica**.

It is difficult to decide which of these forms are unspecialised and which derived. But it is tempting to assume that the slender initially rounded-truncate stamens of the type found in *Laureliopsis* represent the unspecialised condition, because it is easy to visualise the development of either a slenderly aristate or short truncate stamen from them. The stamens of *Laureliopsis* (and *Daphnandra*) are quite rounded at the apex when young, and become truncate or concave truncate after dehiscence.

The anther valves are most markedly elongate-elliptic in *Atherosperma* and *Laurelia*, and characteristically circular in *Doryphora* and to an extent *Daphnandra*. The direction of dehiscence may be latrorse (*Laureliopsis*, *Dryadodaphne pterandrica*), tending introrse (*Doryphora*, *Laurelia*, and *Nemuaron*), tending extrorse (*Dryadodaphne* spp.), or quite extrorse (*Atherosperma*, *Daphnandra*). Latrorse dehiscence may be regarded as the unspecialised condition, and the greatest deviations from it the most derived. Evidence for this comes from the ontogeny of the anthers in both *Atherosperma* and *Daphnandra*. In very young stamens, the pollen sacs are disposed on the lateral faces of the anther. As the anther matures, both gradually converge on the abaxial face.

The anthers themselves are apparently regularly bisporangiate, a feature overlooked by Davis (1966) if she intended to include the Atherospermataceae in her review of the embryological characters of the Monimiaceae. Sampson (1967) examined the anther structure in *Laurelia novae-zelandiae* and, in verifying the presence of only two pollen sacs, concluded that it was derived from a tetrasporangiate anther, the prevalent condition in angiosperms and other members of the

Monimiaceae alliance.

In view of the widely held concept (cf. Foster and Gifford 1959, Eames 1961) that the stamens of woody ranalean plants are modified microsporophylls, attention is drawn to the occasional stamens transitional in form between tepal and stamen in flowers of both species of *Doryphora* (chapter XIII). Sampson (l.c.) also found that, though the patterns of vascularisation in the stamens were particularly variable, some of them were characteristic of the pattern in tepals*. Being differentiated into filament, connoctive, and anther, the stamens of the Atherospermataceae are nevertheless considerably more advanced in their form than those in many woody ranalean plants.

With the exception of the *Siparuna* group, the stamens in all other members of the Monimiaceae alliance differ in possessing apparently tetrasporangiate anthers dehiscing by slits. The mode of anther dehiscence has been stressed by Perkins (1898) and others as one of the principal differences between Atherospermataceae and Monimiaceae, *Hortonia* and *Peumus* included. The anthers of the Monimiaceae, moreover, exhibit a marked tendency to become sessile on the receptacle; the valvular stamens of the *Siparuna* group are similarly short and lack the modified, often prolonged connectives that characterise the Atherospermat-

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* Money et al. (1950) figure the stamens of *Atherosperma* and *Daphnandra* with a single trace only. The vascularisation of the stamens in other genera of the family has not been studied.

aceae. Other differences involving the presence or absence of staminal glands are discussed below.

Stamens with valvular dehiscence are rare in the angiosperms, and known elsewhere only in the Berberidaceae, Hamamelidaceae, and several lauralean families. Their occurrence in all these groups is thought to be largely the result of parallel evolution (Hutchinson 1964, Sampson l.c.). But there can be no doubt that the Atherospermataceae have affinities with the Lauraceae and Gomortegaceae in this character. The anthers in Lauraceae may be bi- or tetra-sporangiate.

The stamens of *Gomortega* are like those of the Atherospermataceae in being apparently bisporangiate, but differ in their strikingly variable form. The outer pair are usually tepal-like and eglandular with the small pollen sacs borne toward the apex on the adaxial face, in a similar way as those in *Austrobaileya* (cf. Canright 1952, Foster and Gifford l.c.). The inner stamens are smaller, biglandular, more clearly differentiated into anther and filament, and resemble in general form those of the Atherospermataceae, particularly *Laureliopsis*.

Staminal Glands

The pair of staminal glands which accompany each stamen and sometimes outer staminodes are constant in form and position for each genus of the Atherospermataceae, except to an extent *Dryadodaphne*, and are characteristic of the tribes. Varying from stipitate stamen-like (*Atherosperma*, *Laureliopsis*) to planate wing-like (*Dryadodaphne*, *Doryphora*), or peltate

(*Daphnandra*, *Laurelia*, *Nemuaron*) structures, they are attached along the sides or abaxial face of the filament. As pointed out in chapter IX and section 8 above, their various modifications of form and orientation are related to their function as nectaries.

Differing views on the origin of such glands in lauralean plants have been put forward by Eichler 1878, Mez 1889, Glück 1919, Engler 1926, Daumann 1931, Money et al. 1950, Kasapligil 1951, Eames 1961, and Sampson 1967. Of these, that interpreting the glands as staminodes which have become aggregated in pairs with fertile stamens, and subsequently transformed into nectaries (Money et al. l.c., Eames l.c., Sampson l.c.) appears to be the one most applicable to the Atherospermataceae. It is supported by patterns of stamen and gland vascularisation: these are variably independent of each other in otherwise "fused" tissues (Money et al. l.c., Eames l.c., Sampson l.c.).

Also consistent with this interpretation is the stamen-like shape of the glands in *Laureliopsis* and *Atherosperma*, genera which in other characters are the least specialised in the family. The glands are not particularly oriented to the position and direction of anther dehiscence, and seem to be poorly modified as nectaries. Furthermore, they are almost as large and cylindrical as the young stamen itself at early stages of stamen ontogeny, but are subsequently outstripped in development.

There has been no convincing explanation as to why there are precisely two glands associated with each stamen; one is not attempted here.

On the assumption that they are staminal in origin, glands with a stamen-like form and attachment towards the base on the sides of the staminal filament may be considered to represent the unspecialised condition in the family. Glands combining all of these features are found in *Laureliopsis*. Those in *Atherosperma* are similar, differing only in their abaxial position on the filament.

The most specialised forms then are the peltate flaps in *Daphnandra* and *Laurelia*, which are attached respectively to the abaxial and lateral-adaxial faces of the filament, and the lanceate-deltate structures in *Doryphora* that are compressed in the same plane as the filament. The form of the basal sub-peltate glands in *Nemuaron* and wing-like glands in *Dryadodaphne pterandrica* may be visualised as representing transitional stages in the evolution of glands of the type found in *Laurelia* and *Doryphora* respectively.

Paired staminal glands are of rare occurrence in other members of the Monimiaceae alliance, being found only in *Hortonia*, *Monimia*, and *Peumus*. They are also absent in the Calycanthaceae. On the other hand, they occur regularly in Lauraceae and Gomortegaceae, and together with the valvular dehiscence of the stamen, provide cogent evidence of relationship with Atherospermataceae. Whether or not the glands in Atherospermataceae and Lauraceae are homologous, or have evolved in parallel, has not been satisfactorily established. Nevertheless, according to the observations of Eames (l.c.) and Sampson (l.c.), those in Lauraceae, and Gomortegaceae, appear to represent staminodes modified in much the same way as in the Atherospermataceae.

Staminodes

The several whorls of staminodes that succeed the stamens in bisexual flowers or replace them in pistilliferous flowers are another distinctive feature of the androecium of the Atherospermataceae. Their arrangement in the flowers of the genera has been described in detail in section 10.

The shape of the staminodes varies from stamen-like or batilliform (*Daphnandra* partly, *Doryphora* p.p., *Laurelia*, *Laureliopsis* p.p., and *Nemuaron*) to rather oblong, slenderly deltoid, scale-like, or subulate (*Atherosperma*, *Daphnandra*, *Doryphora* p.p., *Dryadodaphne*, and *Laureliopsis* p.p.). The flat expanded or scarious apices developed more-or-less distinctly in all genera except *Doryphora* and *Dryadodaphne* appear to represent the anther portion of the functional stamen. Sampson (1967) came to the same conclusion in respect of the staminodes of *Laurelia novae-zelandiae*. In *Doryphora* and *Dryadodaphne*, the respectively long slender attenuate and short acute staminode tips appear to be homologous with the produced connectives of the functional stamens.

Generally isomorphic in other genera, the staminodes in *Laureliopsis*, *Doryphora*, and to an extent *Laurelia sempervirens* vary much in form. In *Laureliopsis*, staminodes of the outer whorl are stamen-like whereas those of inner whorls are scale-like. Such an arrangement also occurs in *Doryphora* but differs in that the inner staminodes have subulate apices. The several outer whorls of staminodes in *Laurelia sempervirens* comprise almost identical batilliform staminodes, but the innermost whorl crowning the rim of the hypanthium is of densely hairy deltate scales.

It is difficult to determine whether this dimorphism represents a derived condition through elaboration or a primitive state in which some staminodes have not yet been lost. It is not unlikely that the inner staminodes in these three taxa are homologous. Evidence for this comes from their similarity of form in *Laureliopsis* and *Laurelia sempervirens*, and their habit of recurving in *Doryphora* when fruiting is initiated, in the same way that the inner elongated staminodes do in *Laureliopsis* to disseminate nutlets. Such homologies would suggest that the androecium with dimorphic staminodes is relatively unspecialised.

It seems that the inner staminodes or their homologues are the ones most likely to have been suppressed in the development of an androecium with isomorphic staminodes. Their diminution can in fact be traced from *Laureliopsis*, in which they are elongated in lieu of the hypanthium to enclose the nutlets in the fruit, to *Doryphora* and *Laurelia sempervirens*, where they are only vestigially present on enlarged fruiting hypanthia. Those genera with ± isomorphic staminodes all have similarly enlarged fruiting hypanthia to enclose the nutlets.

Occasional transitions from fully functional stamens to staminodes with aborted anthers, by way of partial abortion of one or other of the pollen sacs, occur in the androecium of most genera. Such transitional forms are particularly frequent in *Doryphora aromatica*, and are represented in *Dryadodaphne pterandrica* by dimorphic stamens.

Reduction and abortion of staminal glands occur concomitantly with

Laureliopsis and *Doryphora*, and infrequent, often solitary, in other genera. They never assume the characteristic form of their counterparts on fully functional stamens, as a rule merely forming small, rounded, rather ellipsoidal protuberances on the base of the staminode.

As pointed out in sections 7 and 10, staminodes are lacking in all other members of the Monimiaceae alliance except the relatively unspecialised genera, *Hortonia* and *Peumus* (Money et al. 1950), are inconsistently present in Lauraceae, and regularly present in Gomortegaceae and Calycanthaceae.

12. Features of Microsporogenesis

Aspects of microsporogenesis have been investigated briefly in *Atherosperma* by Sastri (1963) and in detail in *Laurelia novae-zelandiae* by Sampson (1967). No data are available for other species of the family.

Sporogenous and wall tissue development in *L. novae-zelandiae* were found to be like that in *Hedycarya* (Monimiaceae). The tapetum is bi-nucleate and of the secretory type. In *Atherosperma*, by contrast, an amoeboid tapetum has been recorded. There appears to be similar variation in tapetum types in Lauraceae (Sastri l.c., Sampson l.c.).

Cytokinesis in *Atherosperma* is of the successive type (Sastri l.c.), whereas in *Laurelia novae-zelandiae* it is simultaneous (Sampson, pers. comm.). Such differences suggest that these two modes of cytokinesis may not have much taxonomic significance, particularly as there is a far greater variety in the modes of microspore cytokinesis among woody ranalean families than in any other angiosperm order. In *Hedycarya arborea* (Sampson l.c.) and Lauraceae (Sastri l.c.), it is simultaneous. In Atherospermataceae, Sampson's observations indicate that simultaneous cell wall formation as found in *Laurelia* is the derived type.

Though it has been suggested that different types of tapetum and cytokinesis in lauralean plants do not have fundamental taxonomic signifiance, it would be valuable to show, by investigation of the remaining genera of the Atherospermataceae, whether the types occurring in *Atherosperma* and *Laurelia* are characteristic of the two tribes recognised in the family.

Differences in the reported mode of cytokinesis in these two genera are particularly intriguing in view of the likelihood that the pollen tetrads formed in each are of the same (tetragonal) type, as concluded below. Eames (1961) has reiterated that tetrahedral tetrads usually result from simultaneous divisions of the type recorded for *Laurelia novae-zelandiae*.

13. Pollen Grains

The uniformly syncolpate, reticulately sculptured, medium-sized atherospermataceous pollen grain is virtually unique among angiosperms. Only the essentially tetragonal arrangement of ~~its~~ the tetrads indicates relationship with the Monimiaceae, as exemplified by the coherent tetragonal tetrads in *Hedycarya*.

Variation in Surface Structure

The form of the pollen grain is remarkably uniform throughout the family. Even the more obvious apparent differences in reticulate sculpturing between the species of several genera, notably *Daphnandra* and *Laurelia*, are vague and difficult to assess.

The genera of the family may nevertheless be grouped in two ways according to their pollen characters. In one, *Atherosperma* and *Doryphora*, with relatively ellipsoidal pollen and very finely reticulate sculpturing, may be separated from the remaining genera which have more spheroidal pollen and more irregularly reticulate surface sculpturing. In the other, *Daphnandra*, *Dryadodaphne*, *Laureliopsis*, and *Nemuaron*, with 1-2 relatively irregular and/or short colpi transversales, may be distinguished from *Atherosperma*, *Doryphora*, and *Laurelia* which are characterised almost invariably by two relatively regular and long colpi.

The latter grouping is more likely to be the significant one, in view of the relationships between the genera according to other morphological characters, and would imply that poorly-defined colpi varying from one to two per grain, as found in *Laureliopsis*, *Daphnandra*, and *Dryadodaphne*, represent an unspecialised condition for pollen in the family. Though such conclusions appear to be consistent with the hypothesis of Money et al. (1950) for the development of dicolpate from monocolpate pollen in this and other woody ranalean groups, it must be emphasised that Money et al. based their interpretation on the meridional not equatorial orientation of the colpi. Rather, the ill-defined nature of the furrows in Laureliopsis and other genera suggests that atherospermataceous pollen could be derived just as easily from an inaperturate grain of the form presently found in the related families Gomortegaceae, Lauraceae, and Monimiaceae.

The importance attached here to the form and size of the colpi may, nevertheless, be exaggerated because of the extent to which they may be affected by acetolysis. The effect varies from preparation to preparation. However , because many grains remain intact after the process, yet may be fractured along the syncolpus by mere heat drying*, it may be that acetolysis does not affect the original colpus size much.

Discrepancies in the shapes and sizes of the colpi between those described here and those briefly discussed and figured by Money et al. (l.c.) and Couper (1960b) for the same species and genera may also reflect different methods of pollen preparation rather than actual differences between the pollen. Money et al. (l.c.), although they did not specifically state so, are likely to have mounted their pollen material in lactic acid.

Orientation of the Syncolpus

Money et al. (l.c.) have interpreted the dicolpate furrow of the atherospermataceous pollen grain as being oriented on a meridian, encircling the grain from pole to pole. According to this interpretation, they suggest that the furrows of atherospermataceous pollen may have developed from a single primitive colpus on the distal face of the grain,

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* Observed in Dryadodaphne pterandrica (Schodde 4816).

of the kind found in *Degeneria* and magnoliaceous genera. Lacking living flowering material, they were unable to form any definite conclusions. Sampson (1967), furthermore, was unable to find any indication of furrow orientation.

Erdtman (1952, f.157E), on the other hand, illustrates the pollen of *Atherosperma* with the furrow oriented equatorially. Although mentioning the interpretation of Money et al. (l.c.), he does not discuss his alternative or how he reached it. He alludes, however, to relationships between monimiaceous pollen and the dicolpate pollen of Calycanthaceae in which, according to the tetrads of *Chimonanthus*, the colpi are also ± equatorial.

In the present study, observation of the young grains in the tetrad about the time of breakdown of the pollen mother cell wall was only possible in *Atherosperma moschatum* (Schodde 3248), owing to the rarity of such stages in collected material of this species and others of *Daphnandra*, *Doryphora*, and *Dryadodaphne*. It appears that meiosis in the anthers occurs at extremely young flower bud stages, and that the development of the tetrad and subsequent breakdown of the pollen mother cell wall takes place in a matter of days. Another obstacle to observing the development of furrows arose from the delicacy of the loosely coherent tetrad, from which the individual pollen grains are freed barely by the time the exine has matured enough to show signs of incipient furrowing.

The arrangement of the pollen cells in the tetrad is of the tetragonal (Erdtman 1943) or "square" (Wodehouse 1935) type, a rather uncommon form in dicotyledons, but occurring also in *Hedycarya* (Monimiaceae) and apparently Annonaceae (Bailey and Nast 1943). Sampson (l.c.) confirms that in *Laurelia novae-zelandiae*, most tetrads are tetragonal in configuration, though some are arranged tetrahedrally.

In *Atherosperma* tetrads, the orientation of the ± ellipsoidal pollen grains is such that the longest axis is in the equatorial plane and the shortest in the polar. In young pollen grains at or just after the "breakdown" of the pollen mother cell wall but still ± holding together in the tetrad, two thinly-walled and obscurely-sculptured elongate depressions appear in a longitudinally equatorial position on the proximal side of the equator (f.44B). From the stages examined, it appears that the two colpi in the mature pollen grain of *Atherosperma* (and probably of the other genera of the family) develop in these depressions which themselves elongate to eventually encircle the grain equatorially.

Two observations by Sampson (l.c.) corroborate independently the equatorial position of the furrow in *Laurelia novae-zelandiae*. First, the widest parts of the furrow (the two colpi) were found to be situated at right angles to the polar axis. As the colpi occur on the long ellipsoidal faces of the ± oblate pollen grains, they must be automatically positioned along the equator.

Second, the generative cell was observed to be at the maximum distance from the germinal furrow. If the generative cell is cut off against the distal or proximal side of the pollen grain, as is usual in angiosperms (La Cour 1949) and reported for the other lauralean taxa, e.g. *Hedycarya* (Sampson l.c.) and *Austrobaileya* (Bailey and Swamy 1949), the colpi must be equatorial. Sampson (l.c.), who supported the meridional interpretation of Money et al. (l.c.), was led to postulate that the generative cell was cut off against what represents a radial wall of the grain at the tetrad stage, a situation which would possibly be unique among angiosperms.

Because the colpi in atherospermataceous pollen are oriented equatorially and developed from germinal areas towards the proximal face of the pollen grain, they appear to have evolved in a different way from those in magnoliaceous genera. The proximal germinal areas may instead be homologous with those in *Amborella*, and the Annonaceae, and the thin proximal walls in the pollen grains of *Drimys* (cf. Bailey and Nast 1943).

Relationships

Money et al. (1950) and Erdtman (1952) have summarised the palynological characters of the rather eurypalynous Monimiaceae alliance. Little can be added from the present study except that the granular exine structure mentioned by them for Trimeniaceae, Monimiaceae, and the *Siparuna* group is apparently micro-reticulate or ± scabrate sculpturing in the former two, but a granular intectate structure (LO-pattern) in the latter.

Features common to the pollen of Monimiaceae and *Siparuna* group are their inaperturate form, micro-mesh to granular extexine sculpture, and rather small size (diameter ca 15-35 μ), quite different from those of atherospermataceous pollen.

The pollen of *Hortonia* is similarly inaperturate, of variable size, and has an extraordinarily ribbed ektexine, comprising a variable number of coarse semi-helical bands extending from one "pole" to another (Money et al. l.c.). It may be that the exine configurations reported for *Mollinedia*, *Macrotorus*, and *Tambourissa* (Money et al. l.c.) are the homologues of these bands.

Among other lauralean groups, there are marked similarities between Atherospermataceae and Calycanthaceae in pollen morphology, notably in the dicolpate germinal areas and equatorial orientation of the furrows (cf. Erdtman l.c.). In Calycanthaceae, nevertheless, the arrangement of grains in the tetrad is tetrahedral (Erdtman l.c.), and the grains, lacking an encircling equatorial furrow, are larger (long.Lt. 45-60 μ), and exhibit a surface sculpture that appears to be finely perforate tectate, at least in *Calycanthus*, ~~(ANU 94-1-1).~~

Gomortegaceae and Lauraceae have inaperturate spheroidal pollen with a relatively "granular" to spinuliferous ektexine that bears a generally closer resemblance to the pollen of the Monimiaceae and *Siparuna* group than to that of the Atherospermataceae (cf. Erdtman l.c., Sastri 1963). Pollen grains in some lauraceous plants are sometimes monocolpate.

14. Gynoecium

The young carpels of the apocarpous gynoecium in the Atherospermataceae resemble in external form those in other members of the Monimiaceae alliance and Calycanthaceae, and the pistil in the Lauraceae. They comprise a basal ovuliferous section or body with a short to long style in terminal or sub-terminal position, terminated by solitary filamentous or somewhat mucilaginous stigmas. Their position and arrangement in the hypanthium has been summarised in section 10. Their ontogeny has been described in *Laurelia novae-zelandiae* (Sampson 1967), but in no other species.

Consistent differences between the genera in gross carpel morphology occur in the position and relative length of the style and the form of the stigmatic parts. Whereas the styles in most genera are ± terminal, they are lateral in *Doryphora*. That this is a derived condition is indicated by their changing position from sub-terminal to sub-basal as the carpel ripens into a nutlet, as described in chapter XIII. *Nemuaron* also has sub-terminal styles which are even more remarkable for their lack of development (f.7C). Reasons for their apparent suppression are inferred in chapter XI.

A characteristic feature of the atherospermataceous flower is the filamentous stigmatic cluster. Comprising the stigmatic filaments from all styles, it may be either ± coherent throughout its length, forming a slender to broad, almost hemispherical cone (*Daphnandra*, *Dryadodaphne*, *Laurelia*, *Laureliopsis*, *Nemuaron* p.p.), or it may branch at the apex in a stellate configuration (Atherosperma, Doryphora, Nemuaron p.p.). There are occasional interchanges of these forms within the genera. The stellate cluster may represent the derived condition on the grounds that it occurs independently in very distantly related genera which in other characters are among the more specialised in the family.

The terminal stigmatic part of the carpel is produced by a terminal solid meristem above the carpellary cleft, below which forms the locule, at least in Laurelia novae-zelandiae (Sampson l.c.). As such it is not homologous with, though perhaps derived from, the stigmatic "crest" region of many other woody ranalean groups, according to Bailey and Swamy's (1951) interpretation of the primitive carpel. The adaxial ridge on the bodies of ripe atherospermataceous nutlets may represent the vestiges of the fused megasporophyll margins and original stigmatic surface of the primitive ranalean carpel. Even in Lauraceae, signs of the cleft of the carpel and sometimes stigmatic "crests" are retained in the style-stigma region (Sampson l.c.).

The locule contains a solitary erect anatropous to hemitropous bitegmic ovule which is attached to the basal part of the locule in all genera. Previous investigators* have suggested that Daphnandra

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* Baillon 1873, Bentham 1880, Pax 1889, Perkins and Gilg 1901, Perkins 1925, A.C.Smith 1941, Pichon 1948, Hutchinson 1964.

and Nemuaron are anomalous and resemble other families in the Monimiaceae alliance in having pendulous orthotropous ovules. As pointed out in chapters XI and XIV, their contention is incorrect.

The carpel of Atherosperma and Laurelia (Money et al. 1950, Sampson l.c.) is vascularised by single abaxial and adaxial strands. The abaxial strand passes into and up the style. The adaxial or ovular strand does not branch in Laurelia but gives off a supra-ovular strand in Atherosperma. Sampson (l.c.) regards the presence of supra-ovular strands here as an ancestral condition possibly indicating the former occurrence of more than one ovule in the locule of atherospermataceous plants. The vascularisation patterns in the ovules of other genera in the family have not been studied.

Externally, the carpels of the Atherospermataceae may be distinguished from those in most other members of the Monimiaceae alliance by their more elongate styles, and variably coherent filamentous stigmas. The concrescence of stigmas in the Siparuna group (cf. Money et al. l.c.) appears to be a parallel development. The stigmas of most genera of Monimiaceae and those of Hortonia are short and broad, and invariably free.

The form and position of the carpels in Calycanthaceae resemble those in Atherospermataceae except for their lack of hairs. The affinities of those in Lauraceae and Gomortegaceae are more difficult to assess because in the former they are solitary and in the latter connate in an epigynous flower. The solid glabrous styles in these two families are almost identical in their external morphology.

The style-stigma section of the carpels of perhaps all members of the Monimiaceae alliance is formed from a solid terminal meristem above the cleft of the carpel as described above for *Laurelia novae-zelandiae*. It appears to have been derived in a similar way in Lauraceae (Sampson l.c.).

The orientation of the anatropous ovule provides one of the more marked distinctions between the Atherospermataceae and related taxa. In the *Siparuna* group and Calycanthaceae, it is erect as in Atherospermtaceae, whereas in all other members of the Monimiaceae alliance, including *Hortonia*, and the Lauraceae and Gomortegaceae, it is pendulous. The ovules in the *Siparuna* group differ, however, in being unitegmic* according to Heilborn (1931), and those in Calycanthaceae are two instead of one per locule. The latter difference does not appear to be fundamental: the persistence of supra-ovular vascular strands in the carpels of various genera of the Monimiaceae alliance (Money et al. l.c., Sampson l.c.) suggests that other ovules were once present in their locules.

15. Features of Megasporogenesis

The modes of megasporogenesis in *Laurelia* and *Hedycarya* (Monimiaceae) revealed no essential differences when compared (Sampson 1967).

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* Disputed by Sampson (1967).

In possessing a monosporic 8-nucleate embryo sac of the Polygonum-type in a crassinucellate ovule (Sampson l.c.), these genera resemble other woody ranalean plants, including some Lauraceae (cf. Sastri 1963). So universal is the Polygonum-type embryo sac in woody ranalean plants that it throws little light on the relationships between the taxa; and it would be surprising if any other type would occur in the other genera of the Atherospermataceae. The Calycanthaceae and most Lauraceae differ only in having a multicellular archesporium (Sastri l.c.).

Megasporogenesis in the few other members of the Monimiaceae alliance studied apparently exhibits peculiar divergences. *Peumus* was suggested by Mauritzon (1935) to have an embryo sac of the bisporic Allium-type. In *Siparuna*, Heilborn (1931) reported the unique development from a multiple archesporium of a uninucleate embryo sac that coiled and burst before nuclear division. One suspects that his material was apomictic.

16. Fruiting Hypanthium

Characteristic of the Monimiaceae alliance is the often bizarre diversity of fructification which in turn reflects adaptation to various modos of dispersal. In most groups ~~it~~ the fruit is variously carnose, often brightly coloured, and presumably attractive to animal vectors. In the Atherospermataceae, however, it comprises a protective lignified oblong-urceolate* hypanthium enclosing, partly or completely, numbers of plumose nutlets that are uniquely adapted to dispersal by wind. As Sampson (1967) has pointed out, this is not a case of one fruit type giving rise to another, but rather of divergent evolution from a basic form.

Except in Laurelia, the hypanthium varies between, never within the genera. Trends in its development suggest that it has evolved to enclose and protect the long plumose, usually persistent styles on the nutlets. The envelopment is incomplete in the genera of the tribe Atherospermateae, and is assisted by elongation of thinly lignified inner staminodes which form a pallisade around the prominently exserted styles. In all genera of the tribe Laurelieae, coalescence of perianth and androecium and elongation and lignification of the hypanthium wall is complete to such an extent that the styles barely protrude beyond its rim. These variations are developmental and reflect the differences in the structure of the flowering hypanthia discussed in section 10.

Marked differences between the genera lie in the persistence of perianth and androecium parts, and patterns of thickening and adornment of the outer hypanthium wall. Perianth and androecium are early caducous in Dryadodaphne, and to an extent in Doryphora and Laurelia novae-zelandiae, but quite persistent in Daphnandra and Laureliopsis. Whereas they are ± smooth in Atherosperma, Daphnandra, Dryadodaphne, Laurelia novae-zelandiae, and Nemuaron, the hypanthium walls are strongly ribbed in Doryphora and

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* Cupular in Atherosperma and globulose-pyriform in Nemuaron.

Laureliopsis, and prominently scarred in *Laurelia sempervirens*.

These hypanthium ribs and protuberant scars are decurrent from the tepals or tepal scars and developed from the lignified bases of caducous tepals and staminodes respectively. Together with the rather frequent occurrence of the outermost bracteoles below the rim on the outer hypanthium wall in *Daphnandra*, they are interpreted as indicating the contributions made by perianth and androecium to the fruiting hypanthium. Moreover, the smooth-walled hypanthia of *Dryadodaphne* and *Nemuaron* are sometimes obscurely tetragonous, a feature which appears to be related to the number of perianth segments.

Nutlet dissemination is effected by longitudinal splitting of the hypanthium wall into 1 to 4 valves and/or by recurving of the protective pallisade of inner staminodes in the tribe Atherospermateae. The mode of dehiscence and number of valves formed may be correlated with or rather independent of the number and arrangement of the perianth-androecium parts, as described in chapter IX. In view of the likelihood that the hypanthium has been formed from such parts, the former condition is regarded as the less specialised.

The fruiting receptacle or hypanthium of other members of the Monimiaceae alliance varies from relatively hard and plate-like to a variably enlarged and sometimes coloured structure. It bears exposed fleshy drupes in most genera of the Monimiaceae. It is baccate in the *Siparuna* group, as a hypanthium enclosing the fruitlets.

Among other related families, only the woody hypanthia of the Calycanthaceae are in any way similar to those of the Atherospermataceae (See also Hutchinson 1964, p.111).

Here the resemblance in shape and scarring between those of *Chimonanthus* and *Laurelia sempervirens* is striking. In Lauraceae, thin hypanthia may or may not enlarge to almost enclose the solitary fleshy drupe, as in *Cryptocarya*. In Gomortegaceae, the ripe "hypanthium" is thick, fleshy, and yellowish, resembling the development in the *Siparuna* group, presumably as an adaptation to dispersal by animals.

17. Nutlet Morphology

Despite the similarity of the young carpels in all members of the Monimiaceae alliance, marked divergences of form develop during fruiting, according to differing modes of dispersal.

In Atherospermataceae, the carpel bodies remain small and dry-skinned, their styles elongate (*Nemuaron* excepted), and they become covered generally with long silky, almost plumose hairs. Such modifications are obviously adapted to dispersal by wind. Observations in *Doryphora sassafras* (chapter XIII) suggest that the hairs also function in slowing the fall of the nutlets, possibly to prevent the nutlets being damaged when they hit the ground.

The styles in all genera except *Nemuaron* and *Doryphora* are terminal and persistent, if rather fragile. The reasons for their persistence and length are inferred above and in section 16. Styles are vestigial in *Nemuaron* and the nutlets compressed into a remarkable hippocrepiform configuration, the reasons for which are discussed in chapter XI. In *Doryphora*, the styles are sub-basal (chapter XIII), and usually caducous soon after the nutlets have been shed. Easily detached styles are an obvious advantage to nutlets falling through tangled vegetation, because, if the styles break off when they are caught up, the nutlets may still reach the ground.

Differences in the pattern of pubescence on the nutlets are characteristic of the genera. The nutlet bodies in the genera *Daphnandra*, *Laurelia*, *Laureliopsis*, and *Nemuaron* are ± uniformly hirsute; those in *Atherosperma* and *Dryadodaphne* are unilaterally glabrous, on the adaxial and abaxial faces respectively; those in *Doryphora* are entirely glabrous. Uniformly hairy nutlets are regarded as representing the unspecialised condition.

It has been mentioned in section 16 that the carpels of other members of the Monimiaceae alliance, and also of Lauraceae and Gomortegaceae, differ from those of the Atherospermataceae by becoming variably fleshy or enclosed in fleshy hypanthia when fruiting; prolongation of the styles does not occur. The Calycanthaceae, however, have nutlets resembling those of the Atherospermataceae in their elongate, though ± hair-less styles.

18. Features of Embryology

An abundant albuminous endosperm, and a straight embryo with erect or slightly spreading cotyledons, are common to all taxa of the Monimiaceae alliance, and also *Gomortega*. Endosperm is lacking or entirely absorbed in Lauraceae and Calycanthaceae. Whereas it is cellular from an early stage in the few genera of the Monimiaceae alliance studied, including *Laurelia* (Mauritzon 1935, Sampson 1967), it is usually nuclear in Lauraceae, and cellular in Calycanthaceae (Sastri 1963, Davis 1966).

It is of note that Lindley (1853) used the character of a solid copious endosperm to associate Atherospermataceae and Monimiaceae with Myristicaceae, Lardizabalaceae, Schisandraceae, and Menispermaceae. Subsequent studies, such as those of Money et al. (1950), have indicated that these families are not quite as closely related to the Monimiaceae alliance as Lindley believed.

19. Chromosome Data

Ehrendorfer et al. (1968) have summarised available chromosome data, quoting numbers of 2n=44 for *Daphnandra repandula* and *Laurelia novae-zelandiae*, and 2n= ± 82 for *Doryphora sassafras*. They use the difference in base numbers between *Doryphora* (X_5=41) and *Daphnandra*-*Laurelia* (X_3=22) to justify the segregation of the family into two tribes, one comprising *Atherosperma* and *Doryphora*, and the other *Daphnandra*, *Dryadodaphne*?, *Laurelia*, and *Nemuaron*?, consistent with the original circumscription by Pax (1889).

Such an assessment, based on counts for 3 species out of 16 and 3 genera out of 7, seems to be premature. It is not consistent with the morphological or ecogeographic affinities between the genera. *Doryphora* is more closely related to *Laurelia* and *Daphnandra* than it is to

Atherosperma, and its anomalous base number, if normal as reported, may merely reflect its rather isolated position within the tribe Laurelieae as defined here.

In related taxa, Ehrendorfer et al. record base numbers of X_3=19, and X_5=43 for the Monimiaceae, X_5=39 for Peumus, X_3=22 for the Siparuna group, X_2=11 for Calycanthaceae, and X_2=12 for Lauraceae. The numbers for Hortonia and Gomortega are not known.

Their pertinent conclusions are that polyploidy has reached high levels and that diploids and lower polyploids have died out in Atherospermataceae, Monimiaceae, and the Siparuna group, though not to such an extent in Lauraceae. These groups are regarded as palaeopolyploids, remnants of formerly well-developed polyploid complexes.

The authors believe that the varied and partly very high chromosome numbers point to the heterogeneity of the Monimiaceae s.l., as conventionally defined. Citing X_5=39 for Peumus (from 19 + 20?), X_5= ± 41 for Doryphora (from 20 + 21?), and X_5= ± 43 for Tetrasynandra (Monimiaceae) (from 21 + 22?), they postulate a series of tertiary base numbers X_3=19(20,21)22 that most likely arose by parallel polyploidy from X_2=12,13,14,15, and ultimately from X=6,7,8.

20. Phytochemical Aspects

The Atherospermataceae are phytochemically interesting because of their essential oils and alkaloids.

Essential Oils

The oils, which impart the characteristic safrol- or citronella-like odour to many members of the family, are carried in secretory cells in the cortex, phloem, and pith of the stems and in the leaves (section 2). The rather persistently aromatic wood of *Atherosperma*, *Doryphora*, *Laurelia*, and *Laureliopsis* indicates the presence of oils in the secondary xylem as well, though the oil cells may not be morphologically obvious.

The composition of the oil in three aromatic Australian species, *Atherosperma moschatum*, *Doryphora aromatica*, and *D. sassafras* has been investigated recently by Petrie (1912), Scott (1912), Penfold (1921), and Jones and Smith (1924 a,b), and its respective components and properties are summarised under each species in the text. Major oils present include safrol, camphor, d-pinene, dα-phellandrine, cineol, and sesquiterpenes, with safrol being often markedly prevalent in the bark. These oils occur in other woody ranalean groups, notably *Beilschmiedia*, *Cinnamomum*, and *Sassafras* and other genera in Lauraceae (Petrie 1912, Hegnauer 1966). Cineol, pinene, and terpenes are recorded also for the Calycanthaceae, according to which the family resembles the Ranales rather than the Rosales (Hegnauer 1964).

Safrol itself is not known in any other members of the Monimiaceae alliance, but probably occurs in the sweetly aromatic *Gomortega*. In the Atherospermataceae, its occurrence appears to be haphazard: it is probably absent in generally odourless *Daphnandra* and *Dryadodaphne*, and ubiquitously present in *Atherosperma* and *Doryphora*, whereas in *Nemuaron*, which has aromatic bark but rather odourless leaves and wood, it is largely confined to cortical and phloem tissue of the stem.

Alkaloids

The alkaloids of the genera of the Atherospermataceae have been the subject of intensive study by I.R.C. Bick and co-workers. Their contributions are reviewed under Atherosperma moschatum, various species of Daphnandra, Doryphora aromatica, species of Dryadodaphne, and Nemuaron vieillardii. Other information on alkaloids has been summarised by Henry (1949) and in Manske (and Holmes) (1950, 1954, 1960, 1967, 1968).

The alkaloids so far isolated fall into two main classes, the aporphine types and bisbenzylisoquinoline types, which may both be formed from a common precursor. Many variants of these two types exist, differing in the number and positions of substituent groups, in stereochemistry, and in other structural features. They have been shown to be characteristically consistent in some species of the family, as in Daphnandra (chapter XIV), and have provided valuable corroborative evidence for species distinguished on otherwise rather slight morphological differences.

Alkaloids of the aporphine type appear to occur exclusively as major alkaloids in Laurelia and Nemuaron, testifying to the close relationship between these genera (chapters XI and XII). They are also present in Doryphora sassafras and constitute the minor alkaloids of Atherosperma. Alkaloids of the bisbenzylisoquinoline type only occur in Daphnandra and

Doryphora aromatica; they are also present as more-or-less major alkaloids in *Atherosperma moschatum*, *Doryphora sassafras*, and species of *Dryadodaphne* (Bick, pers.comm.).

In other members of the Monimiaceae alliance, aporphine alkaloids have been isolated from *Peumus*. Some genera of the Monimiaceae, including *Hedycarya*, *Tetrasynandra*, and *Wilkiea*, have furnished positive alkaloid tests but their alkaloids have not yet been analysed in detail.

Most of the particular alkaloids found in the Monimiaceae alliance are found in no other family. Alkaloids of the bisbenzylisoquinoline type nevertheless occur in Menispermaceae, Berberidaceae, and Magnoliaceae, and both bisbenzylisoquinoline and aporphine alkaloids have been isolated from Annonaceae and Lauraceae (Hegnauer 1966). Though alkaloids are known from the Calycanthaceae, they comprise the divergent types calycanthin and folicanthin which apparently replace the benzyltetrahydroisoquinoline bases generally characteristic of the Ranales (Hegnauer 1964).

Further comparative studies of the alkaloids in these groups and those genera of the Monimiaceae alliance with little known alkaloids are likely to illuminate the relationships between these taxa.

V. TAXONOMIC HISTORY, STATUS, AND RELATIONSHIPS OF THE ATHEROSPERMATACEAE

There has been a historic unanimity of opinion that the Atherospermataceae are related to lauralean plants in general and to the Monimiaceae in particular. The Atherospermataceae have in common with many or all lauralean plants a woody habit, a secondary xylem of a low level of specialisation, sclereids in the pericycle of stems and cortex of petioles, ethereal oil cells in stems and leaves, unilacunar nodes, a basically cyclic arrangement of flower parts*, a choritepalous perianth, biglandular stamens with valvular dehiscence, non-tricolpate or non-monocolpate pollen, a perigynous hypanthium enclosing numerous free uniovulate carpels, and anatropous bitegmic crassinucellate ovules with an embryo sac of the Polygonum type.

The present study confirms the position of the Atherospermataceae among lauralean taxa as defined by Money et al. (1950), and corroborated by Cronquist (1957), Hutchinson (1959, 1964), and Takhtajan (1959) in their circumscription of the order Laurales, and also by Sastri (1963), Buchheim (1964) and Thorne (1968). As is elaborated below, the family has closest affinities with the Gomortegaceae, Monimiaceae (including _Hortonia_ and _Peumus_), Calycanthaceae, and Lauraceae. The remaining lauralean families (Amborellaceae, Austrobaileyaceae, Chloranthaceae,

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* With the exception of carpels, which are spirally arranged.

Hernandiaceae, Lactoridaceae, Trimeniaceae) are related to the Atherospermataceae only through the preceding taxa and are therefore not discussed.

Robert Brown (1814) first recognised that the genera of the Atherospermataceae constituted a distinct taxonomic group. Two genera, Atherosperma and Laurelia, were known at the time, and Brown (l.c.) referred to a further two, undoubtedly Daphnandra and Doryphora, occurring in the region of Sydney. On them he based a new family, Atherospermeae, distinguished from monimiaceous plants by valvate anthers, ovule orientation, and sometimes bisexual flowers.

The conclusions reached on the circumscription of the Atherospermataceae in the present study are in accord with Brown's concept. A reticulate relationship between the component genera is indicated by similarities in various characters. Thus Nemuaron (New Caledonia), which has affinities with Dryadodaphne (New Guinea) on one side and Laurelia (New Zealand and Chile) on the other through leaf, inflorescence, perianth, and androecium structure, and presence and position of bracteoles, resembles Doryphora (Australia) in its inflorescence buds, aromatic bark*, and modified nutlets. And though two tribes are distinguishable, they are linked to a degree by Laureliopsis which, while possessing the critical characters of one (Atherospermateae), approaches the other (Laurelieae) in the characters emphasised at the conclusion of chapter VII.

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* Also Laurelia sempervirens.

The family, consequently, is morphologically closely coherent.

Whereas Lindley (1830, 1853) and Meisner (1841) adopted Brown's view, Endlicher (1837, 1841), Gay (1851 or 1852), and J.D. Hooker (1853, 1855, 1855with Thomson) followed the earlier lead of de Jussieu (1809, 1824) and treated the Atherospermataceae as an infrafamily group within the Monimiaceae. Tulasne's monograph of the Monimiaceae in 1855, in which the Atherospermataceae were included within the Monimiaceae, set a taxonomic precedent. Tulasne distinguished the nutlet-bearing Atherospermataceae as a tribe from the fleshy or drupe-fruited *Siparuna* and *Monimia* groups. Many subsequent revisers maintained it according to Tulasne's circumscription, either as a subfamily (Pax 1889) or a tribe (C.Mueller 1857, A. de Candolle 1868, Baillon 1869, Perkins & Gilg 1901, and Perkins 1925). Others united it with the *Siparuna* group as a tribe (Bentham 1880, Hobein 1888) or subfamily (Perkins 1898, 1925, Perkins & Gilg 1901, followed by Lemée 1929, 1930, 1931, 1932, 1951, Garratt 1934, Metcalfe and Chalk 1950) of Monimiaceae characterised by valved anthers and erect ovules.

Studies of secondary xylem and other anatomical features by Hobein (l.c.), Solereder (1899), and Garratt (l.c.) confirmed a relationship between the *Atherosperma* group, *Siparuna* group, and Monimiaceae, but at the same time drew attention to significant differences in the rays, intervascular pitting, and occurrence of wood parenchyma.

Money at al. (1950) subjected the Monimiaceae to a more searching and broadly-based investigation. Whereas previous revisers had merely considered either flower and fruit characters or anatomical features, Money at al. examined both of these and also characteristics of the pollen. Even though concluding that several groups, Amborella and Trimenia, should be treated as distinct but allied families of the Monimiaceae, they still maintained the Atherospermataceae as a subfamily within the Monimiaceae.

They showed, nevertheless, that the Siparuna group, although resembling the Atherospermataceae in anther dehiscence, ovule orientation, multiseriate ray structure, and nodal anatomy, exhibit divergent trends of floral specialisation and advanced forms of vessels and intervascular pitting. These features were interpreted to imply a fundamental difference between the two groups, and in turn that the similarities between them represented convergence rather than common ancestry. Money et al. therefore also treated the Siparuna group as a distinct subfamily (Siparuneideae) within the Monimiaceae.

The majority of recent reviewers have either adopted the arrangement proposed by Money et al. (Müller-Stoll and Mädel 1962, Buchheim 1964, Rüffle 1965, Thorne 1968) or merely included the genera of Atherospermataceae within the Monimiaceae without indication of rank (Erdtman 1952, Hutchinson 1959, Takhtajan 1959, Sastri 1963).

Other assessments have been put forward by Pichon (1948) and Hutchinson (1964). Pichon, stressing its narrow xylem rays, valved anthers, and erect ovule, advocated the Atherospermataceae as a distinct family, but included the Siparuna group in its circumscription. Good (1964) and

Airy Shaw (1966) also cite it as a family in this sense. Hutchinson, on the other hand, not only united Atherospermataceae ~~and~~ with the *Siparuna* group, but also included them as a subfamily of the Monimiaceae. His treatment combines the most unnatural aspects of the groupings proposed by Bentham (1880) and Pax (1889). It is discussed in more detail in chapters VI and IX.

It has already been mentioned that the Atherospermataceae have close affinities with Gomortegaceae, Lauraceae, and Calycanthaceae as well as with Monimiaceae. Such relationships have been repeatedly mentioned by de Jussieu (1809), Baillon (1868, 1869), Pax (1889), Perkins and Gilg (1901), Perkins (1925), Rendle (1925), Garratt (1934), Money et al. (1950), Erdtman (1952), Stern (1954, 1955), Eames (1961), Müller-Stoll and Mädel (1962), Sastri (1963), Airy Shaw (1966), and Sampson (1967). In the present study, all available characteristics of these families and infra-family groups have been compared in an effort to make an assessment of the taxonomic status of the Atherospermataceae. These characteristics have been discussed in detail in chapter IV and are summarised in table III.

Any character in any one family found to differ from its counterpart in the Atherospermataceae has been examined and tabulated wherever possible for all these families and groups. Forty eight varying characters or groups of characters were extracted for comparison. They are taken from the habit, secondary xylem, vesture, leaf form and arrangement, stomate type, nodal vascularisation, inflorescence structure, sex expression,

TABLE III

	Characters	Lauraceae	Calycanthaceae	Gomortegaceae	Atherospermataceae	*Hortonia*	Monimiaceae	*Peumus*	*Siparuna* group
	growth habit	usu. large trees	shrubs	large tree	usu. large trees	shrub	shrubs, climbers, small trees	small tree	shrubs, small trees
	mode of branching	monopodial, superficially sympodial	-	-	monopodial	-	superficially sympodial	-	-
secondary xylem	vessel shape	± large, round in circumference, and walls ± horizontal	small, end walls oblique	as in Atherospermataceae	narrow, angular, and walls oblique	as in Atherospermataceae	shorter than in Atherospermataceae, end walls more horizontal	as in Monimiaceae	round in circumference, and walls ± horizontal
	perforation plates	simple	simple	scalariform	scalariform	scalariform	scalariform to simple	simple	simple
	intervascular and vessel-ray pitting	alternate, large	alternate large	scalariform	scalariform	scalariform to alternating multiseriate	scalariform to alternating multiseriate	alternating multiseriate	alternating multiseriate
	vessel distribution	frequent radial multiples	usu. radial multiples	solitary	usu. solitary	solitary	frequent radial multiples	frequent radial multiples	frequent radial multiples
	fibre type	frequently septate	fibre tracheids to libriform fibres	exclusively fibre tracheids	usu. fibre tracheids, with some transitions to libriform fibres	non-septate	usu. septate	exclusively septate or libriform fibres	libriform, non-septate except *Glossocalyx*
	fibre pitting	usu. simple	bordered to simple	distinctly bordered	usu. bordered	bordered	transitional from bordered to simple	simple	usu. simple, or vestigially bordered
	multiseriate ray form	± as in Atherospermataceae	relatively short and narrow, 1-2(-3) cells wide	as in Atherospermataceae	relatively short and narrow, 0.2-1.8 mm high x 2-5(-8) cells wide	variable, rather high, 1-10 cells wide	very high, broad, usu. >10 cells wide	as in Monimiaceae, homogeneous	very high, narrow
	parenchyma	paratracheal, abundant	vasicentric, diffuse, or paratracheal, scanty	± diffuse, rather abundant	± absent	diffuse, abundant	± absent	paratracheal or vasicentric	usu. apotracheal bands, abundant
	oil cells	present	absent	absent	rare	present	absent	absent	absent
	secretory cell type	mucilage and oil cells	oil cells only	oil cells only	oil cells only	oil cells only	oil cells only	oil cells only	oil cells only
	odour in vegetative parts	aromatic or not	aromatic	aromatic	aromatic or not	not aromatic	not aromatic	aromatic	not aromatic
	hairs	simple, usu. unicellular	simple, unicellular	simple, unicellular	simple or two-armed, unicellular	stellate scales	stellate, and simple	stellate, tufted	stellate, scale-like, or simple
	leaf arrangement	alternate, sometimes decussate	decussate	decussate	decussate	decussate	decussate to alternate	decussate	decussate to alternate
	leaf node trace	usu. single, arc-shaped	single, arc-shaped, or with small accessory strands	single, arc-shaped	single, arc-shaped, sometimes with several strands	3 or more strands	3 or more strands	3 or more strands	single, arc-shaped
	leaf margins	entire	entire	entire	variably indented	entire	variably indented	entire	variably indented to entire
	stomata type	paracytic	paracytic	± paracytic	predominantly anomocytic	predominantly paracytic	transitional between anomocytic and paracytic	predominantly paracytic	predominantly paracytic
	inflorescence position	axillary or terminal	axillary	axillary or terminal	axillary	axillary	axillary or terminal	axillary	axillary, rarely terminal
	inflorescence structure	divaricately branched or clusered, ± as in Monimiaceae	single flowered	as in Atherospermataceae	monopodial, with simple dichasia in decussate arrangement	as in Atherospermateae	modified to approach a sympodial, clustered, or spike-like structure	as in Atherospermataceae	as in Monimiaceae
	flower sexes	mostly bisexual	bisexual	bisexual	bisexual, or unisexual and monoecious, or transitional	bisexual	strictly unisexual, dioecious	strictly unisexual, dioecious	strictly unisexual, dioecious or monoecious
	floral "receptacle" form (bisexual and pistilliferous flowers)	hypogynous to perigynous (patelliform)	perigynous (poculiform), with well-defined rim	epigynous	perigynous (cupular to poculiform), with well-defined rim	hypogynous (patelliform)	hypogynous (patelliform) to perigynous (cupular)	shallowly perigynous (cupular), with poorly defined rim	perigynous, approaching epigyny
	perianth form	choritepalous; all parts sepaloid to partly petaloid	choritepalous, partly petaloid	choritepalous, all parts sepaloid	choritepalous, partly petaloid	choritepalous, partly petaloid	choritepalous to coalescent and calyptrate, sepaloid	choritepalous, partly petaloid	coalescent, forming a velum and calyptrate structures, sepaloid

Characters	Lauraceae	Calycanthaceae	Gomortegaceae	Atherospermataceae	Hortonia	Monimiaceae	Peumus	Siparuna group
arrangement and number of perianth parts	basically 3-merous, 6(-4) partite	multiseriate	4- to 3-merous, usu. 7-partite	basically 4-merous to 3-merous or compressed spirals, (3-)4-8(-12)-partite	multiseriate, ± 20-partite	multiseriate to 4-merous and 4-partite	several seriate (4-merous?), 10-12-partite	3-, 4-, or 5-merous, 4-8-partite
perianth aestivation	imbricate, rarely valvate	imbricate	imbricate	imbricate	imbricate	imbricate to valvate	imbricate	valvate
androecium structure	stamens and staminodes present	stamens and staminodes present	stamens and staminodes present	stamens and/or staminodes present	stamens and occasional staminodes present	staminodes lacking	staminodes present	staminodes lacking
number of pollen sacs per anther	2 or 4	apparently 4	2	2	4	4	4	apparently 2
anther dehiscence	valvular	vertical fissure	valvular	valvular	vertical fissure	vertical fissure	vertical fissure	valvular
paired staminal glands	present	absent	present	present	present	absent (except Mollinedia)	present	absent
tapetum type	usu. amoeboid	amoeboid	-	amoeboid (Atherosperma), or secretory (Laurelia)	-	secretory (Hedycarya)	-	-
tapetum nuclei arrangement	bi- or tetra-nucleate	multinucleate	-	bi-nucleate (Laurelia)	-	bi-nucleate (Hedycarya)	-	-
mode of cytokinesis	successive	simultaneous	-	successive (Atherosperma), or simultaneous (Laurelia)	-	successive (Hedycarya)	-	-
pollen grain apertures	inaperturate, rarely monocolpate	dicolpate, with equatorial orientation	inaperturate	dicolpate, with equatorial orientation	inaperturate	inaperturate	inaperturate	inaperturate
microsporoderm sculpturing	spinuliferous	finely perforate tectate	granular ?intectate (LO-pattern)	(micro-) reticulate (OL-pattern)	thickened semihelical bands	scabrate	spinuliferous	granular intectate (LO-pattern)
carpel number	1	∞	2-3	(3-)4-∞	∞	∞	∞	4-∞
arrangement of stigmas	-	free	connate (at base)	variably connate	free	free	free	free or connate at base
number of ovules per carpel	1	2	1	1	1	1	1	1
ovule orientation	pendulous	erect	pendulous	erect	pendulous	pendulous	pendulous	erect
number of integuments	2	2	-	2	2	2	2	1?
archesporium type	multisporic	multisporic	-	monosporic (Laurelia)	-	monosporic (Hedycarya)	bisporic?	multisporic
embryo sac type	Polygonum-type	Polygonum-type	-	Polygonum-type	-	Polygonum-type	Allium-type?	-
fruiting "receptacle" form	unenlarged to thin-walled hypanthium, uncoloured	cylindrical-urceolate fleshy to lignified hypanthium, uncoloured	baccate, fruitlets enclosed	cylindrical-urceolate lignified hypanthium, uncoloured -	unenlarged patelliform, drupes exposed	patelliform to disciform, often coloured, drupes exposed or enclosed	hardly enlarged, drupes exposed	ellipsoid to turbinate baccate hypanthium, coloured
fruiting carpel form	apocarpous, enlarged drupaceous, style undeveloped	apocarpous, hardly enlarged, dry, style elongate and glabrous	syncarpous, hardly enlarged	apocarpous, hardly enlarged, dry, style elongate and plumose	apocarpous, enlarged drupaceous, style undeveloped	apocarpous, usu. enlarged drupaceous, style undeveloped	apocarpous, enlarged drupaceous, style undeveloped	apocarpus-sub syncarpous, unenlarged drupaceous, style hardly developed
endosperm structure	usu. nuclear	cellular	-	cellular	-	cellular (Hedycarya)	cellular	-
endosperm persistence	absorbed	absorbed	albuminous	albuminous	albuminous	albuminous	albuminous	albuminous
chromosome numbers	$X_2=12$	$X_2=11$	-	$X_2=22, X_4=41$	-	$X_3=19$, $X_5=43$	$X_5=39$	$X_3=22$
geographic distribution	Asiatic and American tropics and subtropics, incl. Australia and New Zealand; infrequent in tropical Africa and Madagascar	vicarious in China and east North America; N.E. Australia?	Chile	continental borders of southern Pacific ocean: New Guinea, New Caledonia, Australia, New Zealand, Chile	Ceylon	Madagascar, Mascarene islands, Malaysian tropics, Oceania, Australia, New Zealand, American tropics and southern subtropics	Chile	Central and tropical South America; one in tropical west Africa
habitat	tropical to temperate rainforest	temperate or subtropical forest?	subtropical rain-forest	subtropical, temperate, and tropical montane rainforest	tropical and tropical montane rainforest	subtropical, tropical, and tropical montane rainforest, rarely temperate forest	subtropical rain-forest	tropical and tropical montane rainforest

hypanthium form, perianth structure and arrangement, androecium structure, anther dehiscence, microsporogenesis, pollen grain morphology, arrangement of the gynoecium, ovule number and orientation, megasporogenesis, fruiting "receptacle" structure, fruiting carpel form, endosperm type, chromosome number, geographic distribution, and habitat.

The results of the comparison are:

20 characters are common to *Hortonia* and Atherospermataceae out of 41 recorded for both;

17 characters are common to *Peumus* and Atherospermataceae out of 45 recorded for both;

17 characters are common to Monimiaceae and Atherospermataceae out of 48 recorded for both;

11 characters are common to the *Siparuna* group and Atherospermataceae out of 43 recorded for both;

26 characters are common to Gomortegaceae and Atherospermataceae out of 39 recorded for both;

25 characters are common to Calycanthaceae and Atherospermataceae out of 47 recorded for both;

19 characters are common to Lauraceae and Atherospermataceae out of 48 recorded for both.

Because such an analysis does not distinguish between those similarities resulting from convergence and those indicating common ancestry, the differences and divergences tabulated have greater taxonomic significance than the resemblances.

The following conclusions may be drawn. First, the Atherospermataceae are distinct from Hortonia, Peumus, and Monimiaceae rather than necessarily closely allied to Gomortegaceae, Calycanthaceae, and Lauraceae. Second, the Atherospermataceae have, nevertheless, at least as close affinities with Gomortegaceae, Calycanthaceae*, and Lauraceae as they have with Monimiaceae and allied taxa. Third, the Atherospermataceae merit recognition as a family because of these relationships, and are treated so here. Their distinctive features (see diagnosis, chapter III) are equivalent to those used in the order Laurales for separating other families, such as Gomortegaceae and Hernandiaceae from Lauraceae, and Trimeniaceae from Monimiaceae.

Their closest affinities are with Gomortegaceae through which they are related to Lauraceae. So close is the relationship to Gomortegaceae that the problem in future will be whether or not to unite the two rather than to follow the conventional alignment of Atherospermataceae with Monimiaceae.

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* Although Hutchinson (1959, 1964) allocates Calycanthaceae to the order Rosales, recent information on pollen grain structure (Erdtman 1952), micro- and megasporogenesis and embryology (Sastri 1963) and chemical constituents (Hegnauer 1964) is consistent with most assessments based on gross morphology that the family is closely allied to Lauraceae and Monimiaceae (Pax 1889, Perkins and Gilg 1901, Perkins 1925, Rendle 1952, Takhtajan 1959, Buchheim 1964). Baillon (1869), incidentally, maintained it within the Monimiaceae alliance.

The almost perfectly intermediate position of Gomortegaceae itself between Atherospermataceae and Lauraceae has not been realised before. In some features, such as its secondary xylem characters, decussate phyllotaxy with open-veined leaves, inflorescence structure, bisporangiate anthers, and albuminous endosperm, it is almost identical with the Atherospermataceae. In others, such as its rather abundant xylem parenchyma, entire leaves, stomate type, occasionally terminal inflorescences, thick tepals, general stamen form, inaperturate pollen, style structure, and pendulous ovules, it resembles Lauraceae. It differs from both in its epigynous flower, yet shows relationships between both in its transitions from decussate to trimerous arrangement of perianth and perhaps androecium parts. The overall differences between Gomortegaceae and Atherospermataceae are such that it seems inadvisable to unite the families.

Hortonia is more distantly related, differing not only in its entire leaves, inaperturate pollen, and pendulous ovules, but also in having relatively extensive secondary xylem parenchyma, stellate hairs, polytepalous perianth, apparently tetrasporangiate anthers dehiscing by fissures, and a fructification comprising drupaceous carpels on a more-or-less unenlarged receptacle. In all of these features except perhaps the unique presence of xylem parenchyma, it approaches the Monimiaceae.

In ultimately deciding to retain the Atherospermataceae as a subfamily of the Monimiaceae, Money et al. (l.c.) were influenced by the attributes of Hortonia which they believed were intermediate between the two groups. According to their definition, the Monimiaceae "becomes a relatively natural family .... which exhibits diverse trends of floral and vegetative modification from an ancestral stock of which Hortonia appears to be the least specialised surviving representative". Müller-Stoll and Mädel (l.c.), emphasising the common occurrence of abundant parenchyma and oil cells in the wood of fossil Atherospermataceae and Hortonia, have also maintained that the divergent plant forms segregated here in the Atherospermataceae and Monimiaceae evolved from "Hortonia-like ancestors". The way in which Hortonia combines features of both Atherospermataceae and Monimiaceae is described in chapter IV, and illustrated in table III. Its position as a link between Atherospermataceae and Monimiaceae is not disputed.

Nevertheless, it is argued that the occurrence of solitary intermediate forms between two relatively large and distinct taxa does not constitute an *a priori* reason for uniting the two. In the situation here, moreover, there can be made at least as good a case for uniting the Atherospermataceae with Lauraceae through Gomortega as for incorporating it in Monimiaceae through Hortonia. To do either would lead to an unnatural arrangement. To do both would lead ultimately to the reduction of the present order Laurales to the rank of family.

There remains for consideration, albeit brief, the taxonomic position of the other members of the Monimiaceae alliance examined here. Their characteristics are summarised in table III, giving the following figures for the affinities between the Monimiaceae and Hortonia, Peumus, and the Siparuna group:

28 characters are common to Hortonia and Monimiaceae out of 41 recorded for both;

31 characters are common to Peumus and Monimiaceae out of 45 recorded for both;

24 characters are common to the Siparuna group and Monimiaceae out of 43 recorded for both.

These figures, assessed in conjunction with the nature of the differences between the Monimiaceae, Hortonia, Peumus, and the Siparuna group, suggest first, the inclusion of Hortonia and Peumus in Monimiaceae as monogeneric subfamilies, and second, the separation of the Siparuna group as a distinct family more closely related to Monimiaceae than to Atherospermataceae.

It seems, on the basis of available evidence, that recognition of rather narrowly circumscribed families within the Monimiaceae alliance is necessary in order to avoid the serious shortcomings of lumping small but widely divergent groups in a "catch-all" family, such as Monimiaceae s.l.* The lumping of such groups into unwieldy complex families, of which Magnoliaceae s.l. and Saxifragaceae s.l. are examples, tends to obscure the often fundamental morphological and evolutionary differences between them and the problems that they pose.

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* On the basis of varied and high chromosome numbers, Ehrendorfer et al. (1968) have recently come independently to the conclusion that the Monimiaceae s.l. are rather heterogeneous and may need segregation.

VI. TRIBE ATHEROSPERMATEAE

Atherospermateae Pax, Pflzfm. 3,2(1889)96,97,103 p.p. "Atherospermeae"; Garratt, Trop.Woods 39(1934)22 p.p. "Atherospermeae"; Hutchinson, Gen.Fl.Pl. 1(1964)113,122 p.p. "Atherospermeae"; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342 p.p. "Atherospermeae"

TYPE GENUS: *Atherosperma* Labill.

Medium-sized, sometimes shrub-like trees ca (3-)5-25(-35) m high, rarely more, with columnar habit; trunks solitary or 2 to 3 in a close erect group; crowns slender rather cylindrical, as long as or longer than the boles, with branches horizontal-ascending to slightly drooping; bark ± smooth, aromatic; secondary xylem without yellowish hue, the vessel members solitary, rarely up to 5% in radial multiples of 2-3, ca (100-) 120-140(-160) per sq. mm in transection, inner tangential diameter (26-)35-55(-80) μ, the fibres 1.2-1.6 mm maximum length range × (14-) 22-26(-30) μ outer tangential diameter, ± thin-walled, exclusively fibre tracheids, or up to 5% libriform wood fibres with septae, with bordered pits sparse to rather numerous, very small with borders ± indistinct, the multiseriate rays (0.1-)0.3-0.7(-0.9) mm high × 2-4 cells wide, markedly heterocellular, with procumbent cells 5-50 μ in tangential diameter, acicular crystals apparently absent, oil cells absent, the parenchyma apparently absent; hairs on lower face of leaf blades centrifixed, with unequal arms.

Monoecious or polygamous; inflorescences densely sordid greyish silky strigose; flower-subtending bracts or bracteoles ovate-cymbiform, relatively large, ± enclosing mature flower bud; hypanthium of bisexual and pistilliferous flowers rather shallowly cyathiform, the rim concave, sloping into and hardly differentiated from shallow hypanthium chamber; perianth of open flowers cyathiform; stamens truncate at the apex, the filaments relatively slender, ca as long as or longer than the anthers, the staminal glands stamen-like, stipitate, attached towards the base of the filaments; staminodes in bisexual and pistilliferous flowers distributed extensively on rim inside hypanthium chamber, the inner whorls persistent and markedly elongated closely around gynoecium column in fruit, style column exserted prominently (3-)4-6(-7) mm beyond hypanthium rim in fruit; dissemination of ripe nutlets effected by reflexing of staminodes surrounding gynoecium column*.

Genera, Geographic Distribution, and Ecology

The tribe Atherospermateae comprises two genera, Atherosperma, which is confined to mountainous south-eastern Australia and Tasmania, and Laureliopsis, which is confined to southern Chile and western Patagonia (map 1). Both occur in essentially temperate rainforest, where they are often associated with species of the subsections Antarcticae and Quadri-

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* In Laureliopsis, assisted by longitudinal splitting of fruiting hypanthium.

partitae of *Nothofagus*, as defined by van Steenis (1953).

The disjunct geographic distribution of the tribe is interesting in that it excludes New Zealand, and parallels the present distribution of several other temperate rainforest taxa, such as the genera *Eucryphia* (cf. Gilg 1925, Hutchinson 1959, Emberger 1960, and Godley 1960) and *Lomatia* (cf. Berry 1938, Hutchinson 1967), and several closely related deciduous species of *Nothofagus*, *N. pumilio*, *N. antarctica*, and *N. gunnii* (cf. Du Rietz 1960, Fleming in Gressitt 1963). The distribution of *Drimys** and of the acuminately capsuled species of *Euphrasia* (du Rietz 1948, 1960) is of a somewhat similar pattern. It should be pointed out, however, that none of these plants occur consistently side by side with the genera of the Atherospermateae in either Chile or Australia.

Notes on the Characters of the tribe Atherospermateae

The small size of cell members is the most characteristic feature of the secondary xylem. It is exemplified by the frequent narrow vessels (table 1), which highlight the trend in the family from few and wide vessels in tropical-latitude forms to many and narrow vessels in temperate-latitude forms described in chapters IV.2 and IX. It is also evident

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* In the sense of Dandy (1933), A.C.Smith (1943), and Hutchinson (1964), all of whom exclude the New Zealand forms and place them in the genus *Pseudowintera*. Ehrendorfer et al. (1968) have also drawn attention to significant differences between *Drimys* in South America and *Drimys* sect. *Tasmannia* in eastern Australia and New Guinea.

in the shorter fibres and small size of the procumbent ray cells in multiseriate rays that are, as a result, often shorter and narrower than those in the Laurelieae. The multiseriate rays in both genera of the tribe are also rather more heterocellular than in most genera of the Laurelieae. The small size of cell members seems to be correlated with the relatively cool temperate environment in which the genera of the Atherospermateae occur.

The structure of the flowering hypanthium and its differences from that in the Laurelieae have been summarised in chapter IV.10. The descriptions of the "receptacles" of various genera in the family given by Money et al. (1950) are rather misleading in this respect.

The fertile stamens are unique in the family in comprising slender truncate anthers, relatively long filaments, and stamen-like staminal glands attached to the base of the filament. Though Daphnandra has truncate anthers, its staminal glands are thick peltate flaps attached abaxially towards the apex of the short thick filament. Laureliopsis, with narrower truncate anthers, shorter filaments, and ovate, less stamen-like staminal glands than Atherosperma, is the closer to the Laurelieae in stamen morphology. It also approaches the Laurelieae in other characters, which are listed in chapter VII.

The form of the staminal glands is particularly interesting insofar as their consistently stamen-like shape, and basal attachment on the filament, may indicate a lack of modification in their evolution (chapter IV.11). The varied shapes and disposition of their homologues in the Laurelieae makes such a conclusion almost inevitable.

Neither pollen morphology nor ovule placentation appears to shed much light on the relationships between the tribes. By and large, the pollen of *Laureliopsis* is rather more like that of *Dryadodaphne* and *Daphnandra*, while there are resemblances between that of *Atherosperma* and *Doryphora* in form but not size. These characters are discussed in more detail in chapter IV.13.

The characteristic differences in the form of the fruiting hypanthium between the Atherospermateae and Laurelieae have been outlined in chapter IV.16. The hypanthium in the genus *Atherosperma*, though thinly lignified, remains cupular with an unribbed neck and hardly contracted rim. It may be expected from this that the contribution of the perianth-androecium to the development of ~~its~~ the hypanthium is slight. Nutlet dissemination is effected solely by the reflexing of the style-surrounding staminodes.

In *Laureliopsis*, the thinly lignified hypanthium elongates a little and becomes ribbed and contracted towards the rim. The ribs, being the lignified decurrent bases of the persistent tepals, suggest that the contribution of the perianth-androecium to the fruiting hypanthium is considerably greater than in *Atherosperma*. In this respect, the hypanthium approaches the form in the Laurelieae (see chapter VII).

Nutlet dissemination is effected by the reflexing of the staminodes surrounding the styles, together with a splitting of the woody hypanthium wall.

Taxonomic Notes

Suprageneric groupings within the Atherospermataceae were first suggested by Bentham (1880). He separated *Atherosperma* and *Doryphora* from *Daphnandra*, *Laurelia*, and *Nemuaron*. Pax (1889) adopted this grouping and used the names Atherospermeae[*], and Laurelieae for them respectively. Hutchinson (1964) and Ehrendorfer et al. (1968) have since maintained the Atherospermateae as comprising *Atherosperma* and *Doryphora*.

This concept of the Atherospermateae is emended here. *Doryphora* is excluded and referred to the Laurelieae for reasons explained in the treatment of that tribe; and a hitherto unrecognised genus, *Laureliopsis*, is included. *Laureliopsis* is far more closely related to *Atherosperma* than to any other genus in the family; both have in common such features as very narrow and frequent secondary xylem vessels, two-armed leaf hairs, stamen-like staminal glands, and enlarged lignified staminodes in the fruiting hypanthium.

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[*] Other authors, such as de Jussieu (1824), Tulasne (1855), Baillon (1869), Bentham (1880), Hobein (1888), F.M.Bailey (1901,1913), and Solereder (1899) have used the tribe name Atherospermeae for the family Atherospermataceae when treating that group as a tribe of the Monimiaceae.

Key to the Genera of the tribe Atherospermateae

1a. Inflorescence thyrsuliform; fruiting hypanthium urceolate-cupular, with a short (6-)8-ribbed neck, and persistent perianth; leaf blades concolourous, with margins finely serrate, and midribs planate to prominent on upper face; flowers mostly bisexual, sometimes staminate; androecium in staminate and pistilliferous flowers partly sterile, with ± 4 outer stamens; stigmatic column conical .... VII. Laureliopsis Schodde

1b. Inflorescence single-flowered; fruiting hypanthium cupular, without neck, and perianth early caducous; leaf blades ± glaucous on lower face, with margins entire to sparingly toothed, and midribs deeply impressed on upper face; flowers unisexual; androecium in staminate flowers fully fertile, with (10-)12- ± 20 stamens, and in pistilliferous flowers sterile; stigmatic column stellately branched at the apex .... VIII. Atherosperma Labill.

VII. LAURELIOPSIS Schodde, gen.nov.

Laurelia auctt. [non Juss.]: R.Phil., Bot.Zeit. 15(1857)401 p.p.; A.DC., Prod. 16,2(1868)674 p.p.; Benth. in B.& H., Gen.Pl. 3(1880)139,145 p.p.; F.Phil., Cat.Pl.Vasc.Chil. (1881)265 p.p.; Hobein, Bot.Jb. 10(1888)71,73 p.p.; Pax, Pflzfm. 3,2(1889)102 p.p.; Perk. & Gilg, Pflzr. 4(1901)76 p.p.; anonym., Gard. Chron. 3,36(1904)400 p.p.; Dusén, Wiss.ergeb.Schwed.Südpolar-exped. 3,3(1908)4 p.p.?; Stapf, Curtis Bot.Mag. 135(1909) t.8279 p.p.; Perk., Pflzr. 49(1911)46 p.p.; anonym., Garden 79(1915)218, f.p.p.; Skottsberg, Kungl.Sv.Vet.Akad. Handl. 56(1916)37 et seq. p.p.; Perk, Gattung.Monim. (1925)12,13,51 p.p.; Garratt. Trop.Woods 39(1934)20 et seq. p.p.; Berry, Bot. Gaz. 96(1935)751 et seq., f.1 p.p.; Berry, Geol.Soc.Amer.spec. pap. 12(1938)5,16,23,34 et seq., 75 et seq., f.2 p.p.; Metcalfe & Chalk, Anat.Dicot. 2(1950)1139 et seq. p.p.?; Money, Bailey & Swamy, J.Arn.Arbor. 31(1950)381 et seq. p.p.; Core, Plant Taxon. (1955)318 p.p.; Cockayne, Veg.N.Zeal. ed.3, (1958)413 p.p.; Muñoz-Pizarro, Sinops.fl.Chil. (1959)155 p.p.; Godley, Proc.Roy.Soc.Lond. B,152(1960)459,463 p.p.; Skottsberg, ibid. 450 p.p.; Oberdorfer, Pflzsoziol.Stud.Chile (1960)80 et seq. p.p.; Buchheim in Melchior, Syllab.Pflzfm. ed. 12,2(1964)122 p.p.; Hutchinson, Gen.Fl.Pl. 1(1964)112,120 p.p.

Folia varie serrata, concoloria, cum pilis bibrachiatis; inflorescentiae thyrsuliformes, polygamiae; bracteae magnae cymbiformes, et plerumque ante anthesis cadentes; perianthium ordinatum octopartitum, cum tepalis penninervibus, in hypanthio fructificanti persistentibus; stamina ad apices truncata cum glandibus staminalibus staminiformibus; staminodia adsunt in floribus staminatis, in floribus bisexualibus dimorpha, cum staminodiis interioribus in hypanthio fructificanti productis ligneisque; columna stigmatica conico-subulata; hypanthium fructificans cylindrico- vel urceolato-cupulatum, in collo nervatum; nuculae aeque hirsutae.

Ex affinitate Atherospermatis Labill., per formam staminum et structuram perianthii hypanthii fructificantisque.

TYPUS GENERIS: Laureliopsis philippiana (Looser)Schodde, species unica.

Figures 1A, 23, 44A.

Medium-sized to tall polygamous trees, with cylindrical crowns; bark, wood, and leaves ± pungently aromatic; secondary xylem vessels ca (100-)110-130(-150) per sq. mm, inner tangential diameter (35-)45 -55 (-80) μ*; ultimate branchlet stems markedly angular tetragonous, coarsely hispid-strigose; vegetative buds densely strigose; petioles planate; leaf blades large microphyllous to notophyllous, concolorous, margins serrate-serrulate, midribs planate or prominent on upper face,

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* For other secondary xylem data comparable with that given for the genera of the Laurelieae, see data for tribe Atherospermateae.

centrifixed hairs with one arm 1-4 × length of the other, 1-3-layered hypodermis present on upper face*, oil cells confined to mesophyll**.

Inflorescence buds hardly compressed ovoid, shortly stipitate before expansion; mature inflorescences compactly thyrsuliform, with 3-11 flowers, polygamous rarely bisexual; accessory axillary flowers absent; bracts medium-sized, ovate cymbiform, sub-tepaloid, 3-5 mm long × 3-5 mm broad, strigose abaxially with often broadly glabrate margins, glabrous adaxially, caducous usually before anthesis; bracteoles present, ± subtending floral receptacles or hypanthia, similar to bracts in shape, size, and pubescence, and concurrently caducous.

Flowers staminate or ± bisexual; perianth tetramerous, comprising 8 oblong, obtuse, penninerved tepals, $3-4\frac{1}{2}(-5)$ mm long × $1-2(-3)$ mm broad, in 2 ± equal whorls; androecium in staminate flowers of stamens and staminodes, tetramerous, 2-3-seriate, the outer whorl(s) comprising 4 or 4 + 2 stamens, $1\frac{3}{4}-2(-2\frac{1}{2})$ mm long × $\frac{1}{2}-\frac{3}{4}$ mm broad × $\frac{1}{3}$ - $\frac{1}{2}$ mm thick, with ovate to ovoid stipitate staminal glands, and rounded-truncate to sunken-truncate latrorsely-dehiscing anthers, the inner whorl(s) comprising 4 or 8, isomorphic, stamen-like staminodes $(1\frac{1}{4}-)1\frac{1}{3}$ - $1\frac{1}{2}(-2)$ mm long × $\frac{1}{3}$ - $\frac{1}{2}$ mm broad, with reduced or vestigial staminal glands; androecium in bisexual flowers of stamens and staminodes, tetramerous, (4-)5-6-seriate, the outer whorl(s) comprising 4 or 4 + 2 stamens of the same form as in staminate flowers, the inner whorls unequal, the outer-

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* Hobein (1888).

** Hobein (1888), Money et al. (1950).

most comprising 4(+2 or 4) stamen-like staminodes of the same form as in staminate flowers, the innermost whorls of (8 or) 12 or 16 ± eglandular scale-like staminodes, $\frac{3}{4}$-$1\frac{1}{2}$ mm long × $\frac{2}{3}$ - 1 mm broad; pollen grains spheroidal to ellipsoidal, suboblate to oblate, Lg (21-)23-31(-32) μ × long. Lt. (28-)30-34 μ, the colpi transversales of irregular length, (12-)17-24 μ long, sometimes only one (well) developed, the interstitial equatorial depressions relatively extensive though sometimes obscure, the grain walls 1-2 μ thick, the surface sculpture with lumina circular to irregular in outline, ($\frac{1}{2}$-) ± 1(-2) μ long; gynoecium lacking in staminate flowers, comprising in pistill~~ate~~iferous flowers (8-)9-12(-15) carpels with terminal styles and conical-subulate, sometimes branched stigmatic column; ovule ellipsoid-globose, anatropous on basal placenta.

Fruiting hypanthium cylindrical- or urceolate-cupular, (4-)5-8 mm long × 4-6 mm thick, (6-)8-ribbed from tepal decurrences, sparingly haired, dehiscing into 3-4 subequal valves; perianth and androecium persistent, the scale-like staminodes elongated, lignified, ligulate, surrounding the prominently exserted style column; nutlets uniformly silky hirsute, the bodies ovoid-conical, the styles terminal, filiform.

The name Laureliopsis alludes to the superficial resemblance in habit, leaf, and inflorescence form to the genus Laurelia, which occurs in the same geographic region.

Species, Geographic Distribution, and Ecology

The genus Laureliopsis is monotypic, and confined to southern Chile and north-western Patagonia, often in mountains, between ca 36° and 47°S (maps 2,3).

It occurs in primary temperate rainforest, where the single species, L. philippiana, associated generally with Weinmannia trichosperma, Eucryphia cordifolia, and Nothofagus dombeyi, is a prominent, often dominant, element of the forest vegetation.

No data on germination or regeneration have been recorded.

Details of phenology are given under Laureliopsis philippiana.

Notes on Generic Characters

The characteristic features of Laureliopsis - its rather large cymbiform bracts and bracteoles with tepal-like margins, its predominantly bisexual flowers, its penninerved tepals, its truncate stamens with stamen-like staminal glands, and its scale-like staminodes that elongate to surround the prominently exserted style column in the fruit - have not been recognised as such before. Various aspects of the morphological peculiarities are considered below.

The narrow secondary xylem vesselsand centrifixed leaf hairs are unique in the family, Atherosperma excepted. Resembling Atherosperma in these features, Laureliopsis has nevertheless slightly larger, less frequent vessels, and longer hairs in which the arms are more equal. Other characteristics of its secondary xylem are summarised in chapter VI.

Hobein (1888) first recorded its centrifixed hairs and those of Atherosperma, but did not attach any significance to them. Those of Laureliopsis are illustrated in Curtis Bot Mag. 135(1909)t.8279 under the name Laurelia serrata Bert.

Sampson (1967) has drawn attention to the relatively small size of leaves of the base nodes of lateral branchlets in specimens he had seen from Chiloé (Godley 299, 299c). This is a feature of common though not universal occurrence, and is also found, rather less frequently, in the species of all other genera in the family. It is undoubtedly related to the bract-like form and protective function of these leaves in the shoot bud, which have been described in chapter IV.3.

Nowhere in the family is the basically decussate arrangement of parts in the vegetative shoot and inflorescence exhibited better than in this genus. Not only are the stems markedly tetragonous, but the pattern of pubescence also alternates strikingly on successive internodes: the hairs are always densest on the opposite faces adjacent to those decurrent from the superjacent petioles. In the flowers, also, both perianth and androecium parts are as constant in their tetramerous arrangement as they are in Dryadodaphne (Laurelieae). The androecium parts in both staminate and pistilliferous flowers of the more closely related Atherosperma are much more irregular in arrangement (chapter IV.10).

The large size of the bracts and bracteoles reflects their bud-protecting function Their similarity of form and ubiquitous yet transient presence indicate, nevertheless, a lack of specialisation of the inflorescence structure. The flower buds are not enclosed by bracts throughout their development until they are ready to burst, as happens in

Atherosperma and *Doryphora*. Instead, the inflorescence as a whole expands slowly and gradually, while the bracts, seemingly irrespective of their apparent function, fall off.

The distal peduncle bracts and bracteoles also closely resemble the perianth parts in their broadly glabrate tepaloid margins; and the tepals themselves are more bract-like in structure and venation than their counterparts in other genera of the family. The significance of this is discussed in chapter IV.10.

The flowers have generally been described as unisexual in the literature (R.Philippi 1857, Perkins 1911, Muñoz-Pizarro 1959), or inferred to be in descriptions of the genus *Laurelia* which cover the species *L. philippiana*. Only Stapf (1909) and Money et al. (1950) have mentioned the bisexuality of flowers and then in a way that emphasised trends to unisexuality. In the series of specimens examined during the present study, bisexual flowers appear to be the rule rather than the exception; only terminally central flowers are often unisexual (staminate).

It has been mentioned in chapter IV.7 that the staminate flower of *Laureliopsis* appears to represent a stage in the development of staminate flowers of the type found in *Atherosperma* and *Laurelia*. Its androecium comprises both stamens and staminodes confined to the margins of the receptacle in the same way as on the hypanthium of bisexual flowers; the centre of its receptacle, moreover, is hispid as in the hypanthium of bisexual flowers. [The androecium in the staminate flowers of *Athero-*

sperma and Laurelia, is fully fertile, and the stamens are distributed uniformly over the surface of the receptacle.]

The characteristic features of the fruiting hypanthium are reviewed in chapter VI. The contribution of the lignified decurrent perianth parts, and elongated lignified inner staminodes to the structure, is shown more clearly in Laureliopsis than in any other genus of the family.

Affinities

Previous revisers, R. Philippi (1857), Perkins (1911), Looser (1934), and Hutchinson (1964), have not distinguished the genus from Laurelia. Perkins and Gilg (1901) even included it in their circumscription of Laurelia sempervirens, as is indicated by their reference to bisexual flowers.

Laureliopsis, nevertheless, has much closer affinities with Atherosperma, as exemplified by the characteristics of the tribe Atherospermateae. Yet the characters distinguishing Laureliopsis, notably the slightly larger, less frequent secondary xylem vessels, thyrsuliform inflorescence, early caducous bracts, predominantly bisexual flowers and incomplete transitions to unisexual flowers, shorter stamens, pollen form, and relatively urceolate, ribbed fruiting hypanthium that splits to assist dissemination of the nutlets, approach those of the Laurelieae and link the Atherospermateae with that tribe. This relationship, together with the assessment of its critical characters as the least specialised in the family (chapters IV, XVI, table IV), lead to the conclusion that Laureliopsis is the most primitive living genus in the family.

1. *Laureliopsis philippiana* (Looser)Schodde, comb.nov.

Laurelia philippiana Looser, Rev.Asoc.Chil.Quim.y Farm. 21(1934)9 [nom.nov.pro *Laurelia serrata* R.Phil. non Bert.]; Muñoz-Pizarro, Sinops.fl.chil. (1959)155,244, f.136; Oberdorfer, Pflzsoziol.Stud.Chile (1960)80 et seq., f.29 p.p.*; Dansereau in Gressitt, Pacif.Basin Biogeogr. (1963)295 [in errore pro *Laurelia sempervirenti*?].

Laurelia serrata R.Phil., Bot.Zeit. 15(1857)401 [non Bert. 1829]; F.Phil., Cat.Pl.Vasc.Chil. (1881)265; [Hobein, Bot.Jb. 10(1888)71 pro syn. *Laureliae sempervirentis*]; Perk., Pflzr. 49(1911)46; Skottsberg, Kungl.Sv.Vet.Akad.Handl. 56(1916)37 et seq., 277 "*Laurelia serrata* Bert.et Phil."; Perk., Gattung. Monim. (1925)13,51; Looser, Rev.Asoc.Chil.Quim. y Farm. 21(1934)9; Berry, Bot.Gaz. 96(1935)754; Berry, Geol.Soc.Amer.

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* E.J.Godley (pers.comm.), who has had field experience with the species, is of the opinion that the large tree on the far left in f.29 could be *Laureliopsis philippiana*.

spec.pap. 12(1938)75; Money, Bailey & Swamy, J.Arn.Arbor. 31(1950)389,390; Schmithüsen in Schmithüsen, Klapp, & Schwabe, Bonner Geogr.Abh. 17(1957)f.32 p.p.; Cockayne, Veg.N.Zeal. ed.3, (1958)413,443 "Laurelia serrata Bert.et Phil."; v.Bauer, Bonner Geogr.Abh. 23(1958)34; Godley, Proc.Roy.Soc.Lond. B, 152(1960)463,464.

TYPE: Philippi (s.n or 659), Valdivia, "incolis Vauvan" and "Vulg.Vauvan" —— isotypes in K, MEL, US (photograph).

Laurelia sempervirens f. serrata (R.Phil.)Hobein, Bot.Jb. 10(1888)71.

Laurelia sempervirens auctt. [non (Ruiz & Pav.)Tul.]: A.DC., Prod. 16,2(1868)675 p.p.; [F.Phil., Cat.Pl.Vasc.Chil. (1881)265 p.p. pro syn. Laureliae serratae R.Phil. non Bert.et L. aromaticae]; Pax, Pflzfm. 3,2(1889)103 p.p.; Perk. & Gilg, Pflzr. 4(1901)77 p.p.; Hutchinson, Gen.Fl.Pl. 1(1964)120 p.p.?

Laurelia aromatica auctt. [non Poir.]: anonym., Gard.Chron. 3,36(1904)400,f.172; Schenk, Deutsche Tiefsee Exped. 2,1(1905)127?; anonym., Garden 79(1915)218,f*.; Garratt, Trop. Woods 39(1934)19 et seq. p.p.; Schimper & v. Faber, Pflzgeogr. ed 3,2(1935)683 p.p.?

Laurelia serrata auct. [non Bert.]: Stapf, Curtis Bot.Mag. 135(1909)t.8279.

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* The branchlet is figured from the underside.

The following illustrations referred to as *Laurelia serrata* Bert. in Index Londinensis have not been seen but are likely to refer to this species: Castillo & Dey, Jeogr.Vej.Rio Valdivia ed.2,1(1908)53; Skottsberg, Kungl.Sv.Vet.Akad.Handl. 56(1916)f.II.2; Thurston, Brit. & Foreign Trees & Shrubs Cornwall (1930)f.21.

Figures 2, 23, 44A.

Diagnosis

See description of genus.

Detailed Description

Medium-sized to tall trees (10-)15-30(-35) m high; bole ca 20-70 cm or more diameter breast height, sometimes branched from the base with 2-3 trunks, ± unbuttressed, sometimes coppicing; crown narrowly to broadly cylindrical, ca $\frac{1}{3}$ - $\frac{2}{3}$ × length of bole, rarely shorter, with branches horizontal to slightly drooping. Bark ca 5 mm thick* when dry, outer surface rather smooth, or finely striate or scaly, pale grey or slightly brownish, inside drying darker brown. Wood pale greyish cream, growth rings faintly defined or obscure. Branchlet stems relatively closely branched, the ultimate 4-6(-8) internodes ($\frac{3}{4}$-)1-3$\frac{1}{2}$(-5) cm long × 2-3(-4) mm thick, usually markedly tetragonous with angles discernibly flanged on younger internodes, smooth, drying pale fawn-grey to olive-grey or grey-brown, rarely darker, coarsely pale sordid grey or stramineous to dark brown curly hispid-strigose, the hairs dense and widespread over

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* Muñoz-Pizarro (1959).

ultimate 1-2(-5) internodes, below becoming sparse on stem faces subjacent to petioles and remaining dense on adjacent faces, eventually caducous, the leaf and branchlet nodes slightly more compressed, never swollen; shaded and sapling branchlet stems with ultimate 4-6 internodes (1-)2-6 cm long, thicker, the angles more prominently flanged, the hairs finer, more strigose, sparser, sometimes confined to shoots or ultimate 1-2 internodes. Vegetative buds narrowly obcordiform-conical, subsessile, the enveloping pair of bract-like leaves densely sordid stramineous strigose, with more-or-less erect, glabrous, mucronate apices, expanding when buds ca 5-8 mm long. Petioles relatively broad, (3-)4-8(-11) mm long × 1½-2½(-3) mm thick, planate hardly impressed on upper face, drying grey-brown, rarely blackish, usually persistently hispid on upper face, sparsely strigose to usually glabrescent on lower. Leaf blades narrowly elliptic to elliptic, rarely ovate to obovate, (2½-)4-8(-9½) cm long × (1½-)2-3½(-4½) cm broad, usually ± equally narrowed at each end into variously cuneate bases, and narrowly obtuse, rarely broadly obtuse or acute apices; margins serrate to serrulate, slightly to markedly recurved; texture thinly to quite coriaceous, the upper face rather smooth or lined with faintly prominulous to faintly impressed nerves that anastomose obscurely towards the blade margin; colour in dry leaves greyish olive to brownish; nervation on upper face as described, with midrib planate, sometimes prominent, on lower with midrib thickly prominent, and 6-11(-12) main nerves and their anastomoses obscure, hardly more, and sometimes less prominent than on upper face; glabrescent, the stramineous strigose hairs confined to base of midrib on upper face, rarely extending on to blade, more extensive on lower face, persisting along the midrib; leaf blades on shaded and sapling branchlets more ovate or broadly elliptic, (2½-)6-10(-13) cm ×(1½-)2-5(-6)cm broad, with more deeply serrate and flatter margins, thinly coriaceous to chartaceous, nerves and vein reticulum more prominent or impressed on both faces, darker brownish olive when dry, more sparsely haired. Bark, wood, stems, and leaves strongly, persistently, and pungently aromatic, with a clove- or citronella-like odour*.

Inflorescence buds hardly compressed ovoid, initially sub-sessile when 1-2 mm long, the enveloping pair of bracts ovate, shallowly cymbiform, densely sordid greyish to brownish strigose, eventually 3-4(-5) mm long, with shortly recurving mucronate apices; buds subsequently elongating through the development of a short thick stipe (= base internode of peduncle of mature inflorescence) up to 2-3 mm long below the bracts which diverge gradually to allow expansion of the ultimate inflorescence axes and flower buds. Mature inflorescences decurved, borne at ultimate 1-4(-6) leaf nodes among leaves, compactly thyrsuliform, 1-1½(-2) cm long, densely sordid pale grey-stramineous to grey-brown hispid-strigose, bearing 3-11 flowers, polygamous with bisexual and staminate flowers,

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* The odour is fecal, according to Looser (1934), or foetid, according to Stapf (1909) and Muñoz-Pizarro (1959).

sometimes entirely ± bisexual, the terminally central flower often staminate and invariably opening first, other flowers bisexual, infrequently functionally pistillate. Primary peduncles ($\frac{1}{3}$ -)$\frac{1}{2}$-$\frac{3}{4}$(-1) cm long, the base internode 1-$1\frac{1}{2}$ mm thick, rather broadly compressed, the distal internodes slightly slenderer more tetragonous, coarsely pale grey-stramineous hispid-strigose, or the terminal internode more finely and sparsely strigose, 1-3-noded, the subterminal nodes bearing solitary opposite flowers, rarely simple dichasia on secondary peduncles at basal nodes; bracts slightly dimorphic, the base node bracts herbaceous, deeply ovate cymbiform, 3-5 mm long × 3-5 mm broad, with broadly obtuse mucronulate apices and prominently carinate abaxial midribs, densely sordid grey ± strigose abaxially, glabrous adaxially, the distal node bracts sub-tepaloid, shallowly ovate cymbiform, of similar size, densely sordid grey strigose abaxially, with margins broadly glabrate and tepaloid, glabrous adaxially, usually caducous in early bud, sometimes persisting at terminal nodes during flowering; secondary peduncles rare, ca $\frac{1}{4}$ cm long; pedicels short, ± thick, ($\frac{1}{2}$-)1-3(-4) mm long × $\frac{2}{3}$ - $\frac{3}{4}$ mm thick often longest in terminally central flowers, sometimes almost suppressed, ± terete, densely sordid greyish silky strigose; bracteoles usually subtending terminally central and subterminal solitary flowers, regularly absent from lateral flowers of simple dichasia, sub-tepaloid, identical with distal peduncle node bracts in form and size, concurrently caducous. Mature flower buds ellipsoid to ovoid, 3-4 mm long ×2-3 mm thick, densely sordid pale grey strigose, the bracteoles valvate, ± completely enclosing young buds.

Open staminate flowers of medium size. Receptacle patelliform, 1 mm long × $1\frac{1}{2}$ mm broad, densely sordid stramineous-grey silky strigose outside, inside margin broadly glabrous, and centre pilose. Perianth greenish yellow*, cyathiform, 2-seriate or appearing ± uniseriate; tepals 8, oblong obtuse, 3-4(-5) mm long × 1-2 mm broad, ± herbaceous, with broadly glabrate, fimbriately eroded, involute petaloid margins, and thick abaxial costae, penninerved, densely strigose-hirsute on costae abaxially, glabrous adaxially, the inner tepals sometimes shorter and narrower than the outer. Androecium reddish*, of 2-3 tetramerous whorls confined towards receptacle margin, the outer whorl comprising 4 or 4 + 2 stamens, the inner whorls 4 or 8 staminodes; stamens incurving-erect, $1\frac{3}{4}$-2(-$2\frac{1}{2}$) mm long × $\frac{1}{2}$ - $\frac{3}{4}$ mm broad × ± $\frac{1}{3}$ mm thick, glabrous; filaments slender, slightly compressed, $\frac{2}{3}$ - $1\frac{1}{4}$ mm long × ± $\frac{1}{3}$ mm thick; staminal glands ± bilaterally compressed, ovate to ovoid or sub-spheroidal, shortly stipitate, ($\frac{1}{2}$-)$\frac{3}{4}$-1 mm long × ($\frac{1}{3}$ -)$\frac{1}{2}$ - $\frac{2}{3}$ mm broad, attached to basal margins of, and often complanate with filament; anthers cylindrical, $\frac{3}{4}$-$1\frac{1}{4}$ mm long × $\frac{1}{2}$ - $\frac{2}{3}$ mm thick, with rounded truncate (pre anthesis) to sunken truncate (post anthesis) apices, and latrorsely-dehiscing, narrowly elliptic valves; staminodes ± isomorphic, erect to recurving, slenderly clavate, stamen-like, ($1\frac{1}{4}$-)$1\frac{1}{3}$ - $1\frac{1}{2}$(-2) mm long × $\frac{1}{3}$ - $\frac{1}{2}$ mm thick, glabrous, the outer staminodes with reduced ovate to ovoid, shortly stipitate staminal glands, ($\frac{1}{4}$-)$\frac{1}{2}$-$\frac{3}{4}$ mm long × $\frac{1}{4}$-$\frac{1}{2}$ mm thick, the inner staminodes often shorter than the outer, with staminal glands reduced as obtuse obovate-oblong vestiges,

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* Stapf and figure in Curtis Bot Mag. 135(1909)t.8279.

or absent. Carpels lacking.

Open bisexual (or functionally female) flowers of medium-large size. Hypanthium broadly cupular, $1\frac{1}{2}$-$2\frac{1}{2}$ mm long × ($1\frac{1}{2}$-)2-3 mm thick, pubescent outside and inside as in staminate flowers; rim undifferentiated, the perianth and androecium inserted successively down concave margin of hypanthium chamber. Perianth colour, form, and arrangement as in staminate flowers, appearing 2(-3)-seriate; tepals as in staminate flowers, averaging larger, (3-)$3\frac{1}{2}$-$4\frac{1}{2}$(-5) mm long × (1-)$1\frac{1}{2}$-2(-3) mm broad, slightly dimorphic, the outer tepals more bract-like, broader, with nearly entire margins, more obscurely nerved, and more densely pubescent abaxially than the inner. Androecium reddish*, usually partly fertile, of (4-)5-6 tetramerous whorls, the outer whorl comprising 4 or 4 + 2 stamens, the inner whorls dimorphic staminodes; stamens of the same form as in staminate flowers, longer, the filaments 1-$1\frac{1}{2}$ mm long, the anthers sometimes smaller and more rounded obtuse, rarely completely aborted, entirely glabrous; outer staminodes 4(+2 or 4), stamen-like, of the same form and dimensions as in staminate flowers, glabrous; inner staminodes (8 or) 12 or 16, erect, scale-like, shingle-like, or plate-like, flat, with fimbriate, obtuse apices, and scarious margins, glabrous, the outermost oblong, 1-$1\frac{1}{2}$ mm long × $\frac{2}{3}$ - 1 mm broad, with somewhat thickened apices, eglandular or sometimes bearing vestigial staminal glands, the innermost ovate-deltate, $\frac{3}{4}$-1 mm long × $\frac{2}{3}$ mm broad, more markedly fimbriate scarious at the apex and margin, eglandular, all elongating after anthesis, the inner more than

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* Figure in Curtis Bot Mag. 135(1909)t.8279

the outer. Gynoecium of (8-)9-12(-15) carpels; styles exserted to near apices of stamens in a slender finely hispid column; stigmatic column ± coherent, slenderly, often curling conical subulate, sometimes branched, $\frac{1}{2}$-1(-1$\frac{1}{2}$) mm long, exserted beyond apices of stamens to near apex of perianth.

Ripe infructescences borne at ultimate 2-4(-6) leaf nodes usually among leaves on branchlets, 1$\frac{1}{2}$-2 cm long, persistently sordid stramineous-grey strigose, with most hypanthia maturing per infructescence. Primary peduncles $\frac{1}{2}$-1$\frac{1}{4}$ cm long × 1$\frac{1}{4}$-2 mm thick, of the same form as in inflorescence, sometimes more sparingly pubescent, the base internode frequently glabrescent; pedicels 2-4(-5) mm long × $\frac{2}{3}$ - 1 mm thick, of the same form and pubescence as in inflorescence, slightly longer and thicker, hardly expanded under hypanthium. Fruiting hypanthium cylindrical- or urceolate-cupular, hardly or slightly narrowed into an obscure neck $\frac{1}{3}$ - $\frac{1}{4}$ × length of hypanthium, (4-)5-8 mm long × 4-6 mm thick, conspicuously or obscurely (6-)8-ribbed towards rim, drying fawn-grey, sparsely pale sordid stramineous hispid-strigose with hairs denser towards rim, thinly lignified with walls $<$ 1 mm thick, dehiscing lengthwise from the rim between the ribs into 3-4 sub-equal valves; rim ill-defined, perianth and androecium persistent, the tepals decurrent in lignified hypanthium ribs, the inner scale-like staminodes ligulate, lignified, glabrous, and prominently elongated, the inner (5-)± 6(-8) mm long × $\frac{2}{3}$ - 1 mm broad, longer than the outer, surrounding the prominently exserted style column, reflexing at hypanthium dehiscence to disseminate nutlets; hypanthium chamber broadly cupular at the base, sparsely haired, almost glabrous towards the rim, densely sordid silky hirsute towards the base, with nutlets attached superficially to the base and lower sides. Nutlets elongating in maturing hypanthium to increase the exsertion of the style tips to 2-3 mm beyond apex of perianth; bodies of ripe nutlets ovoid-conical, 2-3(-3½) mm long × 1¼-2 mm thick, uniformly sordid brown silky hirsute or often more densely haired abaxially, the hairs straight, 4-6(-7) mm long; styles of ripe nutlets 6-10(-13) mm long, unexpanded at the base into body of nutlet, the hairs becoming markedly shorter towards the apex, ultimately hispidulous-strigillose or absent on apical 2-3 mm.

The epithet philippiana commemorates R.A. Philippi who first recognised and described the species (cf. Looser 1934).

Indian names: Guaguan (Krause: US 1690279, herb. Reed: K), Huahuán (Skottsberg 1916, Garratt 1934, Looser 1934, v. Bauer 1958, Muñoz-Pizarro 1959), Huanhuan (Stapf 1909), Hua Hum (Rasp 140). These are apparently variations of the one name "Huahuán" given to the species by the Araucanian Indians.

Vernacular names: Citronela (madera compensada) (Muñoz-Pizarro 1959), Laurel [? = error for Laurelia sempervirens] (anonym: MA, Rasp 140), Laurela (Muñoz-Pizarro 1959), Vauván (R. Philippi 1857, Perkins 1911, Muñoz-Pizarro 1959).

Series of specimens examined: 28 collections, comprising 3 with young and expanding inflorescence buds, 3 with staminate flower buds, 6 with open staminate flowers, 3 with bisexual flower buds, 8 with open ± bisexual flowers, and 12 with fruiting hypanthia at various stages of maturity.

Geographic Distribution (map 3)

Laureliopsis philippiana occurs in southern Chile, including Chiloé and off-shore islands, and north-western Patagonia along the Chilean border, between ± 36° and ± 47°S (cf. Skottsberg 1916):

Chile. Concepción; Rio Dillo; Rosa Victoria?; Rio Inepe; Temuco; Valdivia; Corral; Puyehue; La Enseñda; Rio Chepu; "Pastahue" Sancta Carola*; Port Laguna (ubi?).

Argentina. San Martin de los Andes; Peninsula Quetrihué; Puerto Blest; Lago Nahuel Huapi; Laguna Frias; Puerto Alegre; Lago Menendez; Cordillera del Chubut.

It has also been recorded from the Taguatagua area (Looser 1934), and near Ancud and Rio Pudeto, Chiloé ("Laurelia cfr. serrata"), Isla San Pedro, Chiloé, S.W. of Caleta Samuel, Isla Huafo (=Guafo), and Rio Aysen, Estero Aysen, and Chacabuco in Aysén province (Skottsberg 1916). Godley (1960) lists other localities as follows: Rio Puelo, Chiloé (fide

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* See under geographic distribution of Laurelia sempervirens.

Kruger), Rio Corcovado, Chiloé (fide Kruger), Rio Palena, Chiloé (fide Reiche), Puntra, Chiloé (fide Schmithüsen), Piriquina, Chiloé (Godley 1960), and Guaitecas Id. (fide Dusén). Schenk's (1905) reference to *Laurelia aromatica* in the Feuerländischen Wald surely refers to this species rather than *Laurelia sempervirens**.

These data suggest that the species has its maximum occurrence between the latitudes of 40°-43°S at the present time, allowing for the local effect of altitude.

Ecology

Laureliopsis philippiana is a canopy, rarely sub-canopy tree of the antarctic (Warming 1925), Chiloé (v. Bauer 1958), or temperate rainforest aspect of what has been termed "Valdivian" forest (Skottsberg 1916, 1960, Schimper and v. Faber 1935, Godley 1960). In Chile, it occurs mainly in the mountains in the northern parts of its range and more extensively in the lowlands in the south. In Patagonia, it is confined to mountain regions of the Andes. Data on its altitudinal occurrence throughout its geographic range are lacking.

Preferred soils are well-drained and derived from volcanic tuffs and sandstones on Chiloé, Guaitecas island, and at the river Aysen (Skottsberg 1916, Reiche 1907 quoting Dusén, and Godley 1960).

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* Stapf (1909) discusses the application of various names to the two species at that time.

In the central parts of its range, 40°- 42°S, the species is most frequent and a forest co-dominant with *Weinmannia trichosperma* between the altitudes of 600-900 m; it is less frequent in the *Fitzroya-Pilgerodendron* associations above, and the *Nothofagus dombeyi-Eucryphia cordifolia* (300-600 m), and particularly the *Nothofagus obliqua-Persea lingue* (150-300 m) subtropical associations below (Oberdorfer 1960). On northern Chiloé, 42°- 43°S, Godley (1960, pers. comm.) records it as frequent in mixed non-*Nothofagus* lowland forest with *Eucryphia cordifolia* and *Weinmannia trichosperma*. On Guaitecas island, it occurs with *Caldcluvia paniculata* and *Weinmannia trichosperma* apart from *Nothofagus-Drimys* forest, according to Dusén (Reiche 1907). On Chiloé, San Pedro island, Guafo island, and at the river Aysen, it is associated variably with the trees *Aextoxicon punctatum*, *Caldcluvia paniculata*, *Drimys winteri* *Eucryphia cordifolia*, *Gevuina avellana*, *Myrceugenia planipes*, *Nothofagus dombeyi*, *Saxegothea conspicua*, and *Weinmannia trichosperma* (Skottsberg 1916).

Its frequent occurrence in mixed or non-*Nothofagus* forest on relatively well-drained soils is in contrast with the ecological attributes of its tribal congener, *Atherosperma moschatum*.

Phenology

Flowering in *Laureliopsis philippiana* is apparently regularly seasonal, taking place from (April-)August to October in the austral winter and spring, under prevailing seasonal conditions of relatively uniform rainfall, and warmer summer and colder winter temperatures.

Fruit is set during summer months between December and March, and inflorescence buds for the ensuing season appear during this period, before dissemination of the nutlets.

Infraspecific Variation

No discernible geographic or altitudinal variation was apparent in the small series of herbarium collections seen, few of which bore altitudinal data. The material available, moreover, came from various parts of the trees collected (from either exposed, semi-shaded, or shaded branchlets, or saplings), making assessment of variation in the vegetative characters virtually impossible.

Taxonomic Notes and Typification

Laureliopsis philippiana has been confused taxonomically (e.g. Perkins and Gilg 1901), and nomenclaturally (see Stapf 1909), with *Laurelia sempervirens*. Aspects of their relationship are discussed under the genus *Laureliopsis* and under *Laurelia sempervirens*. The two species are sympatric. *Laureliopsis philippiana* may be readily recognised by its centrifixed leaf hairs, its predominantly bisexual tetramerous flowers with truncate stamens and stamen-like staminal glands, its small ± ribbed fruiting hypanthia with persistent perianth, and its narrower elliptic leaves with finely serrate margins. Useful field characters are the more finely serrate leaf margins and sharp citronella- or clove-like odour of its bark and leaves.

The determination of type specimens of the name Laurelia serrata R.Phil. is based on the annotation "incolis Vauvan" or "Vulg.Vauvan" on herbarium sheets. Cited also in the original description, this name is the only clear connection between the description and authentic specimens of the species collected by Philippi. All specimens that have been traced with these annotations belong to a single collection in flower bud and opening flower; they are therefore treated as isotypes.

Chemistry

No information is available.

Uses

Stapf (1909) quotes the species as a valuable timber tree, and Godley (pers. comm.) states that the species is logged for timber on Chiloé. Garratt (1934) records a Laurelia with the name Huahuán supplying commercial timber, but his remarks may apply equally or instead to L. sempervirens.

VIII. ATHEROSPERMA Labill.

Atherosperma Labill., N.Holl.Pl.spec. 2(1806)74; Poir. in Lam., Encyc.meth.Bot. 8(1808)817 "Antherosperma"; Juss., Ann.Mus.Hist. Nat.Par. 14(1809)121 et seq.; R.Br. in Flinders, Voy.Terr.Austral. (1814)553; Spreng., Syst.Veg. 2(1825)544; Lindl., Intr.Nat.Syst. Bot. (1830)29; Endl., Gen.Pl. (1837)314; id., Enchir.Bot. (1841) 195,196; Meisn., Pl.vasc.gen. 1(1841)324, 2(1841)236; J.B.Muell., Bot.Wörterb. (1841)42; Rchb., Nomencl.(Herb.buch) (1841)69; Endl., Gen.Pl.suppl. 4,2(1847,8)56; Schnizlein, Icon. 2(1849)n.105; Lind., Veg.Kingd. ed.3,(1853)300; Hook.f., Fl.Tasm. 1(1855)11 p.p.; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)283,291,294,418 p.p.; C.Muell. in Walp., Ann.Bot. 4(1857)117 p.p.; F.Muell., Pl.Colon.Vict. 1(1860)24 p.p.; Hook.f., Handb.N.Zeal.Fl. 1(1864)240 p.p.; A.DC., Prod. 16,2(1868)642,675 p.p.; Baill., Adansonia 9(1868)111,122, 124 et seq. p.p.; Baill., Hist.Pl. 1(1869)319 et seq., 335,343 p.p.; Benth., Fl.Austral. 5(1870)284 p.p.; Baill., Adansonia 10(1873)350 et seq. p.p.; id., Dict.Bot. 1(1877)310 p.p.; F.Muell., Nat.Pl.Vict. 1(1879)21 p.p.; Benth. in B.& H., Gen.Pl. 3(1880)138,139 ,144; Möller, Anat.Baumrinden (1882)100 [n.v.]; F.Muell., Syst.Cens.Austral.Pl. 1(1882)3; C.Moore, Cens.Pl.N.S. Wales (1884)58; F.Muell., Key Syst.Vict.Pl. 1(1887,8)25,541,544, 545; Hobein, Bot.Jb. 10(1888)53,70,73; F.Muell., Sec.Syst.Cens. Austral.Pl. 1(1889)5; Pax, Pflzfm. 3,2(1889)95,96,97,103; Bancroft, Proc.Linn.Soc.N.S.Wales 2,4(1890)1061; Baill., Dict.Bot.

3(1891)206 p.p.; Moore & Betche, Handb.Fl.N.S.Wales (1893)14; Perk., Bot.Jb. 25(1898)552; Solereder, Syst.Anat.Dicot. (1899) [transl. Boodle, Fritsch, & Scott, 2(1908)699 et seq.]; F.M.Bail., Queensl.Fl. 4(1901)1288,1294 p.p.; Perk. & Gilg, Pflzr. 4(1901)3, 8,11,14,77 p.p.; Deane, Rec.Geol.Surv.Vict. 1(1902)26; Rodway, Tasm.Fl. (1903)164 p.p.; Stapf, Curtis Bot.Mag. 135(1909)t.8279; Petrie, Proc.Linn.Soc.N.S.Wales 37(1912)139,143,146,151; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80; Ewart, Handb.For.Trees Vict. For. (1925)122; Perk., Gattung. Monim. (1925)5,10,13,16,51; McLuckie & Petrie, Proc.Linn.Soc.N.S.Wales 52(1927)175; Field Nat.Cl.Vict., Cens.Pl.Vict. ed.2,(1928)29; Francis, Austral. Rain-For.Trees (1929)94; Lemée, Dict.gen.phan. 1(1929)447; Welch, J.Proc.Roy.Soc.N.S.Wales 62(1929)362 et seq.; Ewart, Fl. Vict. (1931)519,520; Willis, Dict.Fl.Pl.Ferns ed.6,(1931)63; Garratt, Trop.Woods 39(1934)21 et seq.; Berry, Bot.Gaz. 96(1935) f.1,n.19 "Antherosperma"; Berry, Geol.Soc.Amer.spec.pap. 12(1938) f.2,n.19 "Antherosperma"; Lemée, Dict.gen.phan. 7(1939)235; A.C.Smith, J.Arn.Arbor. 22(1941)251; Audas, The Australian Bushland (1950)92 p.p.; Gundersen, Fam.Dicot. (1950)65; Metcalfe & Chalk, Anat.Dicot. 2(1950)1139 et seq.; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)374 et seq.; Francis, Austral.Rain-For. Trees ed. 2,(1951)109; Lemée, Dict.gen.phan.(suppl.) 9(1951)56; Croizat, Man.Phytogeogr. (1952)281,f.5,n.19; Botany Dept.University of Melbourne, Fam.Gen.Vict.Pl. (1953)73; Stern, Amer.J.Bot.

42(1955)874; Anderson, Trees N.S.Wales ed.3,(1956)368; L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)49; Hutchinson, Fam.Fl.Pl. ed.2,1 (1959)136; Croizat, Principia Botanica 1A(1960)379; Emberger in Chadefaud & Emberger, Traité Bot. 2(1960)945; Müller-Stoll & Mädel, Trans.Geol.Soc.S.Africa 65(1962)f.6; Burbidge, Dict. Austral.Pl.Gen. (1963)29; Evans in Beadle, Evans, & Carolin, Handb.Vasc.Pl.Sydney & Blue Mts. (1963)129,131; Hutchinson, Gen. Fl.Pl. 1(1964)112,122 p.p.; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed. 7,(1966)104; Curtis, Stud.Fl.Tasm. 3(1967)593.

TYPE SPECIES: *Atherosperma moschatum* Labill., only species.

[*Dendrosma* R.Br.* ex Cromb., J.Linn.Soc.Lond.Bot. 17(1879)395,nom.nud [non *Dendrosma* Panch.& Sebert 1874]]; [Perk. & Gilg, Pflzr. 4(1901)77 pro syn. *Atherospermatis moschati*].

Figures 1B, 15, 24, 44B, C.

Medium-sized monoecious trees, with cylindrical crowns; bark, wood, and leaves strongly, sweetly aromatic; secondary xylem vessels ca (100-)120-140(-160) per sq.mm, inner tangential diameter (25-)40-50(-70)µ **;

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* In his manuscript descriptions and notes, Brown used the name *Dendrosma* for specimens of *Atherosperma moschatum* he had collected in Australia (see also Burbidge 1955).

** For other secondary xylem data comparable with that given for the genera of the Laurelieae, see data for tribe Atherospermateae.

cortex and secondary phloem with rod cells*; ultimate branchlet stems rounded tetragonous, finely hispid-strigose; vegetative buds silky strigose; petioles slenderly sulcate; leaf blades microphyllous, glaucous on lower face, margins sparingly toothed to entire, midribs ± impressed on upper face, centrifixed hairs with one arm > 5× length of the other, hypodermis present** or absent***, oil cells confined to mesophyll****.

Inflorescence buds ovoid, elongate stipitate before expansion; mature inflorescences single-flowered, unisexual; accessory axillary flowers absent; bracts large, enclosing mature flower bud, ovate cymbiform, herbaceous, (4-)5-8(-9) mm long × (3-)4-7 mm broad, uniformly strigose abaxially, silky strigose adaxially, persisting during flowering; bracteoles absent.

Flowers staminate or pistilliferous; perianth tetramerous, comprising 8 elliptic-ovate, obtuse, palmate-parallel-nerved tepals, (5-)6-9(-10) mm long × $(1\frac{1}{2}$-)2-5(-7) mm broad, in 2 slightly unequal whorls; androecium in staminate flowers of (10-)12- ± 20 stamens arranged ± spirally over receptacle, stamens $(1\frac{1}{2}$-)2-4(-$4\frac{1}{2}$) mm long × ($\frac{1}{2}$-)$\frac{2}{3}$ - 1(-$1\frac{1}{4}$) mm broad × $\frac{1}{3}$ - $\frac{1}{2}$ mm

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*Möller (1882) fide Hobein (1888), Solereder (1899).

**McLuckie and Petrie (1927).

***Hobein (1888), Metcalfe and Chalk (1950).

****Hobein (1888), Money et al. (1950).

thick, with lanceate to narrowly ovoid stipitate staminal glands, and broadened truncate extrorsely-dehiscing anthers; androecium in pistilliferous flowers of 24- ± 35(- ± 40)± isomorphic, linear-lanceate or oblong staminodes arranged in (2-)3(-4) sub-spiral whorls, (1-)1½-3(-3½) mm long × (½-)¾-1(-1½) mm broad, usually eglandular; pollen grains ellipsoidal, rarely spheroidal, oblate to suboblate, Lg (16-)18-24(-26)μ × long.Lt.(22-)26-34(-36)μ*, the colpi transversales of regular length, 20-30 μ long, both well developed, the interstitial equatorial depressions short, the grain walls 1-2 μ thick, the surface sculpture with lumina regular and circular in outline, ½(-1)μ in diameter; gynoecium lacking in staminate flowers, comprising in pistill~~ate~~liferous flowers ca 24- ± 40(- ± 50) carpels, with terminal styles, and stellately branched stigmatic column; ovule ellipsoid, anatropous on basal placenta.

Fruiting hypanthium cupular, (3-)4-6(-7) mm long × (4-)6-9(-11) mm thick, ± levigate, densely silky hispid-strigose, ± indehiscent; perianth caducous, androecium persistent, the inner staminodes elongated, lignified, linear, surrounding the prominently exserted style column; nutlets unilaterally silky hirsute, the bodies ellipsoid or slightly conical, the styles terminal, subulate.

The name Atherosperma is formed from ἀνὴρ (=ἀθήρ), a barb or arista, and σπερμα, a seed, in allusion to the aristate nutlets characteristic

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* Erdtman (1952) has recorded pollen grains of A. moschatum with the dimensions 23 × 41 × 29 μ, and occasionally 3 sulculi (= colpi transversales).

of this genus, and also the family (cf. Labillardière 1806, Tulasne 1855, Perkins and Gilg 1901).

Species, Geographic Distribution, and Ecology

The genus *Atherosperma* is monotypic, and confined to south-eastern Australia and Tasmania, usually in mountains, between 32° and 43°40′S (maps 2,4). It is recorded incorrectly for New Guinea by Burbidge (1960, p. 129), and the distribution indicated by Berry (1935, 1938) and Croizat (1952) in published maps, and by Burbidge (1963), is too extensive over eastern mainland Australia.

It occurs in temperate rainforest, in which the single species, *A. moschatum*, is often a dominant element, associated with *Nothofagus cunninghamii* and *Dicksonia antarctica*.

The mode of nutlet germination may be unique in the family. Wherever it was observed (at Brown Mountain, New South Wales, and at Mt.Field, Tasmania), germination took place only on the wet fibrous trunks of the tree fern, *Dicksonia antarctica*, or infrequently on the rough-barked trunks of *Eucalyptus* or *Elaeocarpus holopetalus*, near the ground. No seedlings were ever collected from a substrate of bare soil and leaf litter on the forest floor. Regeneration by coppicing has also been observed frequently.

Details of phenology are given under *Atherosperma moschatum*.

Notes on Generic Characters

Characteristic of *Atherosperma* are the very long and narrow secondary xylem vessel members, the sparingly toothed or ± entire, abaxially glaucous leaves, the large persistent cymbiform bracts, the large unisexual flowers in single-flowered inflorescences, the slender, broadly truncate stamens with stamen-like staminal glands, and extrorsely-dehiscing anthers, and the elongated staminodes that surround the gynoecium in the broadly cupular fruiting hypanthium. In these combined features, the genus is perhaps the most distinctive in the family. Other aspects of its characters are considered below.

The centrifixed hairs on the lower faces of the leaves are much more unequally armed than those of *Laureliopsis*; one of the arms is sometimes so short as to appear vestigial.

Evidence for interpreting the single-flowered inflorescence as reduced, and the single pair of large flower bud-enveloping "bracts" as bracts, not bracteoles, is presented in chapter IV.6. All vestiges of other bract structures are lacking, presumably having been lost in the process of inflorescence reduction. The bracts present resemble closely in their form and herbaceous margins the bracts at the base peduncle nodes in the inflorescence of *Laureliopsis*. They may be readily distinguished, nevertheless, by the silky vesture on their adaxial face. They are also more persistent than in any other genus, and usually remain attached to the peduncle after the fall of staminate flowers and until near the maturation of the fruiting hypanthium. Reasons for this are advanced in chapter IV.6.

The flowers are strictly unisexual. In staminate flowers, stamens only are present, and their anthers dehisce in centrifugal succession. In pistilliferous flowers, the androecium is invariably sterile; the occasional occurrence of perfect anthers in these flowers (Rodway 1903), is not confirmed in the series of specimens examined in the present study.

Though the arrangement of the perianth resembles that in *Laureliopsis* and *Dryadodaphne* (Laurelieae) (chapter IV.10), the tepals in *Atherosperma* differ markedly in their more petaloid form and palmate-parallel venation.

The only data on embryological features have been provided by Sastri (1963), and are reviewed in chapter IV.12.

The characteristics of the fruiting hypanthium and mode of nutlet dissemination are described briefly in chapter VI. The eventual recurving and spreading of the elongated hairy staminodes to effect nutlet dissemination appears to be brought about by the lignification and/or drying of the fruiting hypanthium as it reaches maturity.

Affinities

Notwithstanding its distinctiveness, *Atherosperma* has had a rather chequered taxonomic history since its establishment by Labillardière in 1806, with one species, *A. moschatum*. Brown (1814) suggested that it was closely related to *Laurelia*, and Hooker (1855, 1864) subsequently combined the other then known genera, *Laurelia* and *Doryphora*, under it. This broad definition was corroborated, either directly or indirectly, by Baillon (1868, 1869, 1876), Bentham (1870), F.Mueller (1879), F.M. Bailey (1901), Rodway (1903), and Audas (1950) in respect of *Laurelia*, but not *Doryphora*.

Baillon (l.c.) distinguished Doryphora on account of its aristate anthers and laterifixed styles. Recognising other dissimilar characters in Laurelia, Bentham (1880) broke with convention in relating Atherosperma to Doryphora among the genera of the Atherosperma group in the Monimiaceae alliance. Pax (1889) and Hutchinson (1964) reiterated this view, which was based on the few-flowered involucrate inflorescences common to both genera. It is evaluated in chapter IX.

Species of the very different genus Daphnandra, (D. micrantha, D. repandula), were also originally referred to Atherosperma by Tulasne (1855a, 1855) and F. Mueller (1877) respectively, and maintained under it by C. Mueller (1857), F. Mueller (1860, 1877), A. de Candolle (1868), Baillon (1869), and Perkins and Gilg (1901)*. More recently, A.C.Smith (1941) has suggested that the common presence of bracts beneath the flowers indicates a relatively close relationship between Atherosperma and Dryadodaphne. As indicated in chapter IV.6, however, these "bracts" in the two genera are not homologous.

None of these surmised affinities of Atherosperma have any substance. Instead, as reflected by the characters of the tribe Atherospermateae, the genus is more closely allied to Laureliopsis, and, in virtually all of its morphological characters, is related to the remaining genera of the family only through that genus. The pre-eminent differences between these two genera are mentioned above and in chapter VII.

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* In the case of D. repandula.

1. Atherosperma moschatum Labill.

Atherosperma moschatum Labill., N.Holl.Pl.spec. 2(1806)74,f.224 "Atherosperma moschata"; Poir.in Lamk., Encyc.meth.Bot. 8(1808) 817 "Antherosperma moscata"; Spreng., Syst.Veg. 2(1825)544; Schnizlein, Icon. 2(1849)n.105,f.16 "Atherosperma moschata"; Lindl., Veg.Kingd. ed.3,(1853)300,f.207 "Atherosperma moschata"; Hook.f., Fl.Tasm. 1(1855)11,12 "Atherosperma moschata"; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)276,291,420; C. Muell.in Walp., Ann.Bot. 4(1857)118; F.Muell., Pl.Colon.Vict. 1(1860)24; Zeyer, Jahresberichte (1861)769 [n.v.], Vjschr.prakt.Pharm. 10(1861)504 or 513 [n.v.]; Gladstone, J.Chem.Soc. 17(1864)5; A.DC., Prod. 16,2(1868)676 "A. moschata"; Baillon, Hist.Pl. 1(1869)319,335,336, f.360-365 "A. moschata"; Benth., Fl.Austral. 5(1870)284 "A. moschata"; Gladstone, J.Chem.Soc. 25(1872)12; Baill., Adansonia 10(1873)351 "Atherosperma moschata"; F.Muell., Fragm. 8(1874)142; Baill., Dict.Bot. 1(1877)310,f. "A. moschata"; F.Muell., Fragm. 10(1877)106; F.Muell., Nat.Pl.Vict. 1(1879)22; F.Muell., Syst.Cens.Austral.Pl. 1(1882)3; Moore, Cens.Pl.N.S. Wales (1884)58 "A. moschata"; F.Muell., Key Syst.Vict.Pl. 2(1885)6, 1(1887,8)124,539; Hobein, Bot.Jb. 10(1888)70 "Atherosperma moschata"; Maiden, Useful Nat.Pl.Austral. (1889)9,156, 224,253,315,380 "Atherosperma moschata"; F.Muell., Sec.Syst.Cens. Austral.Pl. 1(1889)5; Pax, Pflzfm. 3,2(1889)104,f.68 A-E; Moore & Betche, Handb.Fl.N.S.Wales (1893)15; Lauterer, Proc.Roy.Soc.

Queensl. 11(1895)21 "Atherosperma moschata"; Solereder, Syst. Anat.Dicot. (1899) [transl.Boodle, Fritsch, & Scott, 2(1908)701, 702]; F.M.Bail., Queensl.Fl. 4(1901)1294 "A. moschata"; Deane, Proc.Linn.Soc.N.S.Wales 25(1901)587, f.XXXVIII.2; Perk. & Gilg, Pflzr. 4(1901)4,5,11,78,f.22A-J; Deane, Rec.Geol.Surv.Vict. 1(1902)26; Rodway, Tasm.Fl. (1903)164 "A. moscata"; Dixon, Pl. N.S.Wales (1906)31 "Atherosperma moschata"; Guilfoyle, Austral. Pl. (1911)65,462; Perk., Pflzr. 49(1911)47; Petrie, Proc.Linn. Soc.N.S.Wales 37(1912)139,143,151,154; Scott, J.Chem.Soc. 101(1912)1612 [n.v.]; F.M.Bail., Compr.Cat.Queensl.Pl. (1913)419 "Atherosperma moschata"; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80; Maiden, For.Fl.N.S.Wales 6(1917)289,f.; Baker, Hardwoods Austral. (1919)332; Penfold, J.Proc.Roy.Soc.N.S.Wales 55(1921)270,272; Brough, McLuckie, & Petrie, Proc.Linn.Soc.N.S. Wales 49(1924)485; Jones & Smith, Proc.Roy.Soc.Queensl. 35(1924) 62; Domin, Bibl.Bot. 89(1925)674; Ewart, Handb.For.Trees Vict. For. (1925)21,122,f.52; Perk., Gattung. Monim. (1925)7,8,13,52, f.40 A-J; Hutchinson, Fam.Fl.Pl. 1(1926)f.10; McLuckie & Petrie, Proc. Linn.Soc.N.S.Wales 52(1927)174,text-f.6; Field Nat.Club Vict., Cens.Pl.Vict.ed.2,(1928)29; Francis, Austral.Rain-For.Trees (1929)20,26,38,95; Welch, J.Proc.Roy.Soc.N.S.Wales 62(1929)352 et seq.,f.2; Patton, Proc.Roy.Soc.Vict. 42(1930)154 et seq.; Ewart, Fl.Vict. (1931)520,f.219; Patton, Proc.Roy.Soc.Vict. 46(1933)117 et seq.; Garratt, Trop.Woods 39(1934)19 et seq., f.I.1; Fraser & Vickery, Proc.Linn.Soc.N.S.Wales 62(1937)289, 63(1938)159,161; Turrill, Curtis Bot.Mag. 165(1948)t.43; de Beuzeville, Austral.Trees Austral.Planting (1947)110,131; Henry, Pl. Alkaloids ed.4,(1949)320; Audas, The Australian Bushland (1950)92,382; Metcalfe & Chalk, Anat.Dicot 2(1950)1141,1144,f. 275H; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)392, text-f.6,f.II.26,III.39; Francis, Austral.Rain-For.Trees ed.2, (1951) 24,48,49,112; Erdtman, Pollen Morph. & Pl.Taxon. (1952)271, f.157E "Atherosperma moschata"; Anderson, Trees N.S.Wales ed.3, (1956)137; Bick, Clezy, & Crow, Austral.J.Chem. 9(1956)111; Curtis, Stud.Fl.Tasm. 1(1956)XXXIV "Sassafras"; Gilbert, Proc. Roy.Soc.Tasm. 93(1959)129,f; Hutchinson, Fam.Fl.Pl. ed.2,1(1959) 137,f.12; Walter, Veg.Erde (1962)140, f.107,108 "Atherosperma moschata"*; Evans in Beadle, Evans, & Carolin, Handb.Vasc.Pl. Sydney & Blue Mts. (1963)131; Buchheim in Melchior, Syllab. Pflzfm. ed.12,2(1964)f.42M; Davies, Geogr.Rev. 54(1964)249 et seq.; Good,Geogr.Fl.Pl. ed.3,(1964)220; Hutchinson, Gen.Fl.Pl. 1(1964)112,122; Bick & Douglas, Chem.& Ind.(London) (1965)694; Costermans, Trees Vict. (1966)66,f.; Curtis, Stud.Fl.Tasm. 3(1967)594,f.125; Curcumelli-Rodostamo & Kulka in Manske, Alkaloids 9(1967) 152,156; Willis in Cochrane, Fuhrer, Rotherham, & Willis, Fl.Pl.Vict. (1968)145,t.451.

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* Incorrectly referred to the family Saxifragaceae.

TYPE: Labillardière, Nova Hollandia [= Recherche Bay, Tasmania] —— isotypes in A, BM, GH, K, MEL, P(?).

Atherosperma integrifolium A.Cunn.ex Tul., Arch.Mus.Hist.Nat.Par. 8(1855)421; [A. DC., Prod. 16,2(1868)676 pro syn. *Atherospermatis moschati*].

TYPE: see under *A. moschatum* subsp. *integrifolium* (Tul.)Schodde.

Atherosperma dilatatum Gdgr., Bull.Soc.Bot.France 66(1919)233.

TYPE: Coghill, Launching Place, Victoria —— holotype in LY, isotype in BO.

Atherosperma elongatum Gdgr., Bull.Soc.Bot.France 66(1919)232.

TYPE: see under *A. moschatum* subsp. *integrifolium* (Tul.)Schodde.

Atherosperma muticum Gdgr., Bull.Soc.Bot.France 66(1919)232.

TYPE: herb.C.Walter, Victoria, 1902 —— holotype in LY, no isotypes traced.

Atherosperma tasmanicum Gdgr., Bull.Soc.Bot.France 66(1919)233.

TYPE: Gunn, Oceania, Tasmania, 1850 —— holotype in LY, no isotypes traced.

[*Dendrosma lucida* R.Br.ex Cromb., J.Linn.Soc.Lond.Bot. 17(1879)395, nom.nud.]; [Perk., Pflzr. 49(1911)47 pro syn. *Atherospermatis moschati*].

[?*Cryptocarya glaucescens* Tul., Arch.Mus.Hist.Nat.Par. 8(1855)420, nom.nud. pro syn. *Atherospermatis moschati* [non *Cryptocarya glaucescens* R.Br. 1810 nec Hassk. 1844 [n.v.]]; C.Muell.in Walp., Ann.Bot. 4(1857)118 pro syn. *Atherospermatis moschati* —— not validly published as not accepted by either author: I.C.B.N. 1966, art.34].

Figures 3, 15, 24, 44B, C.

Diagnosis

See description of genus.

Detailed Description

Medium-sized, less often small or tall trees (3-)5-25(-30)* m high; bole ca 8-40 cm diameter breast height, sometimes branched from the base with 2-3 trunks, ± unbuttressed, often coppicing; crown ± narrowly cylindrical, ca $\frac{1}{2}$-$\frac{3}{4}$ × length of bole, with branches ± horizontal to horizontal-ascending, and leaves ± horizontal on ultimate branchlets. Bark (2-)5-10 mm thick when dry, outer surface rather smooth, or slightly rougher and striately pustuled, pale to mid grey, sometimes brownish, inside dark cream, drying brown to blackish. Wood pale grey-white to mid cream,

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* Tree heights of up to 45 m recorded by J.D.Hooker (1855) and Curtis (1967) may be exaggerated.

growth rings obscure. Branchlet stems relatively closely branched, the ultimate 2-6(-8) internodes $(\frac{1}{2}-)1-2\frac{1}{2}(-4)$ cm long × 1-2(-3) mm thick, sometimes thicker in leader stems, rounded compressed to tetragonous, with angles ± rounded on younger internodes, smooth to wrinkled, drying pale grey-brown, golden, or brown-black, often olive-tinted, finely pale sordid grey or stramineous to sordid blackish brown hispid or hispid-strigose on ultimate 2-4(-6) internodes, the hairs sometimes sparser on stem faces subjacent to petioles, below becoming sparser, shorter, and darker, eventually caducous, the leaf nodes often slightly swollen, and branchlet nodes more broadly compressed; shaded and sapling branchlets with ultimate 4-6 internodes longer, $(1\frac{1}{2}-)2-4(-7)$ cm long, hardly thicker, often washed marone, the hairs finer, more strigose, sparser, sometimes confined to ultimate 2-3 internodes. Vegetative buds of obscure form, subsessile, the enveloping pair of bract-like leaves often obscured by a dense sordid stramineous silky strigose vesture, expanding when buds 6-10 mm long. Petioles slender, (2-)3-6(-8) mm long × $\frac{1}{2}-1\frac{1}{2}$ mm thick, deeply, rarely shallowly impressed on upper face, drying brown to blackish, finely sordid stramineous to brownish hispid-strigose on both faces, eventually glabrescent. Leaf blades linear-elliptic or narrowly lanceate to broadly elliptic or ovate, $(2-)3-7\frac{1}{2}(-12)$ cm long × $(\frac{1}{2}-)\frac{3}{4}-2(-3\frac{1}{2})$ cm broad, ± obtuse sometimes cuneate at the base, acute to narrowly mucronulate obtuse, rarely attenuate at the apex; margins entire to (1-)2-6(-8)-toothed, markedly recurved to revolute; texture thinly to quite coriaceous, the upper face usually finely wrinkled or rugulose, rarely quite smooth, lined with finely impressed, sometimes prominulous nerves that anastomose obscurely towards the blade margin; colour ± glossy mid green on upper face, pale grey-green to glaucous-white with midrib often reddish brown on lower, in dry leaves often nitid pale brown-olive to blackish olive on upper face, remaining ± glaucous on lower; nervation on upper face as described, with midrib shallowly to deeply impressed, very rarely almost planate, on lower with midrib slenderly prominent, and (4-)5-7(-9) slenderly prominulous main nerves anastomosing obscurely towards the blade margin, the vein reticulum absent, rarely obscurely present; glabrescent on upper face, with sordid grey to brown hispid hairs persistent along midrib, persistently cream-grey to brownish strigose on lower face, the hairs browner, denser, more hispid along midrib, eventually caducous; leaf blades on shaded and sapling branchlets usually more broadly ovate, (3-)4-8$\frac{1}{2}$(-10) cm long × ($\frac{3}{4}$-)1$\frac{1}{4}$-3$\frac{1}{2}$(-5) cm broad, with ± acuminate apices, and more deeply (0-)4-14(-18)-toothed flatter margins, subcoriaceous to almost chartaceous, midribs often planate or slightly prominent on upper face, nerves and their anastomoses more prominent on both faces, duller darker on upper face, the glaucous bloom irregular or absent on lower face, almost glabrous. Bark, wood, and stems persistently and sweetly aromatic with the odour of safrol, the leaves equally aromatic, but often with a more citronella-like odour.

Inflorescence buds ovoid, apiculate, (4-)5-7(-8) mm long × (2-)4-5 mm thick at maturity, borne on an elongate stipe (= peduncle of mature inflorescence) described below, the enveloping pair of bracts described below, enlarged and completely enclosing flower bud, opening only when mature flower bud is ready to burst. Mature inflorescences decurved, borne at ultimate 1-2(-3) leaf nodes among leaves, single-flowered, (¾-)1-1¾(-2¼) cm long, densely sordid grey-stramineous silky hispid-strigose, unisexual, the distal node flowers often staminate and invariably opening first, the proximal node flowers pistilliferous. Peduncles (¼-)½-¾(-1¼) cm long × ± 1 mm thick, terete, wrinkled-costate, densely pale grey stramineous hispid-strigose; bracts a single pair subtending the flower, entirely herbaceous, deeply ovate cymbiform, (4-)5-7(-8) mm long × (3-)4-5(-6) mm broad in staminate flowers, (5-)7-8(-9) mm long × (4-)5-7 mm broad in pistilliferous flowers, with broadly obtuse mucronulate apices and prominently carinate abaxial midribs, uniformly greyish strigose abaxially, densely paler silky strigose adaxially, persisting after the fall of staminate flowers and to near maturation of the fruiting receptacle; pedicels ± lacking. Mature flower buds enclosed by valvate bracts, the composite bud being the inflorescence bud as described.

Open staminate flowers of large size, fragrant. Receptacle patelliform to planate, 1-2(-2½) mm long × (2½-)3-4(-5) mm broad, densely sordid pale stramineous to grey-green silky strigose outside, inside finely hispid, rarely glabrous, shortly stipitate, the stipes (≡ pedicels) (½-)1-2(-3) mm long. Perianth white to cream-white, often pink-marone punctate in throat, cyathiform, 2-seriate, the whorls slightly unequal; tepals 8, elliptic-ovate obtuse, (5-)6-9(-10) mm long × (1½-)2-5(-7) mm broad, subpetaloid with entire margins, palmately-parallel-nerved, with usually 3 or

5 main nerves from the base, densely off-white to pale grey-green silky strigose abaxially, with hairs sparser towards the margins, glabrous adaxially, the inner tepals narrower than the outer. Androecium whitish, the connectives washed pink-red, of (10-)12- ± 20 stamens arranged ± spirally over receptacle; stamens recurving-erect, (2-)2$\frac{1}{2}$-4(-4$\frac{1}{2}$) mm long × ($\frac{1}{2}$-)$\frac{2}{3}$ - 1(-1$\frac{1}{4}$) mm broad × $\frac{1}{3}$ - $\frac{1}{2}$ mm thick, the inner longer than the outer, glabrous; filaments slender, terete, 1$\frac{1}{2}$-2(-2$\frac{3}{4}$) mm long × $\frac{1}{3}$ mm thick; staminal glands ± dorsiventrally compressed, narrowly ovoid to ± lanceate, shortly stipitate, (1-)1$\frac{1}{2}$-2(-2$\frac{1}{2}$) mm long × ($\frac{1}{2}$-)$\frac{2}{3}$ - $\frac{3}{4}$(-1) mm thick, attached to basal margins of filament, slightly recurved; anthers dorsiventrally compressed cylindrical, ($\frac{3}{4}$-)1-1$\frac{1}{2}$(-1$\frac{3}{4}$) mm long × ($\frac{1}{2}$ -)$\frac{2}{3}$ - 1(-1$\frac{1}{4}$) mm thick, with broadened truncate apices, and extrorsely-dehiscing, narrowly elliptic valves. Staminodes and carpels lacking.

Open pistilliferous flowers of large size, fragrant. Hypanthium cupular, (2-)3-4(-5) mm long × (4-)5(-7) mm thick, pubescent outside as in staminate flowers, inside sordid hispid-hirsute among staminodes and carpels, ± sessile or infrequently obscurely stipitate on stipes up to $\frac{1}{2}$ mm long; rim undifferentiated, the perianth and androecium inserted successively down concave margin of hypanthium chamber. Perianth colour, form, and arrangement as in staminate flowers, often more deeply cyathiform; tepals as in staminate flowers, averaging a little shorter, 5-8(-10) mm long × (1$\frac{1}{2}$-)2-5(-7) mm broad. Androecium pale green-cream, entirely sterile, of (2-)3(-4) whorls comprising 24- ± 35(- ± 40)± isomorphic staminodes in hemicyclic or spiral arrangement over inner hypanthium wall, packed closely around gynoecium; staminodes recurving, compressed narrowly deltate, linear-lanceate, narrowly oblong, or slightly clavate, with narrowly obtuse to acute entire apices, densely short strigose but glabrous adaxially towards the apices, the outer (1-)$1\frac{1}{2}$-3(-$3\frac{1}{2}$) mm long × ($\frac{1}{2}$-)$\frac{3}{4}$-1(-$1\frac{1}{2}$) mm broad, sometimes bearing vestigial staminal glands up to 1 mm long, the inner shorter, caudate to linguiform at the apices, eglandular, all elongating after anthesis, the inner more than the outer. Gynoecium of ca 24- ± 40(- ± 50) carpels; styles exserted to apices of staminodes in a slender finely hispid column; stigmatic column connate at the base, usually stellately branched at the apex, 1-$1\frac{1}{2}$(-2) mm long, exserted beyond and slightly over-hanging staminodes.

Ripe infructescences borne at ultimate (1-)2-4(-5) leaf nodes among leaves on branchlets, (1-)$1\frac{1}{4}$-$1\frac{3}{4}$(-$2\frac{1}{4}$)cm long, persistently sordid stramineous-grey hispid-strigose, with most hypanthia maturing per branchlet. Primary peduncles $\frac{1}{2}$-1(-$1\frac{1}{4}$) cm long × 1-$1\frac{1}{2}$ mm thick, of the same form as in inflorescences, straightened and slightly thickened; pedicels lacking. Fruiting hypanthium globose-cupular, slightly contracted towards the rim, (3-)4-6(-7) mm long × (4-)6-9(-11) mm thick, levigate, drying pale sordid grey-green, densely silky hispid-strigose, thinly lignified with walls ($\frac{1}{2}$-)$\frac{3}{4}$-$1\frac{1}{4}$(-$1\frac{1}{2}$) mm thick, indehiscent, rarely dehiscing lengthwise into 2(-3) unequal valves; rim ill-defined, perianth caducous, androecium persistent, the staminodes linear, acute sometimes caudate, thinly lignified, generally silky hispid, and prominently elongated, the inner (3-)4-7(-8) mm long × ($\frac{1}{2}$-)± 1(-$1\frac{1}{2}$) mm broad, longer than the outer, surrounding the prominently exserted style column, eventually reflexing to disseminate nutlets; hypanthium chamber broadly cupular, uniformly densely sordid pale brown silky hirsute, with nutlets attached superficially to the base and lower sides. Nutlets elongating in maturing hypanthium to increase the exsertion of the style tips to (2-)3-5(-8) mm beyond apex of androecium; bodies of ripe nutlets ellipsoid or slightly conical, 2-$3\frac{1}{2}$(-4) mm long × ($\frac{2}{3}$-)$\frac{3}{4}$-$1\frac{1}{2}$ mm thick, broadly glabrous adaxially, densely sordid pale brown silky hirsute abaxially, the hairs straight, (4-)5-7(-8) mm long; styles of ripe nutlets (5-)6-10(-15) mm long, hardly expanded at the base into body of nutlet, the hairs becoming gradually shorter towards the apex, the apical 1-2 mm often glabrous.

2-12-noded seedlings* ca 1-16 cm high, the stem internodes tetragonous, 3-15(-25) mm long, smooth, ± stramineous strigose, particularly in smaller seedlings; cotyledons with petioles 1 mm long, and blades elliptic to almost circular, 3-4 mm long × 2-3 mm broad, with obtuse bases, broadly obtuse apices, entire planate margins, chartaceous texture, entirely pale green colour, obscure venation, and without hairs; first 2- ca 6 leaf pairs with petioles 1-2 mm long, and blades elliptic, 5-17 mm long × 3-7 mm broad, with obtuse to cuneate bases, mucronulate obtuse to acute apices, deeply 2-4-toothed planate to recurved margins, chartaceous and finely rugulose texture, ± uniformly pale green colour on both faces, obscure or prominulous venation on both faces, glabrous or

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* Recorded for subsp. *moschatum* only.

sparingly hairy on the upper faces of younger leaves; successive leaf pairs progressively larger and approaching the form of leaves of adult trees, hardly glaucous on lower face, remaining ± glabrous.

The epithet moschatum refers to the aromatic "nutmeg-like" or "musk-scented" odour of the plant (F. Mueller 1860, 1879, Bailey 1901).

Vernacular names: Australian sassafras (Bailey 1913), Black sassafras (Moore & Betche 1893, Turrill 1948a, Anderson 1956, Evans in Beadle, Evans, and Carolin 1963), Native sassafras (F.Mueller 1860, 1887,8), Plume nutmeg (Turrill 1948a), Sassafras (F.Mueller 1879, Maiden 1889, Perkins 1911, 1925, Audas 1950), Sassafras bark plant (Guilfoyle 1911, Turrill 1948a), Southern sassafras (Ewart 1925, 1931, Field Naturalists' Club of Victoria 1928, de Beuzeville 1947, Turrill 1948, Bick, Clezy, and Crow 1956, Willis in Cochrane et. al.1968), Tasmanian sassafras (Guilfoyle 1911 Welch 1929, Turrill 1948a, Metcalfe and Chalk 1950, Hutchinson 1964, Bick and Douglas 1965), Victorian sassafras (Flückinger, quoted by Lauterer 1895, Guilfoyle 1911, Petrie 1912, Scott 1912 [n.v.], Jones and Smith 1924a, Turrill 1948), Xyphalier musqué (Poiret 1808).

Series of specimens examined: 163 collections, comprising 64 with inflorescence (= flower) buds, 40 with open staminate flowers, 31 with open pistilliferous flowers, 42 with fruiting hypanthia at various stages of maturity, and 2 of seedlings.

Geographic Distribution (map 4)

Atherosperma moschatum occurs in the mountains of south-eastern Australia, from the Barrington-Gloucester Tops, New South Wales, 32°S, south-west as far as the Dandenong range and Wilsons Promontory, Victoria, and ± all Tasmania, to 43°40′S. Incorrectly reported distributions include the Cape Otway area, Victoria (F.Mueller 1860, Bentham 1870, Ewart 1925), south Queensland and its border area with New South Wales (Moore & Betche 1893, Bailey 1901, Domin 1925), and the "north and east Australian region" (Good 1964). The provenance "Dividing Ranges (near Geelong)" on a collection of C. Walter (NSW 67857) is also dubious.

Ecology (figures 47-50)

Atherosperma moschatum is confined to temperate rainforest and cool moist tree fern (*Dicksonia antarctica*[*]) gullies throughout its geographic range. In northern parts, on the Barrington Tops, and in the Blue Mountains, and Snowy Mountains, New South Wales, it is confined to altitudes of (500-)1000-1500 m. In southern parts, on Wilsons Promontory and in Tasmania, it extends to lower altitudes, from sea-level to ca 1200 m.

On mainland Australia, *Atherosperma moschatum* is associated with *Nothofagus* over much of its range, except in the central areas between the Blue Mountains and north-east Victoria. At the northern limit of its range on the Barrington Tops, it is largely confined to *Nothofagus moorei-Doryphora sassafras* forest (cf. Fraser and Vickery 1937, 1938);

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[*] See germination, under *Atherosperma*.

in southern Victoria, it is associated with *Nothofagus cunninghamii*. *Elaeocarpus holopetalus* is another frequently associated tree species. In the Blue Mountains where *Nothofagus* is absent, *Atherosperma moschatum* occurs as a minor element in *Ceratopetalum apetalum*-*Doryphora sassafras* forest (Brough et al. 1924, Francis 1951). There it often grows by waterfalls, in association with the conifer *Microstrobos fitzgeraldii*.

It is widespread in Tasmania where it is often co-dominant with *Nothofagus cunninghamii* to form the climax forest over much of the island (Francis 1929, 1951, Turrill 1948a, Gilbert 1959, Walter 1962, Davies 1964, Curtis 1967). Other associated species are *Athrotaxis selaginoides*, *Dacrydium franklinii*, and *Phyllocladus aspleniifolius*, particularly in the rainforests on the west coast of the island.

Confined as a rule to everwet sheltered fern gullies, it commonly extends in such habitat into tall overtopping eucalypt forest, particularly on the Australian mainland where it is often found locally only in such sites (cf. Patton 1930, 1933, Fraser and Vickery 1937, 1938, Turrill 1948a, Gilbert 1959, Walter 1962, Curtis 1967). Though they give the impression of refugia or tension areas (Patton l.c.), such "pockets" or "galleries" of vegetation might well be regarded as trigger units (cf. Herbert 1960). The particular occurrence of *Atherosperma moschatum* in creek beds, for example, may be as much an active means of penetrating and colonising marginal eucalypt forest in suitably cool moist environments in Tasmania, as a means of survival under more adverse climatic conditions in the south-eastern mountains of the Australian mainland.

Phenology and Nutlet Dissemination

Flowering is seasonally regular throughout the range of the species; local populations appear to flower at the same time each year, irrespective of seasonal climatic fluctuations. The young inflorescence (= flower) buds appear in November-December in the early austral summer, before the fruiting hypanthia of the previous flowering season have ripened, and enlarge slowly through autumn and winter until June and July. Flowers usually open between early August and mid September in northern areas and between late August and late October in Tasmania. The duration of the flowering period is about 4-5 weeks, as indicated by a population at Brown Mountain, New South Wales. In this population, flowers open in early September, anthesis follows in mid September, and staminate flowers and the perianth in pistilliferous flowers fall in early October. Fruiting hypanthia usually mature between November and early March in northern areas, and between mid January and early April in Tasmania, over the summer and early autumn months.

As described briefly in chapter VI, dissemination of nutlets is effected by the spreading and recurving of the inner staminode whorls that closely surround the styles and retain the nutlets, allowing the nutlets to fall out and be carried lightly to the ground by wind*. The mature hypanthia remain attached to the tree during nutlet dissemination, but fall within a few days afterwards.

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* Gilbert (1959) records observing the plumose nutlets being blown about like down during dissemination.

The characteristics of the germination of nutlets on fibrous trunks have been described under the genus. In this connection, attention is drawn to Maiden's (1917) publication of a photograph of a sapling of Atherosperma moschatum growing epiphytically on Dicksonia at Ringarooma, Tasmania. If such germination requirements are usual, they would appear to control dispersal by limiting the species to particular habitats.

Infraspecific Variation

Clin~~ic~~al variation is exhibited on a north-south gradient in the following characters: (1) stem compression, which becomes tetragonous on ultimate branchlets, largely because of a slight decrease in the density and length of stem pubescence, (2) leaf blade form, in which breadth, and the frequency and depth of toothing on the blade margin increases, particularly on shaded and sapling leaves, and (3) length of stamens, number of staminodes, length of outer staminodes, and size of mature nutlets, all of which decrease.

The clines are most steeply stepped between the Blue Mountains and the Snowy Mountains - south coast range populations in New South Wales. In conjunction with the other discontinuities in tree size, number of stamens, and geographic distribution, they provide the basis for distinguishing two subspecies. The two subspecies are separated in this region of New South Wales by ca 100-150 miles of relatively dry inhospitable low-lying tableland in the vicinity of Canberra and Goulburn.

a. subsp. *moschatum*

Atherosperma moschatum Labill., 1806, l.c.; Hook.f., 1855, l.c.; Tul., 1855, l.c.; A.DC., 1868, l.c., p.p.; Baill., 1869, l.c., p.p.; Moore & Betche, 1893, l.c., p.p.; F.M.Bail., 1901, l.c., p.p.; Perk. & Gilg, 1901, l.c., p.p.; Dixon, 1906, l.c., p.p.; Domin, 1925, l.c., p.p.; Francis, 1929, l.c., p.3; Patton, 1930, 1933, l.c.; Francis, 1951, l.c., p.3; Bick, Clezy, & Crow, 1956, l.c.; Gilbert, 1959, l.c.; Davies, 1964, l.c.; Costermans, 1966, l.c.; Willis in Cochrane, Fuhrer, Rotherham, & Willis, 1968, t.451.

Atherosperma dilatatum Gdgr., 1919, l.c.

Atherosperma muticum Gdgr., 1919, l.c.

Atherosperma tasmanicum Gdgr., 1919, l.c.

[? *Cryptocarya glaucescens* Tul., 1855, l.c.]

[*Dendrosma lucida* R.Br. ex Cromb., 1879, l.c.]

Figure 3 J - L.

Trees 10-25(-30) m high, with relatively slender crowns; branchlet stems ± quite tetragonous, often blackish, ± shortly hispid-strigose; leaf blades of tree crown elliptic, lanceate, or ovate, (2-)3-$5\frac{1}{2}$(-8) cm long × ($\frac{2}{3}$ -)1-2(-$3\frac{1}{2}$) cm broad, margins (1-)2-6(-8)-toothed, infrequently entire, forking of main nerves discernible on one or both faces; androecium of staminate flowers comprising (10-)12-16(-20) stamens, the outer stamens (2-)$2\frac{1}{2}$-$2\frac{3}{4}$(-3) mm long, the inner ($2\frac{1}{2}$-)3-$3\frac{1}{2}$(-$4\frac{1}{2}$) mm long, all ± recurved after anthesis, particularly the inner stamens; androecium of pistilliferous flowers comprising 24-30(-35) staminodes, the outer staminodes (1-)$1\frac{1}{2}$-2(-3) mm long; ripe nutlet bodies 2-3(-$3\frac{1}{2}$) mm long × $(\frac{2}{3}-)\frac{3}{4}$-$1\frac{1}{4}$(-$1\frac{1}{2}$) mm thick, styles (5-)6-9(-11) mm long.

Series of specimens examined: 135 collections, comprising 56 with inflorescence (= flower) buds, 34 with open staminate flowers, 26 with open pistilliferous flowers, 36 with fruiting hypanthia at various stages of maturity, and 2 of seedlings.

Geographic Distribution (map 4)

Mountain ranges of south-eastern New South Wales, 36°30′S, eastern Victoria, and all Tasmania, to 43°40′S, from sea-level to ca 1200 m altitude.

New South Wales. Tumut; Goobragandra river; Tilba Tilba; Geehi-Khancoban; Cooma; Geehi river crossing; Brown Mountain; Glenbog; Delegate district.

Victoria. Mitta Mitta; Upper Hume (= Murray) river; Mt.Ellery; Big river, between Mts. Bogong and Nelse; Buffalo Hospice; Bendoc towards Orbost; Cumberland Falls; Mt.Margaret Gap toward Lake Mounta Playground; Black's Spur; Marysville; Goulburn river, Marysville; Upper Yarra; Healesville; Don river; Cement Creek; Warburton; Launching Place; Upper Yarra; Powell Mountain; Powelltown; Mt.Baw Baw; Mt.Disappointment; Tomahawk Gap near Beenak; Dandenong range; Ferntree Gully; Sassafras; Kallista; Sherbrooke Forest; Monbulk; Dandenong; Neerim South; Tyers river; Thorpdale; Nyora; Turtons Creek; Sealers

Cove.

Tasmania. King island; Circular Head; Waratah; Ringarooma; Roses Tier; Mt. Barrow; Blue Tier, near Launceston; Forth Falls, near Sheffield; Cradle Mountain; Mersey river; Meander river; Rosebery; Lake St. Clair; Mt. Bishop, Maria island; Mt. Field; Derwent river area; Collinsvale; Mt. Wellington; Mt. Lindon; Ferntree; Hells Gates; Gordon river, Lake Pedder; Picton river; Hartz mountains; Bathurst Harbour; Hastings river; Recherche Bay; Mt. Arrowsmith (ubi?); Kangaroo Bottom (ubi?); Oceania (ubi?).

Infrasubspecific Variation

Characters showing geographic variation are the petioles, which are shallowly impressed and > $1\frac{1}{4}$ mm wide, and leaf blade apices, which are often acuminate, in Tasmanian forms, and the bole bark, which is distinctly rougher in central Victorian populations. Tasmanian forms are also characterised by often markedly broad and deeply toothed leaves.

b. subsp. integrifolium (A.Cunn.ex Tul.)Schodde, comb.et stat.nov.

Atherosperma integrifolium A.Cunn.ex Tul., Arch.Mus.Hist.Nat.Par.8 (1855)421; [A.DC., Prod. 16,2(1868)676 pro syn. Atherospermatis moschati].

TYPE: A. Cunningham 1824, Blue Mountains, April 1826 —— isotypes in K, P(?), SING, W (lost).

Atherosperma elongatum Gdgr., Bull.Soc.Bot.France 66(1919)232.

TYPE: Maiden [= Forsyth], "Jamieson Valley" and "Blue Mountains" [17.].VIII.1899 —— holotype in LY, isotypes in NSW, US.

Atherosperma moschatum auctt. [non Labill.]: A.DC., 1868, l.c. p.p.; Baill., 1869, l.c., p.p.; Moore & Betche, 1893, l.c., p.p.; F.M.Bail., 1901, l.c., p.p.; Perk. & Gilg, 1901, l.c., p.p.; Dixon, 1906, l.c. p.p.; Brough, McLuckie, & Petrie, 1924, l.c.; Domin, 1925, l.c., p.p.; Francis, 1929, l.c., p.4; Fraser & Vickery, 1937, 1938, l.c.; Francis, 1951, l.c., p.5; Anderson, 1956, l.c.; Evans in Beadle, Evans, & Carolin, 1963, l.c.

Figure 3 A-I.

Shrubs or small trees 3-10 m high, with relatively broad crowns; branchlet stems rounded, hardly tetragonous, golden to dark brownish, densely ± hispid; leaf blades of tree crown linear-elliptic or narrowly lanceate, $(2\frac{1}{2}-)4-7\frac{1}{2}(-12)$ cm long x $(1\frac{1}{2}-)\frac{3}{4}-1\frac{1}{2}(-2\frac{1}{2})$cm broad, margins entire, rarely 1-2(-4)-obscurely toothed, forking of main nerves obscure on both faces; androecium of staminate flowers comprising (14-)18-20 or more stamens, the outer stamens $(2\frac{3}{4}-)3-3\frac{1}{2}(-4)$ mm long, the inner $(3\frac{1}{4}-)3\frac{1}{2}-4(-4\frac{1}{2})$ mm long, all ± erect after anthesis or the inner stamens slightly recurved; androecium of pistilliferous flowers comprising (30-)35-40 staminodes, the outer staminodes $(1\frac{3}{4}-)2-3(-3\frac{1}{2})$ mm long; ripe nutlet bodies $(2\frac{1}{2}-)3-3\frac{1}{2}(-4)$ mm long x$1-1\frac{1}{2}$ mm thick, styles (5-)8-10(-15) mm long.

Series of specimens examined: 28 collections, comprising 8 with inflorescence (= flower) buds, 6 with open staminate flowers, 5 with open pistilliferous flowers, and 6 with fruiting hypanthia at various stages of maturity.

Geographic Distribution (map 4)

Barrington-Gloucester Tops, 32°S, and Blue Mountains, 34°S, central east New South Wales, between (500-)1000-1500 m altitude:

Gummi, Manning river; Pheasant creek; Khowlwha (= Kholwha) creek; Home swamp; Barrington Tops; Blue Mountains; between Mt.Wilson and Mt. Irvine; Blackheath; Minnehaha Falls; Jamieson valley; Katoomba; Wentworth Falls; Federal Falls; Lachlan district (watershed?).

Infrasubspecific Variation

The Barringon-Gloucester Tops and Blue Mountains populations are widely separated geographically; the subspecies apparently does not occur on the intervening Mt.Coricudgy massif. These populations show further minor discontinuities in the clinally varying characters discussed above. Barrington-Gloucester Tops trees have rather more rounded stems with a denser and longer pubescence, and more obscurely nerved, and densely pubescent leaf blades than Blue Mountains forms, as well as frequently larger tepals in staminate flowers, averaging 7-8 mm × 4-5 mm against 5-7 mm × $2\frac{1}{2}$-$3\frac{1}{2}$(-5) mm, and longer stamens, averaging $3\frac{1}{2}$-$4\frac{1}{2}$ mm long against $2\frac{3}{4}$-$3\frac{1}{2}$ mm. In the Blue Mountains population, there is a slight increase in the toothing of the leaves, concerning which the southernmost collection seen, from the Lachlan (headwaters?) district (J.Duff: MEL 3178), exhibits a leaf shape and toothing intermediate between this subspecies and *A. moschatum* subsp. *moschatum*.

Taxonomic Notes and Typification

The taxonomic integrity of *Atherosperma moschatum* has been maintained by all previous revisers, except Tulasne (1855), Gandoger (1919), and Airy Shaw (1966).

Tulasne described the rather distinctive Blue Mountains form as a new species, *Atherosperma integrifolium*, and it is noteworthy that its characteristics have not been reviewed again until now. The four species proposed by Gandoger are without basis. The uniformity of the material from which he distinguished his three species from Victoria and Tasmania shows that he had little idea of taxonomic criteria in *Atherosperma moschatum* as a whole. He did recognise the distinctive features of a collection from the Blue Mountains, and, presumably in ignorance of Tulasne's *A. integrifolium*, named it *Atherosperma elongatum*. Airy Shaw records without explanation two species in the genus from Victoria and Tasmania.

The name *Dendrosma lucida* was used by Crombie (1879) merely to refer to a host tree for a lichen, and is apparently based on a manuscript name of R. Brown (see under *Atherosperma*). None of Brown's collections available to me carry any reference to this name, nor does the epithet appear in his manuscript descriptions (cf. also Burbidge 1955).

Although none of the type collections of *Atherosperma moschatum* cited bear the locality "in capite van Diemen" where, according to the protologue, Labillardière gathered them, their similarity to the original illustrations in Labillardière (1806) confirms their authenticity. They were evidently collected in the vicinity of Recherche Bay (= Rocky Bay") in the translation of Labillardière's Relation (1800)) on Labillardière's second visit to Tasmania in 1793. According to the flowering cycle of the species, the specimens would have reached their particular fruit and inflorescence bud stage between December and February, and no later than March. Only the second visit coincides with these months. Topotypical collections are represented by Maiden: NSW 67869 and Schodde 3406, 3412, 3416.

Most of Labillardière's collecting in Tasmania was done in the area of Recherche Bay (43°30′-40′S) between 21 April and 16 May 1792 and 24 January and 15 February 1793. It was this area that he termed, appropriately, "in capite van Diemen". Stearn (1960) and Stafleu (1966) in error put this locality considerably northwards at Storm Bay, at the entrance to the Derwent river. Labillardière on pp. 108,316-317 of the translation of the Relation (l.c.) indicates that Adventure Bay, Cape Tasman (= Tasman Head), and the D'Entrecasteaux Channel were north-east of his "Tempest Bay" and Rocky Bay, which would be impossible if his "Tempest Bay" were the presently named Storm Bay.

The type specimens of Atherosperma integrifolium examined, identical in form and collector's trimming and agreeing in collector and locality data, are labelled with differing dates of collection. One herb. K isotype is dated April 1826, another is undated, and the herb. SING isotype bears the number 1824. Tulasne in the protologue (1855) cites 1824c as a collector's number. According to Heward (1841), Cunningham was in the Blue Mountains area both in January and after October in 1824, and from March to ± August in 1826. Because the date on the sheet in herb. K but not that in herb. SING appears to be written in Cunningham's hand, and the sterile condition of the specimens suggests an autumn collection, April 1826 is the likely date of collection. As indicated by Tulasne, the number 1824 apparently represents a collector's number.

Concerning the typification of *Atherosperma dilatatum*, the locality Launching Place is misspelt "Lunching Place" in the protologue. The precise date of collection, 23 January 1908, is written only on the herb. BO isotype.

Concerning the typification of *Atherosperma elongatum*, J.H.Maiden is cited as collector in the protologue, and the specimen label on the holotype, annotated by Gandoger, also indicates Maiden as collector, Blue Mountains as locality, and "8.99" as collection date. Only the locality and date are written in Maiden's hand, however, while the collector's name has been added by Gandoger. The holotype itself matches perfectly two identical collections of W.Forsyth: NSW 67846, from Jamieson Valley ("near foot of Falls"), 17.VIII.1899, and US 1275465, from Wentworth Falls, VIII.1899. In view of the labelling, there can be little doubt that it is a duplicate of Forsyth's collection sent to Gandoger by Maiden. There is a further collection of Forsyth (NSW 41827) from Wentworth Falls, dated 21.VIII.1899, which differs from the type series only in the slightly higher proportion of female flowers with fallen perianths. It appears to have come from the same tree as the type but, according to the label, at a later date.

Authentic specimens of *Cryptocarya glaucescens* Tul. in herb. W (herb. J.D.Hooker 531 and 857) are apparently lost. The series loaned by herb. K from J.D.Hooker's herbarium offers ambiguous interpretations for authentication. On the one hand, n.531 may refer to the various collections of R.C.Gunn, who always used this number in his collections for Atherosperma moschatum. On the other, the number may be taken from a date written as "5/31 1840" on a J.D. Hooker collection from Kangaroo Bottom. The number 857 has not been traced.

Chemistry

The bark of Atherosperma moschatum contains essential oils, tannin, resin, and various alkaloids. These were first examined by Zeyer (1861) and later reviewed by Maiden (1889).

The essential oils, present also in the leaves and responsible for the characteristic odour of all parts of the tree, were subsequently investigated by Gladstone (1864, 1872) and Scott (1912) (fide Jones and Smith 1924a). Safrol was identified (Jones and Smith 1924a, Turrill 1948); it is present in apparently smaller quantities than in Doryphora sassafras. According to Maiden (l.c.), oil from the bark isolated by steam distillation is thin and light, pale yellowish brown, aromatic, and bitter; it is not rubefacient or irritating when rubbed on skin. Oil from the leaves is distinct, of a greenish colour, and resembles oil of mace (Maiden l.c.) (cf. Doryphora aromatica).

Characteristics of the tannin and resin have been summarised by Maiden (l.c.). The tannin is a yellow liquid of faintly acid and astringent taste. The resins are red-brown and faintly aromatic. A melting point of 114°C and a formula of $C_{21}H_{32}O_5$ is recorded for aromatic resins (Maiden l.c., p.157), while a melting point of 104°C and a formula of $C_{42}H_{32}O_{10}$ is recorded for the apparently non-aromatic resins (Maiden l.c., p.224).

The alkaloids from the bark and leaves have been recently re-examined in detail by Bick, Clezy, and Crow (1956), and Bick and Douglas (1965). The bark contains 1.7-2.0% total alkaloids. The two major alkaloids present, berbamine and isotetrandrine, are of the bisbenzylisoquinoline type with two diphenyl ether linkages. Berbamine has the formula $C_{37}H_{40}O_6N_2$, and crystallises in colourless plates which melt at 129°-134°C. Isotetrandrine, $C_{38}H_{42}O_6N_2$, crystallises in colourless prisms which melt at 182°-183°C.

A number of minor alkaloids have been isolated, though not all have been investigated. One, atherospermoline, is a phenolic alkaloid of the bisbenzylisoquinoline type with two diphenyl ether linkages. It has the formula $C_{35}H_{36}O_6N_2$ and comprises two hydroxy-groups, two methoxy-groups, one methylimino-group, and a secondary amine group.

Others are of the aporphine type: isocorydine, atherosperminine, methoxyatherosperminine, liriodenine (= spermatheridine, Bick et al. 1956), methoxyliriodenine (= atherospermidine, Bick et al. 1956), and spermatherine (in leaves only). Isocorydine is a phenolic aporphine with the formula $C_{20}H_{23}O_4N$, and crystallises in colourless needles with a melting point of 232°-234°C. Atherosperminine, $C_{20}H_{23}O_2N$, crystallises in colourless needles with a melting point of 199°-200°C. Liriodenine, $C_{17}H_{11}O_3N$, is non-phenolic, and crystallises in bright yellow needles which melt at 276°-278°C. Methoxyliriodenine, $C_{18}H_{13}O_4N$, is also non-phenolic, and crystallises in bright yellow needles with the same melting point.

Of these alkaloids, berbamine occurs also in the Berberidaceae, isotetrandrine in the Menispermaceae, isocorydine in the Annonaceae and Papaveraceae, and liriodenine in the Magnoliaceae. No other member of the Atherospermataceae that has been investigated chemically has so many alkaloids in common with other families.

Uses

From the fresh or dry bark and leaves, rather bitter tea- or beer-like infusions have been brewed which act both as a tonic and mild aperient (Lindley 1853, J.D.Hooker 1855, Tulasne 1855, F.Mueller 1860, Baillon 1869, 1877, Maiden 1889, Pax 1889, Perkins and Gilg 1901, Perkins 1925, Ewart 1925, 1931, Garratt 1934, Turrill 1948a, Audas 1950, Anderson 1956, Airy Shaw 1966, Curtis 1967). Lindley, Baillon, and Maiden recommend the adding of milk to improve the taste! These infusions have been used also in the treatment of asthma and some forms of heart disease (Maiden l.c., Bailey 1913, Bick et al. 1956), in which the essential oils may play a role (Maiden l.c., Lauterer 1895, Turrill 1948a).

The timber, with an average lateral hardness of 470 kg (Welch 1929), is rather pale with a dark duramen, and is light, strong, close-grained, yet easily worked; it has been defined as a cabinet softwood by Baker (1919). It is suitable for interior fittings, turnery, and cabinet work, and has been used for sash and door frames, small handles, brush stocks, wooden screws, cask staves, wooden buckets, shoe lasts, carving, sounding boards of musical instruments, and particularly clothes pegs (F.Mueller l.c., Maiden l.c., Welch l.c., Garratt l.c., Audas l.c., Anderson l.c., Willis in Cochrane et al. 1968). According to Tulasne (l.c.) and Baillon (1869), the timber has also been used in the construction of houses and ships. It is not in general use at the present time.

The species is occasionally planted as an ornamental tree in Great Britain (Turrill 1948).

IX. TRIBE LAURELIEAE Pax

Laurelieae Pax, Pflzfm. 3,2(1889)97,102 p.p.; Garratt, Trop. Woods 39(1934)22 p.p.; Hutchinson, Gen.Fl.Pl. 1(1964)113,120 p.p.; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342 p.p.

TYPE GENUS: Laurelia Juss., lectotype.

Small to tall, rarely shrub-like trees, ca (2-)4-45(-50) m high, with widespreading or rather columnar habit; trunks usually solitary*; crowns rather corymbiform to compactly cylindrical, usually and sometimes considerably shorter than the boles, with branches ascending or rather horizontal; bark smooth to very rough, and variably fissured, longitudinally furrowed, or pustuled, aromatic or ± odourless; secondary xylem with yellowish hue, the vessel members solitary or up to 20% in radial multiples of 2-3(-5), ca (30-)45-85(-100) per sq. mm in transection, inner tangential diameter (30-)50-100(-140) μ, the fibres (1.4-)1.9-2.4 (-2.8) mm maximum length range × (17-)24-50(-80) μ outer tangential diameter, thin- to relatively thick-walled, predominantly either fibre tracheids, or libriform wood fibres with septae, or relatively transitional, with bordered pits variably numerous on tracheids, relatively large with borders distinct**, the multiseriate rays (0.2-)0.3-1.1(-1.8) mm high or sometimes more by aggregation ×(2-)3-5(-8) cells wide, heterocel-

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* Sometimes 2 or 3 in a group in Doryphora sassafras (f.19).

** Often rather indistinct in Daphnandra.

lular, with procumbent cells 10-60 μ in tangential diameter, acicular crystals present or absent, oil cells present or absent in marginal cells, the parenchyma absent or very sparse and diffuse; hairs where present on lower face of leaf blades simple, less often tufted.

Bisexual, or monoecious, rarely polygamous*; inflorescences glabrous or glabrescent to rather densely sordid greyish or stramineous-golden strigose; flower-subtending bracts or bracteoles lanceate to ovate, relatively small, not or hardly enclosing mature flower buds**; hypanthium of bisexual and pistilliferous flowers variably deeply poculiform, the rim flat, convex, or rising sub-erect, distinct from deep hypanthium chamber; perianth of open flowers ± rotatiform***; stamens obtusely apiculate to aristate or truncate at the apex, the filaments relatively broad, ± shorter than the anthers, the staminal glands variously wing-like, lanceate-ovate planate, or peltate, stipitate only when peltate, disposed above the base of the filaments according to the genus; staminodes in bisexual and pistilliferous flowers confined to rim distinct from hypanthium chamber, the inner whorls caducous or persistent and not enlarged in fruit; style column hardly exserted or protruding up to 2 mm beyond hypanthium rim in fruit; dissemination of ripe nutlets effected by dehiscence of fruiting hypanthium.

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* Laurelia only.

** Larger and deeply cymbiform only in Doryphora, and completely enclosing mature flower buds only in D. sassafras.

*** Often or usually broadly cyathiform in Laurelia.

Genera, Geographic Distribution, and Ecology

The tribe Laurelieae comprises five genera, *Daphnandra*, *Doryphora*, *Dryadodaphne*, *Laurelia*, and *Nemuaron*, which occur in the mountains of New Guinea, eastern Australia, New Caledonia, New Zealand, and southern Chile (map 1). These genera are associated with essentially subtropical rainforest. The tribe is of much wider occurrence on the eastern and western continental sea boards of the southern Pacific ocean than the Atherospermateae. Only one species, *Laurelia sempervirens*, is found on the eastern sea board. The forests in which the genera occur have been defined ecologically as subtropical or notophyll or sub-montane rainforests in Australia (Baur 1957, Webb 1959, Baur 1962), as subtropical rainforest in New Zealand (Cockayne 1958), and as laurel valley forest with a subtropical aspect in Chile (Warming 1925, Oberdorfer 1960).

In these forests, the genera are associated to a greater or lesser degree with *Nothofagus* subsect. *Bipartitae* as defined by van Steenis (1953) in New Guinea and New Caledonia, the only regions where this group of *Nothofagus* survives today. In Australia, New Zealand, and Chile, they are found in forests where, on climatic and floristic grounds, this group of *Nothofagus* might also have been expected to occur. That this association has historical significance seems to be indicated by the particular occurrence of *Dryadodaphne pterandrica* in the *Nothofagus* forest zone in New Guinea. *D. pterandrica* is the least specialised species of a genus that is the most centrally situated and least specialised in the tribe.

Other trees associated with the genera and species of the Laurelieae in these forests belong to the families Cunoniaceae, Elaeocarpaceae, Escalloniaceae, Eucryphiaceae, Lauraceae, Podocarpaceae, and Winteraceae.

All of these families, with the partial exception of Lauraceae, are essentially southern hemisphere in both distribution and centre of diversity; all have similar if sometimes more extensive ecogeographic distribution patterns. Some of the families, for example Cunoniaceae and Escalloniaceae, are more widespread only because of their occurrence in southern Africa, from where fossils of atherospermataceous plants are known.

Several of the genera, moreover, closely parallel geographic distribution in the Ackama-Spiraeopsis (Cunoniaceae) species group, Quintinia (Escalloniaceae), and the Bubbia (Winteraceae) alliance in Australia, New Guinea, New Caledonia, and New Zealand, and of Aristotelia (Elaeocarpaceae) in Australia, New Zealand, and southern South America.

Whether these associations have a historical basis is unproved but perhaps not unlikely. Any consideration of the phytogeographic origin of the Laurelieae, however, must take into account Dansereau's (1963) warning and the present evidence of the fossil record (chapter XV), which together indicate that these floristic communities, so consistent in their composition today, may nevertheless comprise groups of diverse origin.

Notes on the Characters of the tribe Laurelieae

It has already been noted that the vessels of the secondary xylem in all members of the Laurelieae are wider and fewer per unit transverse area of wood than those of the Atherospermateae (table I). The vessel diameters average smallest in Daphnandra (60 μ), Laurelia (64 μ), and Doryphora (70 μ), the more temperate-latitude genera. In the tropical-latitude genera of the tribe, the vessels are wider, averaging 109μ diameter in *Dryadodaphne*. Even in *Doryphora*, the mean vessel pore width is greater in the northern species, *D. aromatica* (76μ diameter) than in the southern species, *D. sassafras* (64μ diameter), and a similar trend is noticeable in *Daphnandra*, between the northern species *D. repandula* and the southern ones *D. apatela* and *D. tenuipes**. There is a parallel situation in *Nothofagus*, the tropical-latitude species of which have strikingly wider vessels than their higher latitude congeners (Dadswell and Ingle 1954).

The reasons for this pattern of variation are not immediately clear, because both tropical- and temperate-latitude species grow in generally similar cool misty everwet habitats. That these differences in vessel width result from selection in response to seasonal variations in temperature and rainfall in the temperate latitudes, or their near absence in tropical mountain areas, is perhaps the most obvious explanation.

In the Laurelieae, the frequency of vessels per unit transverse area of wood is highest in the temperate-latitude genera, the reverse of the trend in vessel widths. When the mean number of vessels per unit transverse area of wood is multiplied by the mean vessel diameter for each genus, the resulting figures, which gauge the relative vessel area per unit

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* Figures for pore width are not particularly biassed by the occurrence of growth rings, which are rather equally developed in both tropical- and temperate-latitude genera, e.g. *Dryadodaphne* and *Laurelia*.

transverse area of wood, suggest little difference between the genera. In *Daphnandra*, the figure of relative vessel area is rather higher than those of its congeners, and may reflect an increase in vessel capacity in response to the replacement of fibre tracheids by libriform wood fibres in this genus.

The features of the multiseriate rays of the genera of the Laurelieae have been discussed in chapter IV.2. In general, the rays have larger procumbent cells and, except in *Dryadodaphne*, are less markedly heterocellular than in the Atherospermateae.

The staminal glands of the genera of the Laurelieae are remarkable for their diversity of form and total lack of resemblance to stamens. Their modification on the stamens to function as nectaries and landing platforms for insect pollinators has already been mentioned in chapter IV.8,11. That they serve such a purpose is particularly obvious in those genera with peltate glands, *Daphnandra*, *Laurelia*, and *Nemuaron*. In these genera, the glands are oriented and flattened directly beneath the anther valves. In *Dryadodaphne*, their development appears to be at a lower level of specialisation, and the distinctness of the two species groups in the genus is highlighted by differences in the glands. The erect or rather recurved lanceate-ovate glands of *Doryphora* appear to be more obviously modified to fit the symmetry of the flower than to serve as a landing platform for pollinators. Nevertheless, they do recurve slightly relative to the slightly introrse dehiscence of the anther valves, which suggests that they play some part in attracting insects.

The general characteristics of the fruiting hypanthium have been described in chapter IV.16. In all genera except *Nemuaron*, the hypanthium is rather oblong-urceolate.

In Nemuaron, it is quite globose-pyriform; in two species of *Daphnandra*, *D. tenuipes* and *D. johnsonii* it also approaches a globose shape. The value of such a development is unknown. It may be to reduce the amount of tissue put into fruiting: the fruiting hypanthia of *Nemuaron* are the smallest in the tribe, and those of *Daphnandra johnsonii* are the smallest in its genus.

The degree of lignification of the fruiting hypanthium wall varies between the genera. It is thickest (1-3$\frac{1}{2}$(-4) mm thick) in *Dryadodaphne*, and thinnest, almost chartaceous, in some species of *Daphnandra*. In the remaining genera, the lignified walls are from $\frac{1}{2}$ to 2 mm thick.

The number and equality of the fruiting hypanthium valves formed in dehiscence also differ between the genera. They are correlated, to a greater or lesser extent, with the number and arrangement of perianth and androecium parts. In *Dryadodaphne*, *Doryphora aromatica*, and *Nemuaron*, in which the perianth is basically tetramerous, the hypanthia split incipiently into 4 equal valves, of which 2 or 4 develop. The fissures open between the bases, scars, or decurrences of the perianth parts, a feature shown most clearly in the ribbed hypanthia of the species of *Doryphora*. In hexamerous *Doryphora sassafras*, and in *Laurelia* with its more variable number of tepals, the hypanthia dehisce into an irregular number of subequal valves. In *Daphnandra*, with its rather complex dimorphic perianth, the hypanthia ultimately dehisce by a single fissure only.

Patterns of ornamentation of the outer hypanthium wall, and the persistence of perianth and androecium parts, described in chapter IV.16, are also characteristic of many members of the tribe.

Taxonomic Notes

The tribe Laurelieae was introduced by Pax (1889) to separate the three genera Laurelia, Daphnandra, and Nemuaron from the tribes Atherospermateae, comprising Atherosperma and Doryphora, and Siparuneae, comprising Siparuna, Conuleum, and Glossocalyx, within the subfamily Atherospermoideae of the Monimiaceae. Perkins and Gilg (1901), and Perkins (1925) subsequently emended its circumscription to include Atherosperma and Doryphora*, in order to distinguish the group as a whole from the Siparuneae. Garratt (1934), although following Perkins' arrangement, drew attention to the finer distinctions recognised by Pax. Hutchinson (1964) once more separated Atherosperma and Doryphora, but incorporated in their stead those genera that had been referred to the Siparuneae by Pax (l.c.), Perkins and Gilg (l.c.), and Perkins (l.c.). On the basis of chromosome counts in a few genera (Daphnandra, Doryphora, Laurelia, and Siparuna), Ehrendorfer et al. (1968) have corroborated the initial arrangement of Pax (l.c.) (see chapter IV.19).

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* As such, it was equivalent to the Atherospermataceae as defined here. Lemée (1929, 1930, 1951), A.C.Smith (1941), and Money et al. (1950) also used the name for this concept.

The tribe Laurelieae has been redefined here, to include *Doryphora* (and *Dryadodaphne*), and exclude the *Siparuna* group. It has been intimated (chapter IV.6) that the relative similarities in bracts and inflorescence size between *Doryphora* and *Atherosperma* appear to represent convergence in response to similar environments. In all other characters found to be of critical taxonomic value in the family, *Doryphora* exhibits the characteristics of the Laurelieae and bears no resemblance whatever to *Atherosperma*.

Hutchinson's treatment (l.c.) is extraordinary, particularly in view of the clear indications from recent but earlier studies (Garratt l.c., Money et al. 1950) that the *Siparuna* group, including *Bracteanthus*, is no more closely related to the Atherospermataceae than it is to the Monimiaceae or Hortonioideae.

Key to the Genera of the tribe Laurelieae

1a. Inflorescence exclusively 3-flowered, the mature flower buds enclosed by a pair of large cymbiform bracts; mature fruiting hypanthium prominently ribbed; nutlet bodies glabrous, with lateri-, almost basi-fixed styles; flowers white, with acute tepals, (4-)5-13(-18) mm long; stamens flexuously aristate, 5-10(-13) mm long; stigmatic column stellately branched at the apex, rarely conical; fibres of secondary xylem ± exclusively fibre tracheids, never septate .... XIII. *Doryphora* Endl.

1b. Inflorescence variously thyrsiform, never exclusively 3-flowered, the mature flower buds naked; mature fruiting hypanthium levigate, or marked with lignified protuberances; nutlet bodies variously hirsute, with terminal or subterminal styles; flowers pale greenish or reddish, with variously obtuse tepals, 2-6(-7) mm long; stamens narrowly obtuse, truncate, apiculate, or broadly rostrate, ($\frac{2}{3}$ -)1-3$\frac{1}{2}$(-4$\frac{1}{2}$) mm long; stigmatic column variously conical, infrequently branched at the apex; fibres of secondary xylem occasionally to frequently septate .... 2.

2a. Stamens narrowly rounded truncate, obtuse, apiculate, or broadly rostrate, with glands attached to sides of filament; mature fruiting hypanthium with caducous perianth and androecium, rather thickly lignified, with walls ($\frac{3}{4}$-)1-3$\frac{1}{2}$(-4) mm thick; inflorescence thyrsiform, without accessory axillary flowers; (small-)medium-sized to large trees of primary rainforest ... 3.

3a. Flowers unisexual; leaf blades with midribs planate, hardly impressed on upper face; inflorescence densely pubescent; bracteoles tepal-like, contiguous with perianth; mature fruiting hypanthium pusticulate or with lignified protuberances towards base or apex.
.... XII. Laurelia Juss.

3b. Flowers bisexual; leaf blades with midribs markedly impressed on upper face; inflorescence glabrous or sparingly haired-glabrescent; bracteoles bract-like to rather tepal-like, subtending hypanthium to almost contiguous with perianth; mature fruiting hypanthium levigate .... 4.

4a. Mature fruiting hypanthium globulose-pyriform; nutlets incurved hippocrepiform, with vestigial styles; tepals variously 4-6; stamens slender, with obtusely elliptic-ovate sub-peltate glands; carpels ± 5; bark (and leaves) strongly aromatic.
.... XI. Nemuaron Baill.

4b. Mature fruiting hypanthium cylindrical-ellipsoid; nutlets narrowly ellipsoid, with long, thickly subulate styles; tepals regularly 8; stamens thick, with divergent ovate-deltate to obtusely cupular sessile glands; carpels (5-)8-13(-16); bark and leaves ± odourless .... X. Dryadodaphne S. Moore

2b. Stamens broadly truncate, with glands attached to abaxial face of filament; mature fruiting hypanthium with persistent perianth and androecium, thinly lignified or chartaceous, with walls usually < $\frac{3}{4}$ mm thick; inflorescence elaborately thyrsiform, with frequent accessory axillary flowers; small to medium-sized trees of ± secondary rainforest.
.... XIV. Daphnandra Benth.

X. DRYADODAPHNE S.Moore

Dryadodaphne S.Moore, J.Bot. 61(1923)109; [Kosterm., Rec.Trav.Bot. Néerl. 34(1937)605 pro syn. *Levieriae*]; A.C.Smith, J.Arn.Arbor. 23(1942)442; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)373 et seq.; Lemée, Dict.gen.phan. (suppl.) 9(1951)107; Stern, Amer. J.Bot. 42(1955)881; L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)49; Burbidge, Dict.Austral.Pl.Gen. (1963)105; Saunders in Perry et al., CSIRO Land Research Ser.n.15(1965)120; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7,(1966)382; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342.

TYPE SPECIES: *Dryadodaphne celastroides* S.Moore, only species [≡ *D. novoguineensis* (Perk.)A.C.Smith].

Isomerocarpa A.C.Smith, J.Arn.Arbor. 22(1941)250; [id., J.Arn.Arbor. 23(1942)442 pro syn. *Dryadodaphnis*]; [Hutchinson, Gen.Fl.Pl. 1(1964)114 pro syn. *Levieriae*].

TYPE SPECIES: *Isomerocarpa novoguineensis* (Perk.)A.C.Smith, only species [≡ *Dryadodaphne novoguineensis* (Perk.)A.C.Smith].

Daphnandra auctt.[non Benth.]: Perk., Bot.Jb. 52(1915)217 p.p.; Gilg & Schltr., Bot.Jb. 55(1918)196; Perk., Gattung.Monim. (1925)6,8,11,15,47 p.p.; [A.C.Smith, J.Arn.Arbor. 22(1941)250 p.p. pro syn. *Isomerocarpae*, 23(1942)443 p.p. pro syn. *Dryadodaphnis*]; van Royen, Compl.Keys Fam.Gen.Angios.Gymnos.N.Guin.

(1959)115; Good, Geogr.Fl.Pl. ed.3,(1964)101 p.p.; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7,(1966)330 p.p.

Levieria auctt.[non Becc.]: Kosterm., Rec.Trav.Bot.Néerl. 34(1937) 605 p.p.; Hutchinson, Gen.Fl.Pl. 1(1964)114 p.p.

Figures 1C,16,25-27,36B,44D,45A.

Tall bisexual trees, with widespreading, somewhat corymbiform crowns; bark, wood, stems, and leaves ± odourless; secondary xylem vessels predominantly solitary or up to 10% in radial multiples of 2-3(-4), ca (44-)47-55(-64) per sq.mm, (1.2-)1.3-1.5(-1.7) mm long × (30-)80-100(-140) μ inner tangential diameter, the perforation plates and vessel-ray pitting exclusively scalariform; fibres relatively thick-walled, 2.1-2.3 mm long × (20-)30-50(-90) μ outer tangential diameter, varying from predominantly thinner-walled fibre tracheids with bordered pits rather indistinctly bordered in early wood to predominantly thicker-walled libriform wood fibres with occasional septae in late wood; multiseriate rays (0.2-)0.5-0.9(-1.3) mm high × (2)3-6(-8) cells wide, acicular crystals sparingly present in procumbent cells, oil cells present in the margins or absent; ultimate branchlet stems ± angular tetragonous, generally glabrous; petioles shallowly to deeply sulcate; leaf blades large microphyllous to ± notophyllous, with margins shallowly crenate to almost entire, midribs sulcate on upper face, 1-3-layered hypodermis on upper face*.

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* Money et al. (1950).

Inflorescence buds ± compressed, stipitate before expansion; mature inflorescences slenderly thyrsiform, with 3-5(-11), very rarely more, flowers; accessory axillary flowers absent; bracts small, ± isomorphic, (1½-)2-4 mm long × ¾-1¾ mm broad, usually caducous in young bud; bracteoles present, herbaceous and bract-like, subtending floral hypanthium at apex of pedicel, early caducous.

Flowers bisexual; perianth rotatiform, tetramerous, comprising 8 thick, oblong-elliptic, obtuse, obscurely pinnate-palminerved tepals, 1½-4½(-6) mm long × 1-3(-4) mm broad, in 2 whorls; androecium tetramerous, 2-4(-5)-seriate, the outer one or two whorls comprising 4 or 8 stamens, (1-)1¼ - 2(-2½) mm long × ½-2½(-3) mm broad × ⅓-1 mm thick, with divergent, ovate-deltate, planate to shallowly cupular, obtuse staminal glands, and shortly apiculate to broadly rostrate, latrorsely-to ± extrorsely-dehiscing anthers, the inner whorls of ± isomorphic, lanceate-deltoid to almost subulate staminodes, (⅓ -)½-2 mm long; pollen grains spheroidal to slightly ellipsoidal, suboblate, Lg. (22-)24-30(-32)μ × long. Lt (27-)28-33(-35) μ , the colpi transversales of regular to irregular length, (10-)15-25(-30) μ long, sometimes only one well developed, the interstitial equatorial depressions rather extensive, but very shallow and sometimes entirely obscure, the grain walls 1-2 μ thick, the surface sculpture with lumina relatively regular and rather circular in outline, ¼-½(-1) μ in diameter; gynoecium of (5-)8-13(-16) carpels, the styles terminal, ± hispid, the stigmatic column slenderly conical, ± unbranched; ovule narrowly ellipsoid, shortly and obscurely obtusely rostrate at chalazal end, anatropous on sub-basal placenta.

Fruiting hypanthium cylindrical-ellipsoid, 11-40(-45) mm long × 4-13 mm thick, levigate, glabrous, dehiscing regularly into 4, sometimes 2, equal valves; perianth and androecium early caducous; nutlets borne in deep pits on hypanthium wall, unilaterally silky hirsute, the bodies narrowly ellipsoid to obclavate, the styles terminal, subulate

Additional Characters Common to Infrageneric Taxa

Average tree height range 20-45 m; crown branches horizontal-ascending in open decussate arrangement; wood pale cream to pale brownish cream or yellowish, drying sordid brown; ultimate branchlet stems smooth or finely striate, drying usually blackish, broadened and smooth at branchlet and leaf nodes, the branchlet nodes often swollen and (2-)4-12 (-15) mm broad on leader stems; vegetative buds narrowly attenuate conical, the enveloping pair of bract-like leaves generally glabrous, or sometimes irregularly, rarely uniformly or densely sordid stramineous tomentose, with markedly divergent mucronate apices, expanding when buds (5-) 8-10 mm or more long; leaf blades with midribs shallowly to deeply impressed on upper face, conspicuously prominent on lower, entirely glabrous, bearing sparse, brownish to blackish, small, pellucid glandular pits.

Inflorescence buds ± compressed, narrowly obcordiform to sub-hippocrepiform, initially sessile and complanate with stem when 1-2 mm long, the enveloping pair of bracts slenderly lanceate, navicular, glabrous, eventually 2-4 mm long, with often markedly recurving apices; buds subsequently elongating through the development of a compressed stipe

(= base internode of primary peduncle of mature inflorescence) up to 2-3(-4) mm long below the bracts which diverge gradually to allow expansion of the ultimate inflorescence axes and flower buds; mature inflorescences ± decurved, usually glabrous or glabrescent*, borne at ultimate (1-)2-4(-5) leaf nodes among leaves; peduncles often broadly compressed at base internode, and more slender, tetragonous at distal internodes, the subterminal nodes bearing usually solitary opposite flowers, rarely simple dichasia or secondary peduncles; central flower in terminal dichasia, rarely solitary flowers at subterminal nodes opening first; peduncular bracts herbaceous, linear to narrowly ovate, navicular to carinate, with mucronate apices and finely fimbriolate margins, usually glabrous, rarely tomentulose - hispidulous abaxially; pedicels rounded compressed, often tetragonous where terminally central; bracteoles in single pairs, narrowly deltate to ovate, navicular, $\frac{3}{4}$-$2\frac{3}{4}$(-3) mm long × $\frac{2}{3}$ - $2\frac{1}{2}$ mm broad, with mucronate apices and fimbriolate margins, usually glabrous, rarely tomentulose-hispidulous abaxially, bilaterally compressed when enclosing young flower bud; mature flower buds obtusely to rather acutely obovoid or ellipsoid, the outer tepals valvate to imbricate, incompletely enclosing inner tepals.

Open flowers of medium-~~small~~size; hypanthium broadly-based turbinate-poculiform, glabrous or glabrescent**, the rim flat to sloping

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* Except D. novoguineensis var. macra.

** Except D. novoguineensis var. macra.

slightly upwards, and glabrous except for a ring of short stramineous hispid hairs on the inner margin; perianth pale yellowish green to pink, marone, or purplish, the tepals with entire or ± finely fimbriolate margins, variably sparsely puberulous; stamens thick, apically recurving, the filaments thick, ± terete, sparsely puberulous abaxially, glabrous adaxially, the staminal glands broadly and obliquely attached along the sides of the filament from just above its base adaxially to just below the anther abaxially, the anthers glabrous or sparsely strigillose abaxially, with elliptic valves; staminodes thickened towards the base, with a ± prominent abaxial midnerve, glabrous or abaxially hispidulous-strigillose, the outer staminodes longer, broader, thicker, and more hairy than the inner, often bearing vestiges of staminal glands as small obtuse lobes or dark hyaline areas in the base margins.

Ripe infructescences borne at ultimate (1-)2-5(-7) leaf nodes among leaves on branchlets, with 1-2, rarely more, hypanthia maturing per infructescence; pedicels of the same colour and form as in inflorescence, but thicker, ± broadly expanded under fruiting hypanthia, glabrous; fruiting hypanthium variously thickly lignified, with walls 1-3½(-4) mm thick, in dehiscence with two opposite fissures usually extending further towards the base than the other two, which sometimes remain as obscure notches at the rim; hypanthium rim as in flower or broader, scarred levigate, with hair-ring persistent on inner margin; hypanthium chamber narrow; nutlets attached to sides and base of hypanthium chamber, with straight hairs confined to adaxial face, the styles broadly expanded at the base into bodies of nutlets, with hairs gradually shorter towards the hispidulous, ultimately glabrous apex.

The name *Dryadodaphne* is derived from δρύάς , a dryad or nymph whose life was bound with that of her tree, and δάφνη for the sweet bay or laurel (*Laurus nobilis*).

Species, Geographic Distribution, and Ecology

The genus *Dryadodaphne* comprises three species, two in New Guinea, and one in north-east Australia, between 1° and 16°35′S (maps 2,5). The records of *Daphnandra* from New Guinea (Perkins 1915, 1925, Gilg and Schlechter 1918, Gilg and Diels 1925, van Royen 1959, Good 1964, and Airy Shaw 1966) are all attributable to this genus.

The species occur in primary cool subtropical and montane rainforests between the altitudes of (500-)600-2800 m. They are rarely prominent, and apparently never dominant elements of the forest. In New Guinea, one of the species is associated consistently with *Nothofagus* forest, and the other with lower altitude mixed forest.

Germination of seeds occurs freely in the leaf litter and soil of the forest floor (personal observations and seedlings and young saplings of *Dryadodaphne novoguineensis*: Schodde 4878, and *D. pterandrica*: Schodde 4817, 4919). No data are available for *D. trachyphloia*. Some regeneration by coppicing, but not suckering, has been recorded.

Flowering in the New Guinea species appears to take place all year round in an environment in which there is relatively little seasonal fluctuation in rainfall, day-length, and temperature. The flowering cycle of the Australian species is inadequately documented.

Notes on Generic Characters

Dryadodaphne is characterised among the genera of the Laurelieae by its large umbrageous tree form, its secondary xylem with relatively large pores, thick-walled fibres, and frequent oil cells* in the rays, its relatively odourless bark and leaves, a general glabrousness, its small bracteoles that subtend the flowering hypanthium, its bisexual, regularly tetramerous flowers, its thick stamens with broadly apiculate to rostrate apices and broadly acute wing-like to obtusely cupular staminal glands, and its levigate, cylindrical, thickly woody fruiting hypanthia in which unilaterally glabrous nutlets are borne in deep pits on the hypanthium wall.

In both New Guinea species, which occur over the widest altitudinal range for the genus, the higher altitude forms have smaller but generally thinner canopy leaves where thicker leaves might be expected (cf. van Steenis 1957). [The higher altitude forms of Nemuaron also show this trend.]

The constantly 8-partite perianth of Dryadodaphne, arranged in two tetramerous whorls, is unique in the tribe Laurelieae, and resembles the condition in the Atherospermateae. Its thick tepals, moreover, have an obscure pattern of venation that appears to be transitional between the unspecialised pinnate type found in Laureliopsis and Doryphora, and the

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* Except D. pterandrica.

derived palmate-parallel type characteristic of Atherosperma, Daphnandra, and Laurelia. In these characters Dryadodaphne links genera of both tribes.

It has been indicated in chapters IV.6 and VIII that, contrary to the suggestion of A.C.Smith (1941), the small, early caducous bracteoles that regularly subtend the flowering hypanthia in all species of Dryadodaphne are unlike and not homologous with the flower-subtending bracts of Atherosperma. Their more likely homologues are the outermost pair(s) of herbaceous perianth parts (= perianth bracteoles) in the flowers of Daphnandra, Laurelia, and Nemuaron (cf. chapter IV.6).

Money et al. (1950) also associate Dryadodaphne with Atherosperma where they describe the staminal glands of both as being relatively "free" from the filament. For Dryadodaphne this is inaccurate. Though its glands arise from near the base of the filament on the adaxial face, they are still clearly attached to it; abaxially they are connate with the filament towards the anther. The short staminal filaments make this a difficult character to measure.

The variation that occurs in the form of the staminal glands and anthers between and within the species of Dryadodaphne is not found in any other genus of the family. It is referred to in chapter IX, and discussed in more detail in following sections. The outer staminodes of all species usually bear the vestiges of staminal glands.

Why the species of Dryadodaphne, living in a relative uniform tropical latitude environment, have developed or retained a fruiting hypanthium that is much more thickly lignified than in members of any other genus, is not known. It is noteworthy that the hypanthium walls in the more southern Queensland species are considerably thinner, (1-1$\frac{1}{2}$(-1$\frac{3}{4}$) mm thick), than those of the two New Guinea species, ((1-)1$\frac{1}{2}$-3$\frac{1}{2}$(-4) mm thick). The deep pits in which the nutlets are borne on the inner hypanthium wall resemble the hypanthial ingrowths that enclose the carpels in the genus *Siparuna* (*Siparuna* group).

Relatively few, often only one, fruiting hypanthia mature per infructescence, a feature which is more marked and consistent in this genus than in any other of the family. The reasons for such apparent infertility or non-development of the hypanthia are not known.

Affinities

Despite its frequent confusion with *Daphnandra* in the literature, *Dryadodaphne* is a well-defined genus which has closer affinities with *Nemuaron* than any other genus of the Laurelieae. In referring it to *Levieria*, a member of the Monimiaceae closely related to *Hedycarya*, Kostermans (1937) and Hutchinson (1964) have misidentified or misinterpreted its characters. A.C.Smith (1941) published it as a new genus, *Isomerocarpa*, without knowing of its earlier description under the name *Dryadodaphne* by S.Moore. Moore had described it in the Lauraceae which implies that he recognised valved anthers even though he did not mention them.

Dryadodaphne resembles *Nemuaron* in its secondary xylem features (relatively wide vessels of which up to 10% are in radial multiples, and relatively thick-walled fibres which show transitions from fibre tracheids to libriform fibres), in the form and glabrousness of its leaves, branchlets, and spare thyrsiform inflorescence, in its bisexual flowers, in the texture and venation of its tepals, and in the isomerous dehiscence of its fruiting hypanthium. It also approaches the other genera of the Laurelieae in other characters. In respect of *Daphnandra*, these are its green or red-pigmented bisexual flowers with rotate perianth, its trend to extrorse anther dehiscence and abaxial staminal glands which are reduced to obtuse cupular flaps in *Dryadodaphne novoguineensis* and *D. trachyphloia*, and its shortly or obscurely rostrate ovule. In respect of *Doryphora*, they are the form of its secondary xylem multiseriate rays, its bisexual flowers with a constant number of perianth parts, to some extent the form of its ± rostrate stamens and relatively wing-like staminal glands, and the structure of its fruiting hypanthium with its completely caducous perianth and androecium. In respect of *Laurelia*, they are the structure of its inflorescence, and the form of its fruiting hypanthium and nutlets.

In summary, *Dryadodaphne* is hardly more closely related to one genus than it is to another, except *Nemuaron*. The form and combination of its morphological characters place it in the centre of the reticulate pattern of relationships between the genera of the Laurelieae. This position is particularly well demonstrated by the above-mentioned features of its secondary xylem, through which it links *Doryphora* and *Laurelia* (vessels predominantly solitary, and fibres almost exclusively fibre tracheids) with *Daphnandra* (up to 20% vessels in radial multiples, and fibres frequently libriform and septate). The characters of *Dryadodaphne* indicating its central position among the genera of the Laurelieae are enumerated in table IV and reviewed in chapters IV and XVI. They suggest that the genus is the least specialised in the tribe.

Interspecific Relationships

The three species of *Dryadodaphne* fall into two alliances, one comprising *D. pterandrica* (New Guinea), and the other *D. novoguineensis* (New Guinea) and *D. trachyphloia* (north-east Queensland).

D. pterandrica stands apart in its relatively broadly obtuse, frequently retuse leaves, generally cream-green flowers, equal whorls of tepals, two unequal whorls of stamens, broad wing-like staminal glands attached nearer to the base of the filament, shortly apiculate outer anthers, latrorse anther dehiscence, and shorter if thicker fruit.

It is geographically sympatric with *D. novoguineensis* over its entire range, but ecologically allopatric, occurring generally at higher altitudes (figure 51). The occurrence of red or purplish pigmented flowers and a single fertile whorl of stamens in some collections of *D. pterandrica* from lower altitudes may indicate introgression with *D. novoguineensis*. One collection from Edie Creek, Morobe District (Henty: NGF 27169)*, for example, possesses not only these characters, but also the more acute flower buds and unequal tepal whorls of *D. novoguineensis* with the elliptic-obovate leaves and apiculate stamens with wing-like

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*Treated as *D. pterandrica* in the text and index to collections examined.

staminal glands of D. pterandrica. Perhaps significantly, the specimen was collected in "disturbed forest" at an altitude of 2000 m where the altitudinal range of the two species overlaps. Nevertheless, no evidence of introgression was found in populations of both species in the adjacent Aseki area studied cursorily by me in April 1966.

The single western New Guinea collection (Brass and Versteegh 11194) of D. pterandrica from the Oranje range approaches in its general leaf and stamen form and flower colour several western New Guinea collections of D. novoguineensis subsp. occidentalis, particularly the most westerly collection (van Royen and Sleumer 7387) from Mt. Nettoti, Arfak mountains. These collections promote an overall impression that D. pterandrica and D. novoguineensis, distinct in form and altitudinal occurrence in east and central New Guinea, merge or grade into each other in west New Guinea. This situation resembles the overlapping ring pattern of speciation recorded in certain birds (cf. Mayr 1942), except that here the ring has an altitudinal as well as geographical basis. Available collections of Dryadodaphne from west New Guinea, six in all from widely separated localities, are nevertheless too few to allow adequate assessment of their position between D. pterandrica and D. novoguineensis.

Common to both D. novoguineensis and D. trachyphloia are usually red- or purple-pigmented flowers, rather unequal tepal whorls in which the inner series are narrower and more petal-like, and a single whorl of 4 stamens with prolonged ovate to linguiform apices, rather extrorse dehiscence, and usually obtusely cupular or short flat glands. These characters are more specialised than those in *D. pterandrica*, according to the evaluations given in chapters IV and XVI. For example, the red-pigmented flowers of the *novoguineensis-trachyphloia* group are probably more effective in attracting insect pollinators. Moreover, the two unequal staminal whorls of *D. pterandrica*, in which the inner stamens are narrower with smaller appendages and more closely resemble those of *D. novoguineensis* and *D. trachyphloia*, may represent a stage in the reduction of the androecium in *Dryadodaphne* to a single staminal whorl, as found in *D. novoguineensis* and *D. trachyphloia*. The staminal glands also are more clearly modified to function as landing platforms for insect pollinators in the latter species than in *D. pterandrica*, being attached closer to the anther as shallow cupular protuberances directly below the anther valves on the abaxial face of the filament.

D. novoguineensis and *D. trachyphloia* are vicarious species. *D. novoguineensis* is rather polymorphic, with two subspecies and one variety. *D. trachyphloia* is distinguished from it by its shaggy brown trunk bark, absence of vein reticulum on the lower face of crown leaves, smaller inflorescence and flowers, more slender stamens with characteristically rounded linguiform apices, and relatively thin-walled fruiting hypanthia, all of which are characters of lesser taxonomic significance in the genus.

D. trachyphloia also appears to possess a higher frequency of oil cells in the xylem rays (cf. Schodde 3352) than *D. novoguineensis*, in which they are occasionally present, or *D. pterandrica* in which they are apparently always absent.

Key to the Species and Infraspecific Taxa of Dryadodaphne

1a. Stamens 8 (very rarely 4); outer stamens including appendages broader than long, with apiculate apices $\frac{1}{4}$-$\frac{1}{2}$(-$\frac{2}{3}$) mm long, and widely divergent, deltate-ovate, ± acute glands, ($\frac{1}{2}$-)1-1$\frac{1}{3}$(-1$\frac{1}{2}$) mm long; leaf blades narrowly to broadly obovate, rarely elliptic, with rounded obtuse, frequently retuse apices; tepals ± pale cream-green, rarely pink to marone, in ± equal whorls.

. ... 1. D. pterandrica Schodde

1b. Stamens 4; stamens including appendages longer than broad*, with lanceate to ovate or linguiform rostrate apices $\frac{1}{2}$-1(-1$\frac{1}{4}$) mm long, and slightly divergent, lanceate to cupular, rather obtuse glands, $\frac{1}{3}$ - 1 mm long; leaf blades variously lanceate to elliptic, with attenuate to acuminate, rarely rounded obtuse apices; tepals pale marone-brown, pinkish, or purplish, rarely cream-green, in unequal whorls 2

2a. Leaf blades with ± extensive ± fine vein reticulum on lower face; tepals (2-)2$\frac{3}{4}$-4(-6) mm long; fruiting hypanthia (11-)17-40(-45) mm long, with walls (1-)1$\frac{1}{2}$-3 mm thick, and pubescence in chamber densest towards rim; bark rather smooth, finely cracked to shallowly fissured 3

3a. Staminal glands ± thick, ovate-oblong, obtuse, or shallowly cupular, $\frac{1}{2}$-$\frac{3}{4}$(-1) mm long; crown leaf blades with acuminate, rarely rounded obtuse apices, and

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* Infrequently as broad as long in west New Guinea forms.

distinctly undulate-crenate to crenulate margins; fruiting hypanthia 2-4 times longer than broad.

.... 2a. *D. novoguineensis* (Perk.)A.C.Smith subsp. *novoguineensis*

4a. Inflorescences generally glabrous; crown leaf blades (2-)4-10(-12) cm long × ($\frac{3}{4}$-)1$\frac{1}{2}$-3$\frac{1}{2}$(-4$\frac{1}{2}$) cm broad, relatively thinly coriaceous, with finely prominulous to rather obscure vein reticulum on lower face.

.... 2b. *D. novoguineensis* (Perk.)A.C.Smith var. *novoguineensis*

4b. Inflorescences finely to densely tomentulose; crown leaf blades (3-)5-12(-17) cm long × (2-)2$\frac{1}{2}$-5(-6$\frac{1}{2}$) cm broad, relatively thickly coriaceous, with conspicuously prominent vein reticulum on lower face.

.... 2c. *D. novoguineensis* var. *macra* Schodde

3b. Staminal glands ± planate, lanceate to ovate, rather acute, $\frac{3}{4}$-1 mm long; crown leaf blades with narrowly obtuse, hardly acuminate apices, and obscurely undulate-crenate, almost entire margins; fruiting hypanthia 1$\frac{3}{4}$-2 times longer than broad.

.... 2d. *D. novoguineensis* subsp. *occidentalis* Schodde

2b. Leaf blades with vein reticulum absent on lower face except for intramarginal forking (and anas-tomosing) of nerves; tepals 1$\frac{1}{2}$-2$\frac{1}{2}$ mm long; fruiting hypanthi~~um~~a 11-22(-24) mm long, with walls 1-1$\frac{1}{2}$(-1$\frac{3}{4}$) mm thick, and pubescence in chamber densest towards base; bark very rough, coarsely fissured and flaking.

.... 3. *D. trachyphloia* Schodde

1. *Dryadodaphne pterandrica* Schodde, sp.nov.

Dryadodaphne novoguineensis auctt. [non (Perk.)A.C.Smith]: A.C.Smith, J.Arn.Arbor. 23(1942)433 p.p.; L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)49 p.p.?

Isomerocarpa novoguineensis auct. [non (Perk.)A.C.Smith]: A.C.Smith, J.Arn.Arbor. 22(1941)251 p.p., [23(1942)443 p.p. pro syn. *Dryadodaphnis novoguineensis*].

Arbor magna 20-30 m alta, folia comparate lata, obtusa saepe retusa, series tepalorum aequiformatae, plerumque virellae, stamina fungentia octo rare quattuor, cum apiculis brevibus, dehiscentia valvarum antherarum revera laterali, et glandulis divergentibus, late aliformibus, planis-cupulatis, ovatis-lanceatis, acutis vel aliquantum obtusis, $\frac{1}{2}$-$1\frac{1}{3}$(-$1\frac{1}{2}$) mm longis, et hypanthia fructificantia comparate brevia, (15-)18-23(-27) mm longa × (5-)6-10(-11) mm lata, crasse ligneaque. Ab omnibus speciebus *Dryadodaphnis* combinatione horum characterum differt.

TYPUS: Schodde 4816, Angabena ridge, ca 3 miles east of Aseki —— holotypus in CANB (167641), isotypi in A, B, BH, BO, BRI, CANB, CONC, G, K, L, LAE, P, US.

Figures 4, 25, 44D.

Diagnosis

Trees 20-30 m high; bark rather smooth, rarely coarsely lined, cracked, or fissured, pale grey to brownish grey; wood with growth rings ± obscure; leaf blades narrowly to broadly obovate, infrequently elliptic, often retuse, ($\frac{3}{4}$-)$2\frac{1}{2}$-6(-10) cm long × ($\frac{1}{2}$-)1-3(-4) cm broad, with extensive though finely prominulous vein reticulum on lower face.

Mature inflorescences (¾-)1½-3(-5) cm long; pedicels slightly more slender than primary peduncle, (1-)3-9(-13) mm long × ⅔ - 1 mm thick, ± expanded under hypanthium; bracteoles (1½-)2-2¾(-3) mm long × 1½-1¾(-2½) mm broad; flower buds obtuse, almost turbinate.

Open flowers with perianth pale cream- or yellow-green, rarely whitish or reddish, the tepal whorls ± equal, with tepals broadly obtuse oblong-linguiform to elliptic, (1½-)3-4½(-5) mm long × (1½-)2-2¾(-3) mm broad; androecium pale cream- or yellow-green, the two outer whorls comprising 4 stamens each; stamens of outermost whorl broader than long, (1-)1⅓ - 2 mm long × (1¼-)1½-2½(-3) mm broad, with widely divergent, ± planate, wing-like, ovate- to lanceate-deltate, ± acute staminal glands, (½-)1-1⅓(-1½) mm long, latrorsely dehiscing valves, and apiculate apices; stamens of inner whorl ± as broad as long, (1-)1¼-1¾(-2) mm long × 1-1¾(-2¼) mm broad, with shorter, sub-cupular, ovate to circular, ± obtuse staminal glands, ½-¾(-1) mm long, latrorsely dehiscing valves, and longer apiculate-rostrate apices; styles exserted (¾-)1-1¼(-1½) mm beyond hypanthium rim, stigmatic column protruding beyond apices of staminodes to near apices of outer stamens.

Ripe infructescences (2½-)3-5(-6) cm long; pedicels (3-)5-12(-15) mm long × 1-1¾ mm thick; fruiting hypanthium (15-)18-23(-27) mm long × (5-)6-10(-11) mm thick, thickly lignified, with walls (1½-)2-3½(-4) mm thick, dehiscing into 4, rarely 2, isomerous valves, the chamber evenly sparsely haired; nutlet bodies (3-)5-6 mm long, styles (5-)7-10(-14) mm long, with tips exserted 1-1¼(-1½) mm beyond the hypanthium rim.

Detailed Description

Trees ca 20-30 m high, rarely more; bole ca (25-)40-70(-90) cm diameter breast height, ± unbuttressed, rarely coppicing; crown narrowly umbrageous, rather dense, shorter than the bole. Bark (4-)7-15(-18) mm thick when dry, outer surface rather smooth to finely, rarely coarsely lined, cracked, or fissured, pale mid- to brown-grey, rarely darker or browner, inside stramineous or pale brownish cream, exceptionally light orange. Wood usually pale brownish yellow, sometimes paler cream, growth rings obscure or faintly discernible. Branchlet stems relatively closely branched, the ultimate 4-6 internodes (½-)1-4(-9) cm long × 1-3(-4) mm ~~broad~~ thick, with lateral stems slightly slenderer than leader stems, compressed and usually tetragonous with sharp, less often rounded angles, drying blackish or brownish black, glabrous, or shoots and buds sometimes unevenly sordid buff tomentulose, or with scaly incrustation; shaded and sapling branchlet stems less compressed. Petioles (3-)5-9(-14) mm long × (½-)1-1½(-2) mm thick, usually longest on shaded branchlets, deeply impressed, with narrow, or obscure, rarely broad marginal flanges on upper face, glabrous. Leaf blades narrowly to broadly obovate, sometimes rounded cuneate, infrequently elliptic, (¾-)2½-6(-10) cm long × (½-)1-3(-4) cm broad, ± attenuately cuneate at the base, broadly, less often narrowly obtuse, frequently retuse at the apex; margins faintly undulate, or obscurely or obtusely crenulate, rarely markedly crenulate or entire, ± markedly recurved, almost revolute towards the petiole; texture quite, rarely thinly coriaceous, the upper face smooth, with nerves sometimes faintly prominulous; colour slightly glossy mid yellowish green to dark green on upper face, duller and paler on lower, in dry leaves glossy to dull pale olive-brown or mid greyish olive on upper face, browner on lower; nervation on upper face as described, on lower with (4-)6-8(-11) conspicuously prominulous main nerves anastomosing often more obscurely towards margins of blade, the vein reticulum more finely prominulous, sometimes obscure, extending towards the midrib; bearing very sparse to frequent pale to brown-black glandular pits; leave blades on shaded and sapling branchlets more elliptic and larger, (2-)3-7(-12) cm long × (1-)2-3$\frac{1}{2}$(-4$\frac{1}{2}$) cm broad, with often narrower, sometimes acuminate apices, and more markedly crenate, planate margins, more thinly coriaceous, generally duller green, nerves and vein reticulum more prominulous on both faces. Bark, stems, and leaves not or faintly aromatic when crushed with an odour like that of *Evodia**, the odour evanescing in these parts when dried.

Mature inflorescences sparse, rarely congested on ultimate branchlets, spare thyrsiform, ($\frac{3}{4}$-)1$\frac{1}{2}$-3(-5) cm long, glabrous, or glabrescent with a sparsely sordid stramineous to rusty strigillose tomentulum on upper parts, bearing (1-)3 or 5, rarely 7, 9, or 11 flowers. Primary peduncles ($\frac{1}{4}$-)$\frac{3}{4}$-2$\frac{1}{4}$(-3)cm long × ($\frac{2}{3}$ -)1(-1$\frac{1}{2}$) mm thick, variously compressed, striately wrinkled or finely costate, rarely quite smooth, drying blackish, rarely

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* Data from Hartley 11651.

red-brown or dark olive, glabrous, or glabrescent with fine sparse tomentulum persistent on young parts, 1-2(-3)-noded, the subterminal nodes single-flowered, very rarely bearing simple dichasia; bracts lanceate-deltate to narrowly ovate, rarely oblong, ($1\frac{1}{2}$-)2-3(-4) mm long × $1\frac{1}{4}$-$1\frac{3}{4}$ mm broad, early caducous, rarely persisting until anthesis; secondary peduncles ± $\frac{1}{2}$ cm long, slenderly compressed, glabrous; pedicels slightly more slender than peduncles, (1-)3-9(-13) mm long × $\frac{2}{3}$ - 1 mm thick, slightly to rather conspicuously expanded under hypanthium, drying red-brown, paler, or blackish, glabrescent, sordid stramineous to grey-white tomentulose when young; bracteoles lanceate-deltate to ovate-deltate, ($1\frac{1}{2}$-)2-$2\frac{3}{4}$(-3) mm long × $1\frac{1}{2}$-$1\frac{3}{4}$(-$2\frac{1}{2}$) mm broad, glabrous, or glabrescent with a sparse to dense tomentulum abaxially, rarely adaxially, sometimes persisting until anthesis. Mature flower buds obtuse, sometimes almost turbinate, ($1\frac{1}{2}$-)$2\frac{1}{2}$-4 mm long × ($1\frac{1}{2}$-)2-3(-$3\frac{1}{2}$) mm thick, glabrous, or sparsely grey-white to sordid stramineous tomentulose on hypanthium and margins of tepals.

Open flowers. Hypanthium 1-2(-$2\frac{1}{2}$) mm long × (1-)$1\frac{1}{2}$-$2\frac{1}{2}$(-3) mm thick, glabrescent, or persistently sparse fine off-white to greyish stramineous tomentulose; rim 1-$1\frac{1}{2}$ mm broad. Perianth pale cream- or yellow-green, rarely whitish, pinkish lilac, purple, or marone adaxially, the whorls ± equal, the tepals obscurely 3(or 5)-nerved from near the base; outer tepals oblong-linguiform to elliptic, rarely narrowly obovate, ($1\frac{1}{2}$-)$3\frac{1}{2}$-$4\frac{1}{2}$(-5) mm long × ($1\frac{1}{2}$-)2-$2\frac{3}{4}$(-3) mm broad, with broadly obtuse apices, sepaloid or subpetaloid, glabrous or rarely sparsely sordid strigillose abaxially, usually finely sordid tomentellous adaxially towards the apex; inner tepals of similar shape, form, and texture, $(1\frac{1}{2}-)3-4(-5)$ mm long × $(1\frac{1}{2}-)2-2\frac{1}{2}(-3)$ mm broad, often thinner, variably sparsely sordid stramineous puberulous on both faces, rarely entirely glabrous. Androecium pale cream-green or yellow-green, sometimes dull purplish red, (3-)4(-5)-seriate, the outer two whorls comprising 4 stamens each, the inner 4 infrequently with aborted anthers, the inner whorls comprising staminodes; stamens of outer whorl somewhat incurved-recurved upright, $(1-)1\frac{1}{3} - 2$ mm long × $(1\frac{1}{4}-)1\frac{1}{2}-2\frac{1}{2}(-3)$ mm broad × $\frac{2}{3} - 1$ mm thick; filaments $(\frac{1}{3}-)\frac{1}{2}-\frac{3}{4}(-1)$ mm long × $(\frac{1}{2}-)\frac{2}{3} - 1(-1\frac{1}{4})$ mm broad × $\frac{1}{2}-\frac{3}{4}$ mm thick; staminal glands widely divergent, wing-like and planate or shallowly cupular at the base, ovate- to lanceate-deltate, acute to narrowly obtuse, $(\frac{1}{2}-)1-1\frac{1}{3}(-1\frac{1}{2})$ mm long; anthers broadly short apiculate, the apiculum ± dorsiventrally compressed, rarely broadly conical, rather obtuse to broadly acute, $\frac{1}{4}-\frac{1}{2}(-\frac{2}{3})$ mm long × $\frac{1}{2}-\frac{3}{4}$ mm broad, the pollen sacs with latrorse or very slightly extrorse dehiscence, $(\frac{1}{3}-)\frac{1}{2} - \frac{2}{3}(\frac{3}{4})$ mm long; stamens of inner whorl smaller and more slender, similarly incurved-recurved, $(1-)1\frac{1}{4}-1\frac{3}{4}(-2)$ mm long × $1-1\frac{3}{4}(-2\frac{1}{4})$ mm broad; filaments $(\frac{1}{4}-)\frac{1}{2}-\frac{3}{4}(-1)$ mm long × $(\frac{1}{2}-)\frac{2}{3} - \frac{3}{4}$ mm broad; staminal glands less divergent, shorter, more cupular, ovate to circular, ± obtuse, $\frac{1}{2}-\frac{3}{4}(-1)$ mm long, sometimes aborted; anthers obtusely apiculate-rostrate, the apiculum thicker, more broadly conical, $(\frac{1}{4}-)\frac{1}{3} - \frac{2}{3}$ mm long × $\frac{1}{2} - \frac{2}{3}$ mm broad, the pollen sacs with similar dehiscence, $(\frac{1}{3}-)\frac{1}{2} - \frac{2}{3}$ mm long; staminodes upright to recurving, compressed narrowly to broadly lanceate or deltoid to subulate, $(\frac{1}{3}-)\frac{1}{2}-1\frac{1}{2}(-1\frac{3}{4})$ mm long × $\frac{1}{3}$ - 1 mm broad, apiculate, acute, or narrowly obtuse, the outer staminodes often with vestigial staminal glands. Gynoecium of (5-)8-12(-15) carpels; styles exserted $(\frac{3}{4}-)1-1\frac{1}{4}(-1\frac{1}{2})$ mm beyond hypanthium rim in a slender column $\frac{1}{2}$ - $\frac{2}{3}$ mm wide; stigmatic column narrowly conical, curling, $\frac{1}{2}$-1 mm long, exserted beyond apices of staminodes, sometimes to apices of outer stamens.

Ripe infructescences $(2\frac{1}{2}-)3-5(-6)$ cm long, glabrous. Primary peduncles $(1-)1\frac{1}{2}-2\frac{1}{2}(-3\frac{1}{2})$ cm long × $\frac{3}{4}-1\frac{1}{2}$ mm thick, of the same form and colour as in inflorescence, but usually less markedly tetragonous, and sometimes more broadly compressed at the nodes; pedicels (3-)5-12(-15) mm long × $1-1\frac{3}{4}$ mm thick. Fruiting hypanthium cylindrical-ellipsoid, sometimes almost clavate, (15-)18-23(-27) mm long × (5-)6-10(-11) mm thick, levigate, often conspicuously 4-, rarely to 8-ribbed or -angled towards the rim when immature, slightly glossy pale to dark green, drying dark grey or brown to blackish, thickly lignified with walls $(1\frac{1}{2}-)2-3\frac{1}{2}(-4)$ mm thick, dehiscing regularly into 4, rarely 2, equal valves; rim $1-1\frac{3}{4}$ mm broad, relatively levigate with inner staminodes variably persistent; hypanthium chamber sparsely sordid stramineous hispidulous-strigollose near the rim, equally sparsely long silky pale fawn hirsute towards the base, with hairs ± confined to the rims of the nutlet pits. Nutlets elongating in maturing hypanthium to maintain the exsertion of the style tips $1-1\frac{1}{4}(-1\frac{1}{2})$ mm beyond the hypanthium rim; bodies of ripe nutlets narrowly ellipsoid, almost fusiform, or narrowly obclavate, (3-)5-6 mm long × $1-1\frac{1}{2}(-1\frac{3}{4})$ mm thick, sordid stramineous to pale fawn silky hirsute, the hairs (6-)8-12(-14) mm long; styles of ripe nutlets (5-)7-10(-14) mm long.

6-12-noded seedlings ca 15-30 cm high, the ultimate 4-6 internodes rounded compressed, 10-20 mm long × $\frac{2}{3}$ - $1\frac{1}{2}$ mm thick, smooth, drying dark olive-brown to blackish, glabrous, the nodes hardly compressed; cotyledons caduous; subsequent leaf pairs with petioles deeply impressed on upper face, 3-4 mm long × $\frac{1}{2}$ mm thick in early leaves, 5-7 mm long × 1-$1\frac{1}{2}$ mm thick in later, and leaf blades oblanceate to narrowly obovate, 26-40 mm long × 12-18 mm broad in early leaves, 90-120 mm long × 35-40 mm broad in later, with attenuately cuneate bases, narrowly to acuminately obtuse apices, shallowly crenate margins that are planate in early leaves and somewhat recurved in later, chartaceous to thinly coriaceous texture, dull or slightly glossy mid green colour, deeply impressed midrib on upper face, prominulous nerves and vein reticulum on both faces, particularly in chartaceous leaves, glabrous, glandular pits sparingly present.

The epithet *pterandrica* is derived from πτερον, a wing, and ἀνδρικός, of a man or male, in allusion to the broad wing-like glands on the stamens of this species.

Melanesian names: Dafa (Nerenavip village, Telefomin area —— Frodin NGF 28507, 28519), Katan (Kiliga, Mt. Hagen area —— Saunders 670; Togoba, Mt. Hagen area —— Saunders 843, 866), Korgi (Chimbu area —— Robbins 1189; Waimambuno village, Chimbu area —— Saunders 817), Mowku (Enga language, Laiagam-Wabag area —— Walker ANU 768), Mugu (Enga language, Wabag area —— Flenley ANU 2367), Muk (Enga language, Laiagam area —— Saunders 1030), Nopohn (Togoba, Mt. Hagen area —— Saunders 862), Piljim (Mt.Hagen area —— Robbins 1050), Piltimo or Piltimu (Kornia, Mendi area —— Saunders, pers.comm.), Pohn (Togoba, Mt. Hagen area —— Pullen 563), Onda or Onde (Aseki area, Kukukuku ranges —— Schodde 4816, 4832, 4918).

Series of specimens examined: 56 collections, comprising 8 with inflorescence buds, 31 with flower buds, 24 with open flowers, 22 with near or fully mature fruiting hypanthia, and 1 of seedlings.

Geographic Distribution (map 5)

Dryadodaphne pterandrica occurs in the mountains of central and south-east New Guinea, north-west at least to the Oranje range, 3°40′S to 9°30′S:

Oranje range. Baliem river.

Hindenburg range. Nerenavip area.

Central highlands. Kepilam; Sirunki; Kupalis near Wabag; Sau valley divide; Mt. Hagen; Mt. Oga; Mt. Kum.

Bismarck range. Mt. Wilhelm; Waimambuno; Marafunga, Omahaiga valley; Mt. Otto area; Daulo area.

Saruwaged range, Huon Peninsula. Wantoat; Abe; Matap; Ogeramnang; Mt. Rawlinson; Samanzing; Sambanga; Yunzaing; Mannasat.

East highlands. Spreader Divide; Angabena ridge near Aseki; Edie creek; Mt. Kaindi.

Wharton range. Garaina - Mt.Dickson.

Owen Stanley range. the Gap; Mt. Ganeve; Alola; Lala river; Mt. Dayman.

Although frequent throughout its geographic range in its preferred habitat, and now the most commonly represented species of the genus in herbarium collections, Dryadodaphne pterandrica has been found only recently. The earliest collections are those of J. and M.S.Clemens, gathered in the Huon Peninsula in 1936-7.

Ecology (figure 51)

Dryadodaphne pterandrica occurs sparingly to frequently as a mature tree of the forest canopy in primary, rarely old secondary, montane rainforest. In the north-western and central parts of its range, it is found between the altitudes of 2000 and 2800 m, and in the south-east between (1350-)1600-2400 m in the East highlands, and Saruwaged and Owen Stanley ranges. It grows in fairly well-drained sites, usually on the slopes and towards the crowns of mountains and ridges. Flenley has recorded the soil on which one plant (ANU 2367) was growing as a latosol, pH 5.5 to 6.0; there are no other soil data.

The species is associated generally with forests dominated by Nothofagus. Locally, however, it often occurs in forests of mixed tree species in which species of Ascarina, Castanopsis, Cinnamomum, Claoxylon, Cryptocarya, Dacrydium, Drimys, Elaeocarpus, Evodia, Galbulimima, Halfordia, Ilex, Opocunonia, Planchonella, Platea, Prunus, Quintinia, Schizomeria, Sloanea, Syzygium, Timonius, Weinmannia, Xanthomyrtus, and Zanthoxylum are commonly found (Saunders n.1965;personal observations). Towards the upper limit of its altitudinal range, it extends also into conifer forests dominated by species of Papuacedrus, Phyllocladus, and Podocarpus. There it often becomes rather stunted and heavily mossed.

Phenology

Flowering and fruiting takes place continuously throughout the year, irrespective of season, altitude, and locality. Both have been recorded in July and December in the Owen Stanley range (Brass 22425; Carr 13799, 13839), and also in December in the Oranje range (Brass and Versteegh 11194), at the other end of the known geographic range of the species.

As a rule, flowering and fruiting occur successively rather than contemporaneously on any one tree. In the mountains of the Huon Peninsula, from where the greatest number of collections (14) throughout the year are available, it appears that flowering occurs predominantly between December and August-September, and fruiting between June and November.

Infraspecific Variation

In the eastern and central parts of its range, Dryadodaphne pterandrica is a fairly uniform species; the only variation exhibited is that correlated with altitude. Lower altitude forms tend to have more slender stems with less compressed nodes, larger, more elliptic, thicker leaves, with narrower apices, and almost entire margins; and often four (or six) instead of eight stamens, which are usually somewhat transitional in form between the stamens of the outer and inner whorls of 8-stamen flowers. In such flowers, there are frequent signs of abortion of pollen sacs in the stamens of the inner whorl and of the staminal glands on those of the outer whorl (Hartley 12709, Henty 27169, Schodde 4918). All flowers in which the tepals and/or androecium have been coloured marone, pink-lilac, or purplish are from lower altitude collections. The possibility that these variations result from introgression with *D. novoguineensis* has been discussed. Trees from higher altitudes tend to have smaller, more obovate, retuse leaves, flower parts that are consistently pale greenish-cream, and regularly eight stamens per flower.

A single collection from the Oranje range (Brass and Versteegh 11194), at the western limit of the geographic range of the species, is rather distinct from eastern populations in the following characters: relatively small ± entire leaves; reddish flowers; four small stamens, of which the shortest has the form of an outer whorl stamen, and the other three the form of inner whorl stamens of 8-stamen flowers; and very thick fruit (10-11 mm thick). Further collections are needed from the region, however, before the significance of such differences can be determined.

Chemistry

No information has been published. According to Bick (pers.comm.), one of the minor alkaloids of *D. pterandrica*, a yellow one related to the aporphines, has been found also as a major alkaloid of *Nemuaron vieillardii*, and in very small amounts in *Atherosperma moschatum*.

Uses

According to Robbins (n.1050, 1189), the timber of *D.pterandrica* is used in the Mt. Hagen and Chimbu areas, Central highlands.

2. Dryadodaphne novoguineensis (Perk.)A.C.Smith

Dryadodaphne novoguineensis (Perk.)A.C.Smith, J.Arn.Arbor. 23(1942) 443 p.p.; L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)49 p.p.

Daphnandra novoguineensis Perk., Bot.Jb. 52(1915)217,f.5; Gilg & Diels, Notizbl.Bot.Gart.Mus.Berl. 9(1925)467; Perk., Gattung Monim. (1925)50,f.38; [A.C.Smith, J.Arn.Arbor. 22(1941)251 pro syn Isomerocarpae novoguineensis, 23(1942)443 pro syn. Dryadodaphnis novoguineensis].

TYPE: Ledermann 8939, Etappenberg —— holotype in B (lost), isotype in K.

Isomerocarpa novoguineensis (Perk.)A.C.Smith, J.Arn.Arbor. 22(1941) 251 p.p., [23(1942)443 p.p. pro syn. Dryadodaphnis novoguineensis].

Dryadodaphne celastroides S.Moore, J.Bot. 61(1923)109; Kosterm., Rec.Trav.Bot.Néerl. 34(1937)605; [A.C.Smith, J.Arn.Arbor. 23(1942) 443 pro syn. Dryadodaphnis novoguineensis]; Lemée, Dict.gen.phan. (suppl.) 9(1951)108.

TYPE: Forbes 724, Wori Wori Mt. —— holotype in BM, isotypes in K, MEL.

Daphnandra perkinsiae Gilg & Diels, Notizbl.Bot.Gart.Mus.Berl. 9(1925)466; A.C.Smith, J.Arn.Arbor. 22(1941)252.

TYPE: Ledermann 8934, Sepik-Gebiet (SING), Etappenberg (Gilg & Diels l.c.) —— holotype in B (lost), isotype in SING.

Figures 5, 26, 36B, 45A.

Diagnosis

Trees (10-)20-40(-50) m high; bark rather smooth or finely cracked to broadly fissured, pale whitish grey to brownish; wood with growth rings obscure; leaf blades narrowly to broadly elliptic, infrequently lanceate or ovate, ± acuminate, (2-)4-12(-17) cm long × ($\frac{3}{4}$-)$1\frac{1}{2}$-5(-$6\frac{1}{2}$) cm broad, with extensive, often conspicuously prominulous vein reticulum on lower face.

Mature inflorescences ($1\frac{1}{2}$-)2-$3\frac{1}{2}$(-5) cm long; pedicels more slender than primary peduncle, (2-)4-8(-12) mm long × $\frac{1}{3}$ - 1 mm thick, hardly expanded under hypanthium; bracteoles ($1\frac{1}{2}$-)2(-$2\frac{1}{2}$) mm long × (1-)$1\frac{1}{2}$-$2\frac{1}{2}$ mm broad; flower buds ± ellipsoid, often ± acute.

Open flowers with perianth variously reddish, rarely entirely cream-green, the tepal whorls slightly unequal, with outer tepals obtusely oblong-linguiform, (2-)3-4(-6) mm long × $1\frac{1}{2}$-3(-4) mm broad, and inner tepals narrowed towards the apices, more petaloid, (2-)$2\frac{3}{4}$-$3\frac{1}{2}$(-5) mm long × ($1\frac{1}{4}$-)$1\frac{1}{2}$-$2\frac{1}{2}$(-$3\frac{1}{2}$) mm broad; androecium reddish, the outer whorl only comprising 4 stamens; stamens longer than broad, ($1\frac{1}{3}$ -)$1\frac{1}{2}$-2(-$2\frac{1}{2}$) mm long × 1-$1\frac{3}{4}$ mm broad, with slightly divergent, planate, ovate to shallowly cupular, ± obtuse staminal glands, $\frac{1}{2}$-1 mm long, slightly to markedly extrorsely dehiscing valves, and lanceate to ovate rostrate apices; styles exserted $\frac{1}{2}$-1 mm beyond hypanthium rim, stigmatic column protruding to apices of inner staminodes.

Ripe infructescences 4-8 cm long; pedicels 8-12(-13) mm long × 1-$1\frac{1}{2}$ mm thick; fruiting hypanthium (11-)17-40(-45) mm long × (4-)7-13 mm thick, thickly lignified with walls (1-)1½-3 mm thick, dehiscing into 4, rarely 2, equal valves, the chamber with hairs densest towards the rim; nutlet bodies (3-)5-6(-7) mm long, styles (5-)7-14(-15) mm long, with tips exserted 1-1½ mm beyond the hypanthium rim.

Detailed Description

Variably large trees (10-)20-40(-50) m high, young trees sometimes flowering when ± 3 m high; bole ca (40-)50-90(-115) cm diameter breast height, often buttressed, the buttresses short and thick, 2-3(-4) m high, rarely coppicing; crown variably umbrageous, openly branched, shorter than the bole. Bark 7-15(-20) mm thick when dry, outer surface rather smooth to slightly roughened, finely cracked, or shallowly and broadly fissured, pale whitish grey to grey-brown or dark brown, inside pale yellowish brown to pale buff-brown. Wood cream to brownish yellow in sapwood, browner or brown-cream in heartwood, growth rings usually obscure. Branchlet stems relatively openly branched, the ultimate 4-6 internodes (½-)2-4(-5) cm long × (1-)1½-4 mm thick, with lateral stems ± markedly slenderer than leader stems, compressed and usually conspicuously tetragonous with sharp, less often rounded angles, drying blackish, rarely greyer or browner, generally glabrous, or shoots, sometimes apical internodes, sparsely to densely sordid stramineous to pale grey-fawn hispidulous or tomentulose. Petioles (5-)7-15(-22) mm long × (¾-)1-3(-3½) mm thick, rarely longer on shaded branchlets, narrowly impressed with narrow marginal flanges to broad and shallowly impressed with broad marginal flanges on upper face, generally glabrous, rarely sparsely strigillose. Leaf blades narrowly to broadly elliptic, infrequently lanceate, ovate, or narrowly obovate, (2-)4-12(-17) cm long × ($\frac{3}{4}$-)1$\frac{1}{2}$-5(-6$\frac{1}{2}$) cm broad, obtuse to widely cuneate, very rarely narrowly cuneate at the base, narrowly or acuminately obtuse, rarely broadly obtuse at the apex; margins conspicuously, if shallowly undulate-crenate, rarely almost entire, slightly to markedly recurved; texture thinly to quite coriaceous, the upper face smooth or finely lined with prominulous nerves and vein reticulum; colour ± dull mid to dark green on upper face, paler on lower, in dry leaves often rather glossy pale to dark greyish olive on upper face, dull pale or brownish grey on lower; nervation on upper face as described, on lower with (5-)6-11(-13) ± obscurely to conspicuously prominent main nerves anastomosing obscurely to conspicuously towards margins of blade, the vein reticulum obscure to almost as prominent as nerves, extending in a fine open mesh from the margin of the blade towards the midrib, sometimes uniformly prominulous over entire blade; occasionally bearing sparse, pale brown to blackish glandular pits; leaf blades on shaded and sapling branchlets 6-12 cm long × 2$\frac{3}{4}$-4$\frac{1}{2}$ cm broad, with sometimes narrower bases, and more markedly crenulate, planate margins, chartaceous to thinner coriaceous, brilliant glossy green on both faces, nerves and vein reticulum more and equally prominulous on both faces, glandular pits often more frequent. Bark and sapling leaves often fragrant, if weakly aromatic*, the odour evanescing in these parts

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* Data from Schodde 4878, Smith NGF 1016, and White NGF 9592.

when dried.

Mature inflorescences congested, rarely sparse on ultimate branchlets, thyrsiform, (1½-)2-3½(-5) cm long, glabrous or glabrescent to persistently and densely off-white, pale grey, or yellowish tomentulose-strigillose on upper parts, bearing 3-5(-11), very rarely up to 17 flowers. Primary peduncles (½-)1-3(-4½) cm long × (¾-)1-2(-2½) mm thick, terete to compressed, rather smooth to striate or finely costate, drying dark brown to blackish, glabrous, or glabrescent with a fine sparse to dense sordid grey-white or stramineous tomentulum ± persistent on nodes and distal internodes, 1-3(-5)-noded, the subterminal nodes usually single-flowered, rarely bearing simple dachasia; bracts variously lanceate-deltate, rarely linear-oblong, (1½-)2½-4 mm long × 1-1½ mm broad, very early caducous; secondary peduncles* (5-)7-12(-15) mm long × < 1 mm thick, slenderly compressed, glabrous or sparsely tomentulose, the bracts ± shorter and broader than those on primary peduncles, 2½ mm long × 1½ mm broad, often finely tomentulose; pedicels slenderer than peduncles, (2-)4-8(-12) mm long × ⅓ - 1 mm thick, rarely much expanded under hypanthium, drying grey-brown to blackish, glabrous to rather densely pale grey or yellowish tomentulose; bracteoles lanceate to ovate-deltate, (1½-)2(-2½) mm long × (1-)1½-2½ mm broad, glabrous or spar~~e~~sely sordid strigillose to densely cream-grey tomentulose abaxially, very rarely sparsely silky sericeous adaxially, rarely persisting until anthesis. Mature flower buds often

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* Present regularly only in var. macra.

narrowed acutely at apex, 3-5(-7) mm long × 2-3(-4) mm thick, either almost glabrous with hairs confined to margins of tepals or entirely ± densely glaucous to sordid golden grey tomentulose.

Open flowers. Hypanthium $1-2(-2\frac{1}{2})$ mm long × $(1-)1\frac{1}{2}-2\frac{1}{2}$ mm thick, glabrous to rather densely sordid pale grey tomentulose; rim $1-1\frac{1}{2}$ mm broad. Perianth pale marone-brown to purplish, pinkish, or reddish brown, abaxially sometimes greenish, rarely entirely cream-green, the whorls slightly unequal, the tepals obscurely 3- or 5-nerved from near the base, with a midnerve; outer tepals oblong-linguiform, rarely narrowly obovate, (2-)3-4(-6)mm long × $1\frac{1}{2}-3(-4)$ mm broad, with broadly, rarely narrowly obtuse apices, and relatively thick margins, sepaloid, ± glabrous to pale sordid grey tomentulose abaxially, usually finely tomentulose-strigillose adaxially towards the apex; inner tepals usually smaller, elliptic, $(2-)2\frac{3}{4}-3\frac{1}{2}(-5)$ mm long × $(1\frac{1}{4}-)1\frac{1}{2}-2\frac{1}{2}(-3\frac{1}{2})$ mm broad, with narrow apices and thinner margins, subpetaloid, variably sparsely tomentulose on both faces, particularly towards the apex, rarely entirely glabrous. Androecium red, purple, or pink-marone, 2-3-seriate, the outer whorl comprising 4 stamens, the inner whorls staminodes; stamens recurving upright, $(1\frac{1}{3}-)1\frac{1}{2}-2(-2\frac{1}{2})$ mm long × $1-1\frac{3}{4}$ mm broad × $\frac{1}{3}-\frac{1}{2}$ mm thick; filaments $(\frac{1}{4}-)\frac{1}{2}-\frac{2}{3}(-\frac{3}{4})$ mm long × $(\frac{1}{4}-)\frac{1}{2}-\frac{3}{4}(-1)$ mm broad × $\frac{1}{3}-\frac{2}{3}$ mm thick; staminal glands slightly divergent, planate, lanceate- or ovate-oblong, narrowly obtuse, rarely acute, to thick, cupular, obtuse, $\frac{1}{2}-1$ mm long, often protruding conspicuously from the abaxial face of the stamen; anthers broadly rostrate, the rostrum dorsiventrally compressed, narrowly lanceate to broadly ovate, acute, $(\frac{1}{2}-)\frac{3}{4}-1(-1\frac{1}{4})$ mm long × $\frac{1}{2}-1$ mm broad, the pollen sacs with slightly to markedly extrorse dehiscence, $\frac{1}{3}-\frac{1}{2}$ mm long; staminodes ± upright, lanceate, deltoid, or subulate, $(\frac{1}{2}-)\frac{3}{4}-2$ mm long × $\frac{1}{4}-\frac{3}{4}$ mm broad, acute, the outer staminodes often with vestigial staminal glands. Gynoecium of 8-13 (-16) carpels; styles exserted $\frac{1}{2}-1$ mm beyond hypanthium rim in a slender column $< \frac{1}{2}$ mm wide; stigmatic column narrowly conical, curling, $(\frac{1}{3}-)\frac{1}{2}(-1)$ mm long, exserted to apices of inner staminodes, rarely beyond.

Ripe infructescences 4-8 cm long, generally glabrous, with pedicels sometimes persistently sparse puberulous. Primary peduncles of the same dimensions, form, and colour as in inflorescence, 1-2-noded, the distal internodes often caducous; pedicels 8-12(-13) mm long × $1-1\frac{1}{2}$ mm thick. Fruiting hypanthium cylindrical-ellipsoid, rarely rather urceolate when immature, (11-)17-40(-45) mm long × (4-)7-13 mm thick, levigate, often finely to broadly ribbed when immature, drying dark grey-brown to blackish, thickly lignified, with walls $(1-)1\frac{1}{2}-3$ mm thick, often narrowed into a thick turbinate stipe 5-6 mm long at the base, dehiscing regularly into 4, rarely 2, equal valves; rim $1\frac{1}{4}-1\frac{3}{4}$ mm broad, levigate, with inner staminodes early caducous; hypanthium chamber often densely, rarely sparsely pale stramineous-fawn hispidulous-strigillose towards the rim, more sparsely and longer, somewhat silkier, pale fawn hirsute towards the base with hairs often confined sparingly to the rims of the nutlet pits. Nutlets elongating in maturing hypanthium to maintain the exsertion of the style tips $1-1\frac{1}{2}$ mm beyond the hypanthium rim; bodies of ripe nutlets narrowly ellipsoid, almost fusiform, or narrowly obclavate, (3-)5-6(-7) mm long × 1-1½ mm thick, sordid stramineous to dark fawn silky hirsute, the hairs 7-10 mm long; styles of ripe nutlets (5-)7-14(-15) mm long.

20-25-noded seedlings* ca 20-25 cm high, the ultimate 4-6 internodes obscurely tetragonous, 5-20 mm long × ± 1 mm thick, often striate, drying brownish or darker, sparsely sordid stramineous in parts, the nodes hardly compressed; cotyledons caducous; subsequent leaf pairs with petioles deeply impressed on upper face, 5-7 mm long × $\frac{2}{3}$ mm thick, and leaf blades narrowly obovate to elliptic, 45-65 mm ~~cm~~ long × 12-20 mm broad, with attenuately cuneate bases, acuminately obtuse apices, distantly shallowly crenate, subplanate margins, chartaceous texture, brilliantly glossy mid green colour, shallowly impressed midrib on upper face, prominulous nerves but not vein reticulum on both faces, glabrous or very sparsely curling strigose towards base on lower face, glandular pits frequent.

Melanesian names: Andengambi (Chimbu area —— Smith NGF 1016), Anona (Akuna area —— Smith NGF 1016), Anonya (Aiyura area —— Smith NGF 1016), Goekaai (Kapaukoe language, Wissel lakes area —— Vink & Schram BW 8717), Kamo (Okapa, Aiyura area —— White NGF 9592), Nasapu (Anona or Arona, Aiyura area —— Smith NGF 1016), Onda or Onde (Aseki area, Kukukuku ranges —— Schodde 4875, 5081).

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* Recorded for var. novoguineensis only (Schodde 4878).

Series of specimens examined: 21 collections, comprising 5 with inflorescence buds, 13 with flower buds, 11 with open flowers, 13 with near or fully mature fruiting hypanthia, and 1 of seedlings.

Geographic Distribution (map 5)

Dryadodaphne novoguineensis occurs throughout the mountains of all New Guinea, 1°- 9°30'S: Arfak mountains; Oranje range; Toricelli mountains; Central highlands; Kratke range; Saruwaged range, Huon Peninsula; East highlands; Wharton range; Owen Stanley range.

Ecology (figure 51)

Dryadodaphne novoguineensis occurs sparingly to frequently as a solitary mature tree of the forest canopy in primary hill and montane rain forest, and rarely as a remnant in secondary forest. It sometimes grows to great and pre-eminent proportions in the forest. Throughout its geographic range, it is found between the altitudes of (500-)700-1800 (-2400) m, generally below those occupied by *D. pterandrica*. It prefers gullies, slopes, and fairly well-drained ridge crowns. The only information of associated soil is provided by Vink and Schram (BW 8717) who recorded a young tree on sandy clay.

Growing in forests of mixed tree species, it has been recorded associated with species of *Agathis*, *Calophyllum*, *Cryptocarya*, *Elaeocarpus*, *Galbulimima*, *Nothofagus*, *Opocunonia*, and *Syzygium*, and with *Pandanus* in dense, well-mossed forest at 850 m at Etappenberg (Gilg and Diels 1925). Only once, at Mt. Nettoti (1750 m), has it been found associated specifically with *Nothofagus* forest (van Royen and Sleumer 7387).

Phenology

Although the number of collections available of this species are still very few and the period May to August inclusive is represented by only three specimens, all of them other than those of seedlings and young saplings are fertile, and either in flower or fruit or both. This indicates that flowering and fruiting takes place continuously throughout the year, as in the case of _Dryadodaphne pterandrica_, apparently irrespective of the season, altitude, or area. As a rule, flowering and fruiting appear to occur successively rather than contemporaneously on any one tree: only one third of the collections studied bear both flowers (or mature flower buds) and relatively mature fruit.

Infraspecific Variation

Dryadodaphne novoguineensis is more polymorphic than the other species of the genus. Three infraspecific taxa are distinguishable.

a. subsp. _novoguineensis_

Daphnandra novoguineensis Perk., 1915, l.c.
Dryadodaphne celastroides S.Moore, 1923, l.c.
Daphnandra perkinsiae Gilg & Diels, 1925, l.c.
Isomerocarpa novoguineensis (Perk.)A.C.Smith, 1941, l.c. p.p.
Dryadodaphne novoguineensis (Perk.)A.C.Smith, 1942, l.c. p.p.

Trees (10-)20-40(-50) m high when flowering; crown usually wide-spreading; bark smoothly striate to shallowly fissured, whitish grey to mid brownish grey; sapwood cream, heartwood pale brownish yellow or cream-brown; bases of lateral branchlets frequently swollen; ultimate

4-6 branchlet internodes ± angular tetragonous; leaf blades of tree crown lanceate to elliptic, rarely ovate to broadly elliptic, (2-)4-10 (-12) cm long × ($\frac{3}{4}$-)1$\frac{1}{2}$-3$\frac{1}{2}$(-4$\frac{1}{2}$) cm broad* or (3-)5-12(-17) cm long × (2-)2$\frac{1}{2}$-5(-6$\frac{1}{2}$) cm broad**, with variously acuminate obtuse, rarely narrowly or rounded obtuse apices, and distinctly, if shallowly, undulate-crenate to crenulate, rarely almost entire,** slightly recurved margins, thinly to quite coriaceous, the upper face usually lined with prominulous nerves and vein reticulum, the lower with nerves and vein reticulum obscurely to often conspicuously prominulous; outer tepals (2-)3-4(-6) mm long × (1$\frac{1}{2}$-)2-3(-4) mm broad, the inner tepals usually slightly smaller and narrow at apex and base, with broadly petaloid margins; staminal glands relatively amplexicaul, variably thick, ovate-oblong obtuse to obtusely shallow cupular, $\frac{1}{2}$-$\frac{3}{4}$(-1) mm long; outer staminodes narrowly deltoid, abaxial midnerve usually prominent, vestiges of staminal glands often absent; fruiting hypanthium (11-)18-40(-45) mm long × (4-)7-13(-13) mm thick, the length/breadth ratio 2-4:1.

Series of specimens examined: 16 collections, comprising 5 with inflorescence buds, 10 with flower buds, 8 with open flowers, 11 with fruiting hypanthia, and 1 of seedlings.

Geographic Distribution (map 5)

East New Guinea, 3°10′- 9°30′S, between 500-2400 m s.m.: all locali-

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* Var. *novoguineensis*.

** Var. *macra*.

ties east of the Toricelli mountains and central highlands.

Within the region of occurrence of subsp. *novoguineensis*, two varieties are distinguishable.

b. var. *novoguineensis*

Daphnandra novoguineensis Perk., 1915, l.c.

Dryadodaphne celastroides S. Moore, 1923, l.c.

Daphnandra perkinsiae Gilg & Diels, 1925, l.c.

Isomerocarpa novoguineensis (Perk.)A.C.Smith, 1941, l.c., p.p.

Dryadodaphne novoguineensis (Perk.)A.C.Smith, 1942, l.c., p.p.

Figure 5A - D.

Ultimate 4-6 branchlet internodes $(1-)1\frac{1}{2}-3(-4)$ mm thick, the nodes not broadly compressed, the bases of lateral branchlets often swollen; petioles ± slender, $(5-)7-14(-22)$ mm long × $(\frac{3}{4}-)1(1\frac{1}{2})$ mm thick, narrowly sulcate on upper face, with narrow or obscure marginal flanges; leaf blades of tree crown lanceate to elliptic, $(2-)4-10(-12)$ cm long × $(\frac{3}{4}-)1\frac{1}{2}-3\frac{1}{2}(-4\frac{1}{2})$ cm broad, with distinctly acuminate, very rarely narrowed apices, and distinctly undulate-crenate to crenulate margins, often thinly coriaceous, main nerves $(5-)6-10(-12)$, ± widely-spaced, prominulous, vein reticulum finely prominulous to rather obscure on lower face; inflorescences with upper peduncle nodes, pedicels, and flower buds ± glabrous, or early glabrescent with very sparse, sordid, obscure, tomentulose or strigose hairs sometimes persistent on bracteoles and perianth of flower buds; primary inflorescence peduncles $(\frac{1}{2}-)1-2(-3\frac{1}{2})$ cm long × $\frac{3}{4}-1\frac{1}{4}$ mm thick towards base, with $1-2(-3)$ nodes, bearing $3-5(-11)$

flowers; inflorescence pedicels $\frac{1}{3}$ - $\frac{3}{4}$ mm thick; infructescences (4-)5-6 cm long; fruiting hypanthium (11-)18-25(-35) mm long x (4-)7-10(-13) mm thick.

Series of specimens examined: 13 collections, comprising 4 with inflorescence buds, 7 with flower buds, 6 with open flowers, 10 with fruiting hypanthia, and 1 of seedlings.

Geographic Distribution (map 5)

East New Guinea, between 500-1950 m s.m.:

Toricelli mountains (Mt.Sapau area); Etappenberg, near Hunstein range; Mt.Hunstein; Okapa; Wanatabi; Aiyura; Yunzaing, Saruwaged range; Angabena ridge, Aseki; Dieni, Ononge road; Subitana area, Sogeri plateau; Mt. Wori Wori.

c. var. <u>macra</u> Schodde, var. nov.

Laminae foliorum coronarum arborum saepe longiores quam 10 cm, latiores quam $3\frac{1}{2}$ cm, et petioli ($1\frac{1}{2}$-)2-$2\frac{1}{2}$(-$3\frac{1}{2}$) mm crassi, inflorescentiae relative tomentulosae dense glauco-griseae vel alutaceae, et hypanthia fructificantia 35-45 mm longa. A var. <u>novoguineensi</u> inflorescentiarum tomentello ± dense glauco-griseo vel alutaceo et hypanthiorum fructificantium foliorumque magnitudine majore valde recedit.

TYPUS: Schodde 5081, Aseki valley, ca 3 miles south-east of Aseki —— holotypus in CANB (163726), isotypi in A, B, BO, BRI, CANB, CHR, CONC, K, L, LAE, US.

Figure 5 H.

Ultimate 4-6 branchlet internodes 2-4 mm thick, the nodes usually very broadly compressed, the bases of lateral branchlets rarely swollen; petioles broad, (8-)10-15(-20) mm long × (1½-)2-3 (-3½) mm thick, shallowly sulcate on upper face, with broad marginal flanges; leaf blades of tree crown broadly elliptic, sometimes ovate or obovate, (3-)5-12(-17) cm long × (2-)2½-5(-6½) cm broad, with broadly obtuse, sometimes shortly acuminate apices, and obscurely undulate-crenate, often almost entire margins, quite coriaceous, main nerves 9-11(-13), closely parallel, prominent, vein reticulum conspicuously prominulous on lower face; inflorescences with upper peduncle nodes, pedicels, and flower buds finely to densely pale to cream- or yellow-grey tomentulose, the tomentulum invariably dense and persistent; primary inflorescence peduncles (½-)1½-3(-4½) cm long × (1-)1½-2(-2½) mm thick towards base, with (1-)2-3(-5) nodes, bearing (3-)5-11(-17) flowers; inflorescence pedicels $\frac{2}{3}$ - 1 mm thick; infructescences 5-8 cm long; fruiting hypanthium ca. 35-45 mm long × (6-)10-13 (or more) mm thick.

Series of specimens examined: 3 collections, comprising 1 with inflorescence buds, 3 with flower buds, 2 with open flowers, and 1 with submature fruiting hypanthia.

Geographic Distribution (map 5)

East New Guinea, between 1000-2400 m s.m.:

Porget, north of Wabag; Aseki valley; Wau area.

The collection from Porget (Womersley (VII.1959): CANB, L, LAE) is the only record of the species above the altitude of 2000 m.

d. subsp. *occidentalis* Schodde, subsp. nov.

Isomerocarpa novoguineensis (Perk.)A.C.Smith, 1941, l.c., p.p.

Dryadodaphne novoguineensis (Perk.)A.C.Smith, 1942, l.c., p.p.

Cortex relative asper fissuratusque, folia coronarum arborum relative anguste obtusa vix acuminata ad apices, et obscure undulato-crenata paere integra, glandulae staminum planae, lanceatae ad ovatae, $\frac{3}{4}$-1 mm longae, et hypanthia fructificantia $1\frac{3}{4}$-2 plo longiora quam latiora. A subsp. *novoguineensis* glandulis staminum divergentibus longioribus et planioribus, apicibus foliorum rotundioribus et marginibus integrioribus, hypanthiis fructificantibus crassioribus, et cortice asperiore magis brunneoque recedit.

TYPUS: Brass & Versteegh 11984, 15 km S.W. of Bernhard Camp, Idenburg river —— holotypus in A, isotypi in BO, K, LAE.

Figure 5 E-G.

Trees 3-30(-35) m high when flowering; crown often or usually (?) slender; bark often rather rough and fissured, dark brown; sapwood yellowish, heartwood brown-yellow; bases of lateral branchlets ± unswollen; ultimate 4-6 branchlet internodes ± rounded tetragonous; leaf blades of tree crown broadly elliptic to ovate or obovate, (3-)4-9 (-10) cm long x $(1\frac{1}{2}$-$)2$-$3\frac{3}{4}($-$4\frac{1}{2})$ cm broad, with narrowly to attenuately obtuse, hardly acuminate apices, and obscurely undulate-crenate, often ± entire, distinctly recurved margins, ± quite coriaceous, the upper face usually smooth with nerves only prominulous, the lower with nerves and vein reticulum finely to rather obscurely prominulous; outer tepals $2\frac{3}{4}$-$3\frac{1}{2}$ mm long × $1\frac{1}{2}$-2(-$2\frac{1}{2}$) mm broad, the inner tepals similar in size or slightly narrower, with slightly petaloid margins; staminal glands relatively divergent, planate, lanceate- or ovate-oblong, narrowly obtuse to almost acute, $\frac{3}{4}$-1 mm long; outer staminodes ± compressed, lanceate, abaxial midnerve usually obscure, vestiges of staminal glands usually present; fruiting hypanthium17-23 mm long × 10-12 mm **thick**, the length/breadth ratio $1\frac{3}{4}$-2: 1.

Series of specimens examined: 5 collections, comprising 3 with flower buds and open flowers, and 2 with fruiting hypanthia.

Geographic Distribution (map 5)

West New Guinea, 1°-4°S, between 900-1800 m s.m.:

Mt. Nettoti, Nettoti range; Motito, Wissel lakes; vicinity of Bernhard Camp (= "P keten"), Idenburg river.

The few collections are likely to reflect the meagreness of botanical exploration in the central ranges of West Irian rather than any rarity of the subspecies, which is probably fairly common in the primary forests there at the above stated altitudes.

Infraspecific Relationships

D. novoguineensis subsp. *occidentalis*, at the western end of the species range, is readily distinguished from subsp. *novoguineensis* by its apparently rougher and browner bark, its more rounded and entire leaf blades, its larger, more divergent staminal glands, and its apparently thicker fruiting hypanthia. In most of these characters it approaches D. pterandrica, the significance of which has been discussed above.

There are no collections as yet between "P keten"*, the most easterly known locality of subsp. occidentalis, and the Toricelli and Hunstein ranges respectively, the most westerly known localities for subsp. novoguineensis, a distance of about 200-250 miles. Because of this, it is not known whether the distributions of the two subspecies are disjunct or continuous. The latter seems more likely in view of the continuity of mountain ranges and primary mountain forest in that sparsely inhabited and poorly explored region of New Guinea. If the distributions are continuous, it becomes important to know whether or not the characters distinguishing the subspecies are linked clinally. Examination of all collections of subsp. novoguineensis throughout its geographic range (ca 500 miles) reveals no marked trend towards the west in the rounding of leaf apices or the lenghthening and spreading of the staminal glands. Two of the most westerly collections from the central range at the Etappenberg have, respectively, the most attenuately acuminate leaves found in the species (Ledermann 8939), and quite short obtuse, rather cupular staminal glands (Ledermann 8934). A third collection (Hoogland 10953) from Mt. Hunstein in the same region, has leaves with quite shortly acuminate apices and almost entire margins, approaching the leaf form of

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* The Times Atlas of the World, vol.1 (1958) pl.15.

subsp. *occidentalis*; it lacks flowers. The occurrence of trees with such differing leaf form in this region suggests that the two subspecies are rather discrete geographically, that their ranges abut immediately west of the Hunstein range, and that clines in their distinguishing characters, if present at all, are steep. The possibility that this differentiation of forms may be correlated with the development of a minor but significant zoogeographic barrier for mountain birds between the Telefomin and Hagen regions in the same sector of the central New Guinea highlands (Gilliard and Lecroy 1961) should not be overlooked.

Though *D. novoguineensis* subsp. *occidentalis* is known from only three localities in the Oranje range, Wissel Lakes area, and Arfak mountains separated over a distance of 400 miles, the specimens from these distant areas are very similar in form, particularly in the structure of the staminal glands. The most western collection (van Royen and Sleumer 7387) from Mt. Nettoti has particularly broadly rounded leaf apices, approaching *Dryadodaphne pterandrica* in this character more than the others. The higher altitude specimens,moreover, have smaller, more crenate, and thinner leaves (Brass and Versteegh 11984, van Royen and Sleumer 7387) than those from lower altitudes. In both varieties of subsp. *novoguineensis*, a similar trend in overall size is apparent, with Hartley 13154 from 1500 m at Wanatabi possessing the smallest leaves so far recorded in the species.

Higher altitude forms of both subspecies, e.g. those cited above, appear to possess more elongate and flatter staminal glands than forms from lower altitudes. It may, on the one hand, be a further indication of possible introgression between *D. novoguineensis* and the higher altitude species, *D. pterandrica*. On the other, it may merely reflect differing selection pressures at high and low altitudes. The value of this observation is uncertain because of the paucity of comparative material, and also because the staminal glands in the specimen from the highest known station for *D. novoguineensis*, at 2100-2400 m (Womersley (VII.1959): CANB, L, LAE), are as short and obtusely cupular as those in the lowest altitude forms.

D. novoguineensis var. *macra* is a large leaved, large fruited form with conspicuously tomentulose inflorescences. It has so far been found entirely within the geographic range of subsp. *novoguineensis*. The features distinguishing it among populations of subsp. *novoguineensis* have not been found in subsp. *occidentalis*, except perhaps for the rounded apices and more entire margins of the leaves. Both varieties of subsp. *novoguineensis* have been recorded in close proximity in the Aseki area, var. *novoguineensis* from a ridge crest (Schodde 4875), and var. *macra* from the foot of a river gully (Schodde 5081). Their ecological occurrence appears to be similar, though var. *macra* may be adapted to wetter or more poorly drained situations in gullies (cf. Schodde 5081), and possibly higher altitudes.

Taxonomic Notes and Typification

Perkins' remarks when describing *Daphnandra novoguineensis* indicate the specimen in herb. B as the holotype. This collection, like most type material of *D. perkinsiae*, has been lost (chapter II), and the only duplicate traced during the present study, has been that in herb. K. It is sterile.

The holotype of *Dryadodaphne celastroides* S. Moore was seen from a photograph of the sheet in herb. BM annotated by Moore. The collecting ~~It~~ falls within the range of variation of *Dryadodaphne novoguineensis* var. *novoguineensis*.

Daphnandra perkinsiae Gilg & Diels, of which one sheet of the type collection (Ledermann 8934), but none of the paratypes, were available for study, falls within the range of variation of *Dryadodaphne novoguineensis* var. *novoguineensis*. As A.C.Smith (1941) has already predicted, it was originally distinguished on what have proved to be insignificant differences in the leaf.

Chemistry

No information has been published.

Uses

The bark of the species is chewed and rubbed on the chest by Chimbu natives in the case of certain illnesses (fide Smith NGF 1016).

3. *Dryadodaphne trachyphloia* Schodde, sp.nov.

Dryadodaphne novoguineensis auct. [non (Perk.)A.C.Smith]:
L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)49 p.p.

Arbor magna gracilisque 35-45 m alta, cortex asperissimus cum fissuris profundis, lignum eburneum cum annulis conspicuis, folia sine reticulata venationum, inflorescentiae floresque minores, pedicelli comparate crassi pedunculis aequantesque, rostra staminalia linguiformia, anguste obtusa, $\frac{1}{2}$ mm longa × $\frac{1}{3}$ mm lata, columnae stigmaticae infra staminodia persistentia immersae, et pila cavitatum hypanthiorum fructificantium versus basim confertissima. Species in Queenslandia reperta et *D. novoguineensis* proxima, cujus fabricam florium foliorumque formam habet, sed in combinatione characterum praecedentium vero differt.

TYPUS: Schodde 3340, Churchill Creek, Mt. Lewis Range —— holotypus in CANB (128459), isotypi in AD, BRI, CANB, L.

Figures 6, 16, 27.

Diagnosis

Trees 35-45 m high; bark very rough, coarsely fissured, and flaking, mid- to rusty-brown; wood with growth rings usually conspicuous; leaf blades linear-lanceate to broadly lanceate, ± attenuately acuminate, $(3-)4-8(-10)$ cm long × $(\frac{3}{4}-)1-3(-3\frac{1}{2})$ cm broad, without vein reticulum on lower face.

Mature inflorescences $(\frac{3}{4}-)1-1\frac{1}{2}(-2)$ cm long; pedicels ± as thick as primary peduncle, $(3-)4-5(-6)$ mm long × ± $\frac{3}{4}$ mm thick, hardly expanded under hypanthium; bracteoles $\frac{3}{4}$-1 mm long × $\frac{2}{3}$ - $\frac{3}{4}$ mm broad; flower buds ± obovoid, acute.

Open flowers with perianth apparently reddish, the tepal whorls slightly unequal, with outer tepals obtusely oblong-linguiform, 2-2$\frac{1}{2}$ mm long × 1$\frac{1}{4}$ - 1$\frac{1}{2}$ mm broad, and inner tepals narrowed towards the apices, more petaloid, 1$\frac{1}{2}$-2 mm long × 1 mm broad; androecium reddish, the outer whorl only comprising 4 stamens; stamens longer than broad, 1$\frac{1}{3}$ mm long × $\frac{1}{2}$ - $\frac{2}{3}$ mm broad, with hardly divergent, shallowly cupular, obtuse staminal glands, $\frac{1}{3}$ - $\frac{1}{2}$ mm long, ± extrorsely-dehiscing valves, and linguiform, obtuse, rostrate apices; styles exserted $\frac{1}{3}$ - $\frac{1}{2}$ mm beyond hypanthium rim, stigmatic column sunk below apices of inner staminodes.

Ripe infructescences (2$\frac{1}{2}$-)3-3$\frac{1}{2}$(-4) cm long; pedicels (4-)5-7(-8) mm long × 1-1$\frac{1}{2}$ mm thick; fruiting hypanthium 11-22(-24) mm long × 4-7 mm thick, lignified with walls 1-1$\frac{1}{2}$(-1$\frac{3}{4}$) mm thick, dehiscing into 2, rarely 4, equal valves, the chamber with hairs densest towards the base; nutlet bodies 3-5 mm long, styles (3-)5-10(-12) mm long, with tips exserted up to $\frac{1}{2}$ mm beyond the hypanthium rim.

Detailed Description

Large trees 35-45 m high; bole ca (30-)50-100 cm or more diameter breast height, slightly to often extensively buttressed, sometimes coppicing; crown broadly umbrageous, openly branched, shorter than the bole. Bark 10-15 mm thick when dry, outer surface very rough, coarsely fissured and flaking, mid- to rusty-brown, the fissures sometimes deeply orange-tinted, inside cream. Wood uniformly rich mid cream, growth rings usually conspicuous. Branchlet stems relatively openly branched, the ultimate 4-6 internodes (½-)1-3(-6) cm long × 1-2(-3) mm thick, with lateral stems ± markedly slenderer than leader stems, broadly compressed, becoming tetragonous with rounded, less often sharp angles, drying dark olive grey to reddish brown, often with blackish tints, glabrous or shoots unevenly sparsely sordid tomentulose; shaded and coppice branchlet stems with ultimate 4-6 internodes (2-)3-7(-10) cm long × 2-3(-4) mm thick, often more broadly compressed, the branchlet nodes 8-15(-20) mm broad. Petioles (5-)8-14(-18) mm long × 1-1¾(-2) mm thick, longest and thickest on shaded and coppice branchlets, narrowly impressed with narrow marginal flanges on upper face, glabrous. Leaf blades linear-lanceate to broadly lanceate, sometimes elliptic, rarely ovate, (3-)4-8 (-10) cm long × (¾-)1-3(-3½) cm broad, narrowly to broadly cuneate at the base, attenuately ± acuminately obtuse at the apex; margins shallowly, distantly, often obscurely undulate-toothed, slightly to markedly recurved, texture thinly to quite coriaceous, the upper face smooth, sometimes obscurely lined with prominulous nerves; colour rather glossy dark green on upper face, dull pale to bright green on lower, in dry leaves mid to dark brownish or greyish olive on upper face, brownish olive on lower; nervation on upper face as described, on lower with 6-9 faintly or distinctly prominulous widely-spaced main nerves forking obscurely towards margins of blade, the vein reticulum absent; glabrous, occasionally bearing sparse brownish glandular pits; leaf blades on shaded and coppice branchlets more elliptic, 8-17 cm long × (3½-)5-6(-7) cm broad, with more shortly acuminate or obtuse apices, and subplanate margins, chartaceous to thinly coriaceous, slightly glossy green, nerves more prominulous on both faces, vein reticulum obscurely present, extending from the margin of the blade towards the midrib, glandular pits not more frequent. Bark and wood with a faint sour or <u>Ananas</u>-like odour, the leaves sometimes with a faint safrol-like odour*, the odour evanescing in these parts when dried.

Mature inflorescences sparse to congested on ultimate branchlets, shortly thyrsiform, $(\frac{3}{4}-)1-1\frac{1}{2}(-2)$ cm long, glabrous, or glabrescent with a fine sparse sordid whitish to greyish tomentulum often persistent on pedicels and flower buds, bearing 3(-5) flowers. Primary peduncles $(\frac{1}{2}-)\frac{2}{3}-\frac{3}{4}(-1)$ cm long × $(\frac{2}{3}-)\frac{3}{4}(-1)$ mm thick, terete to compressed, rather wrinkled finely costate, drying blackish to blackish olive, generally glabrous, 1(-2)-noded, the subterminal node single flowered; bracts linear-lanceate, 2-3 mm long × $\frac{3}{4}$-1 mm broad, generally glabrous, very early caducous; secondary peduncles absent; pedicels ± as thick as peduncles, (3-)4-5(-6) mm long × ± $\frac{3}{4}$ mm thick, rarely much expanded under hypanthium, drying blackish, generally glabrescent, rarely sparse pale grey tomentulose towards the base; bracteoles ovate-deltate, $\frac{3}{4}$-1 mm long × $\frac{2}{3}-\frac{3}{4}$ mm broad, glabrous, rarely persisting until anthesis. Mature flower buds acute at the apex, $(2-)2\frac{1}{4}-2\frac{3}{4}(-3)$ mm long × $1\frac{1}{4}-1\frac{1}{2}$ mm thick, usually sparsely pale grey tomentulose on hypanthium and margins of tepals.

Open Flowers. Hypanthium $1-1\frac{1}{4}$ mm long × $1\frac{1}{4}$ mm thick, sparsely grey-

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* Data from Schodde 3340, 3352.

white tomentulose-strigillose; rim ($\frac{1}{2}$-)± $\frac{2}{3}$(-$\frac{3}{4}$) mm broad. Perianth apparently marone-brown to purplish, the whorls slightly unequal, the tepals obscurely nerved; outer tepals oblong-linguiform, 2-2$\frac{1}{2}$ mm long × 1$\frac{1}{4}$-1$\frac{1}{2}$ mm broad, with broadly obtuse apices and relatively thick margins, sepaloid, entirely glabrescent, or persistently pale stramineous strigillose adaxially towards the apex; inner tepals smaller, elliptic, 1$\frac{1}{2}$-2 mm long × 1 mm broad, with narrow apices and hardly thinner margins, subpetaloid, usually sparsely strigillose towards the apex, sometimes almost glabrous. Androecium apparently reddish or purplish, 3-4-seriate, the outer whorl comprising 4 stamens, the inner whorls staminodes; stamens upright hardly recurved, 1$\frac{1}{3}$ mm long × $\frac{1}{2}$ - $\frac{2}{3}$ mm broad × ± $\frac{1}{3}$ mm thick; filaments $\frac{1}{3}$ - $\frac{1}{2}$ mm long × ± $\frac{1}{2}$ mm broad × ± $\frac{1}{3}$ mm thick; staminal glands hardly divergent, thick, cupular, obtuse, $\frac{1}{3}$ - $\frac{1}{2}$ mm long, protruding conspicuously from the abaxial face of the stamen; anthers rostrate, the rostrum dorsiventrally compressed, linguiform, hardly broadened, rather obtuse, $\frac{1}{2}$ mm long × $\frac{1}{3}$ mm broad, the pollen sacs with markedly extrorse dehiscence, $\frac{1}{3}$ - $\frac{1}{2}$ mm long; staminodes ± upright, lanceate-deltoid to lanceate, $\frac{2}{3}$ - 1$\frac{1}{3}$ mm long × $\frac{1}{4}$ - $\frac{1}{3}$ mm broad, obtuse to acute, the outer staminodes without vestiges of staminal glands. Gynoecium of ca 10 carpels; styles exserted $\frac{1}{3}$ - $\frac{1}{2}$ mm beyond hypanthium rim in a slender column ± $\frac{1}{3}$ mm wide; stigmatic column short, acutely conical, $\frac{1}{4}$ - $\frac{1}{3}$ mm long, sunk below apices of inner staminodes.

Ripe infructescences (2$\frac{1}{2}$-)3-3$\frac{1}{2}$(-4) cm long, generally glabrous. Primary peduncles ($\frac{2}{3}$ -)$\frac{3}{4}$-1$\frac{1}{2}$(-2) cm long × 1-1$\frac{1}{2}$ mm thick, of the same form and colour as in inflorescence; pedicels (4-)5-7(-8) mm long × 1-$1\frac{1}{2}$ mm thick. Fruiting hypanthium slenderly cylindrical-ellipsoid, sometimes narrowed into an obscure neck, 11-22(-24) mm long × 4-7 mm thick, levigate, often striate when immature, drying blackish, lignified, with walls 1-$1\frac{1}{2}$(-$1\frac{3}{4}$) mm thick, dehiscing regularly into 2, rarely 4, equal valves; rim $\frac{2}{3}$ - $\frac{3}{4}$ mm broad, relatively levigate, with inner staminodes ± persistent; hypanthium chamber sparsely pale stramineous to off-white strigillose-hispidulous towards the rim, more densely, longer, somewhat silkier, fawn hirsute towards the base, particularly about the rims of the nutlet pits. Nutlets elongating in maturing hypanthium to maintain the exsertion of the style tips up to $\frac{1}{2}$ mm beyond the hypanthium rim; bodies of ripe nutlets narrowly ellipsoidal or almost fusiform, 3-5 mm long × ($\frac{3}{4}$-)1 mm thick, pale fawn silky hirsute, the hairs (6-)7-10 mm long; styles of ripe nutlets (3-)5-10(-12) mm long.

Seedlings unknown.

The epithet <u>trachyphloia</u> is derived from φλοιος , bark, and τραχμς rough, and alludes to the characteristically rough brown bark of this species.

Vernacular names: Ladei (local wood and timber cutters, Mt. Molloy area, North Queensland). The name has been taken from Podocarpus ladei, by mistake.

Series of specimens examined: 5 collections, comprising 1 with inflorescence buds, 2 with flower buds, 1 with open flowers, 3 with near or fully mature fruiting hypanthia, and 2 of coppice leaves. The collections of C.T.White 10689, A.G.Hanson 51/62, and E. Volck 54/89 cited by L.S. Smith (1958) were unavailable for comparison.

Geographic Distribution (map 5)

Dryadodaphne trachyphloia is so far known only from the Mt.Lewis-Mt.Spurgeon range, between Mt. Molloy and Mossman, north-east Queensland, 16°25′- 16°35′S:

Churchill creek; Bushy creek logging area; near Mt. Molloy.

Ecology (figure 52)

Dryadodaphne trachyphloia occurs sparingly as a mature tree of the forest canopy in creek beds and swampy sites at the foot of gullies in primary mountain rainforest of mixed tree species at altitudes between 600 and 1000 m. Its confinement in few numbers to such everwet sites is striking, both in the forest of the area, and in comparison with the habitat preferences of the New Guinea species of the genus. Coupled with a lack of seedlings and saplings observed in the forest on Mt. Lewis, it gives the impression that the species is surviving in the refuge of everwet gullies under an otherwise unfavourable environment.

Phenology

Present information, even when data from the above examined collections are combined with those given by L.S.Smith (1958), is insufficient to define flowering and fruiting cycles. Flowering specimens have been collected in April and May, and specimens with submature fruit only in late August.

Infraspecific Variation

Although the series studied is too small to permit a reliable assessment of variability, it does indicate some variation in the shapes and breadths of canopy leaves from tree to tree. Leaf shapes range from linear-lanceate and $\frac{3}{4}$-1$\frac{3}{4}$(-2) cm broad in Hanson:

CANB 30809 to broad lanceate or elliptic and 2-2½ cm broad in Schodde 3340, 3352. L.S.Smith (1958) has already drawn attention to the narrowness of the leaves.

Chemistry

According to Bick, Douglas, and Taylor (unpubl., Bick, pers. comm.), the major alkaloid extracted from samples of bark of this species (voucher: Webb 5313) has been identified as dryadine, of the bisbenzylisoquinoline type.

Uses

The timber of the species is used locally in the Mt.Molloy area in the construction of buildings. It has the characteristics of brittleness and of warping during seasoning.

(Page 253 follows)

XI. NEMUARON Baill.

Nemuaron Baill., Adansonia 10(1873)351; Benth. in B. & H., Gen. Pl. 3(1880)138,139,145; Hobein, Bot.Jb. 10(1888)52; Pax, Pflzfm. 3,2(1889)97,102; Baill., Dict.Bot. 3(1891)423; Perk., Bot.Jb. 25(1898)551; Perk. & Gilg, Pflzr. 4(1901)4,14,73; Schltr., Bot.Jb. 39(1906)106; Perk., Gattung.Monim. (1925)6, 15,47; Hutchinson, Fam.Fl.Pl. (1926)89, map "Nemualon"; Willis, Dict.Fl.Pl.Ferns ed.6,(1931)446; Lemée, Dict.gen.phan. 4(1932)673; Garratt, Trop.Woods 39(1934)21,23; Berry, Bot. Gaz. 96(1935) f.1,n.16 p.p.; Berry, Geol.Soc.Amer.spec.pap. 12(1938)f.2,n.16 p.p.; Guillaum., Fl.Anal.Synopt.Nouv.-Calédonie(Phan.)(1948)122; Money, Bailey, & Swamy, J.Arn. Arbor. 31(1950)381 et seq.; Croizat, Man.Phytogeogr. (1952)281, f.V.16 p.p.; Stern, Amer.J.Bot. 42(1955)881; Hutchinson, Fam. Fl.Pl. ed.2,1(1959)136, map "Nemualon"; Hutchinson, Gen.Fl.Pl. 1(1964)120; Müller-Stoll & Mädel, Trans.Geol.Soc.S.Africa 65(1962)f.6 p.p.; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7, (1966)764; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342.

TYPE SPECIES: Nemuaron vieillardii (Baill.)Baill., lectotype (Hutchinson 1964).

Doryphora? auct. [non Endl.]: Baill., Adansonia 9(1868)128, (1869)129,134 p.p.; Baill., Hist.Pl. 1(1869)317,335 p.p.; [Baill., Adansonia 10(1873)350 p.p. pro syn. Nemuaron].

Atherosperma auct. [non Labill.]: Baill., Hist.Pl. 1(1869)343 p.p.?

Figures 1D, 28, 45B.

Medium-sized bisexual trees, with spreading, somewhat corymbiform crowns; bark strongly aromatic, the odour weak in stems and leaves; secondary xylem vessels predominantly solitary or up to 10% in radial multiples of 2-3(-4), ca 50-100 per sq. mm, inner tangential diameter (40-)60-90(-130) μ, the perforation plates and vessel-ray pitting exclusively scalariform; fibres relatively thick-walled, outer tangential diameter (20-)25-40(-50) μ, varying from thinner-walled fibre tracheids with bordered pits rather distinctly bordered in early wood to predominantly libriform wood fibres with occasional septae in late wood; multiseriate rays (0.2-)0.35-0.55(-0.8) mm high × (2-)3(-4) cells wide, acicular crystals present in procumbent cells or absent, oil cells absent; ultimate branchlet stems often angular tegragonous, usually glabrescent; petioles shallowly sulcate, rarely planate; leaf blades microphyllous to small notophyllous, with margins shallowly undulate-crenate to almost entire, midribs sulcate on upper face, 2-3-layered hypodermis present on upper face*

Inflorescence buds broadly compressed, stipitate before expansion; mature inflorescences slenderly thyrsiform, with 3-5(-9) flowers; accessory axillary flowers absent; bracts small, ± isomorphic, 2-3 mm long ×

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*Cf. Hobein 1888, Perkins 1898, Money et al. 1950.

$1\frac{1}{2}$-2 mm broad, usually caducous in young bud; bracteoles present, herbaceous to tepaloid, usually borne on hypanthium and often contiguous and persistent with perianth, rarely subtending floral hypanthium and earlier caducous.

Flowers bisexual; perianth rotatiform, comprising usually an outer pair of tepaloid bracteoles, and 4-6 elliptic, obtuse, obscurely pinnate-palminerved tepals, $1\frac{1}{2}$-$3\frac{1}{2}$ mm long × 1-2 mm broad, in ± decussate arrangement; androecium 2-3-seriate, the outer whorl comprising (4-)6(-7) stamens, $1\frac{1}{4}$-$1\frac{3}{4}$ mm long × $\frac{2}{3}$ - 1 mm broad × $\frac{1}{4}$ - $\frac{1}{3}$ mm thick, with elliptic to ovate obtuse subpeltate staminal glands, and rounded truncate to obscurely apiculate, ± introrsely-dehiscing anthers, the inner whorls of 4-8 isomorphic batilliform staminodes, ($\frac{3}{4}$-)1-2 mm long; pollen grains ellipsoidal, rarely approaching spheroidal, oblate to suboblate, Lg (17-)22-26(-29) μ × long. Lt. (29-)31-38(-44) μ, the colpi transversales of regular to irregular length, (10-)15-20(-25) μ long, occasionally only one well developed and up to 25 μ long, the interstitial equatorial depressions narrow and variably extensive, the grain walls 1-2(-$2\frac{1}{2}$) μ thick, the surface sculpture with lumina relatively irregular in outline, ($\frac{1}{2}$-)$\frac{3}{4}$-$1\frac{1}{2}$ μ long; gynoecium of ± 5 carpels, the styles vestigial, sub-terminal, glabrous, the stigmatic column slenderly filamentous, sometimes branched; ovule ellipsoid, often acuminate at chalazal end, hemitropous on sub-marginal placenta.

Fruiting hypanthium globulose-pyriform, 6-8 mm long × 4-7 mm thick, levigate, glabrous or very sparsely haired, dehiscing into 2 or 4 equal valves; perianth and androecium eventually caducous; nutlets attached superficially to hypanthium wall, enveloped by hairs, the bodies reniform-hippocrepiform, incurved on median axis, the styles subterminal, vestigial, glabrous apicula.

The name *Nemuaron* is taken from "Nemuaro", the name given to *Nemuaron vieillardii* by the natives of New Caledonia (Baillon 1873).

Species, Geographic Distribution, and Ecology.

The genus *Nemuaron* is monotypic and endemic in New Caledonia, 20°30′-22°20′S.

It is confined to the ± subtropical rainforests of mountain ranges, where *N. vieillardii* is a relatively insignificant element of the forest vegetation.

Germination of seeds occurs freely in the leaf litter and soil of the forest floor (personal observations, and seedling saplings of *N. vieillardii*: Schodde 5248).

Details of phenology are given under *Nemuaron vieillardii*.

Generic Characters

Nemuaron is the least known of the genera of the Atherospermataceae. Although the herbarium material examined during the present study is far more extensive than that available to earlier investigators such as Baillon (1873), Bentham (1880), and Perkins and Gilg (1901), it comprised only 21 collections. A mere three of these (Balansa 3457, McKee 12800, 13429) had open flowers.

The genus is distinct from all others of the family in having perianth and androecium parts very similar to those of *Laurelia* in bisexual flowers, small globose-pyriform fruiting hypanthia with isomerous dehiscence, and carpels of extraordinary form and arrangement in both flower and fruit. In particular, the up to 2 mm or more long filamentous stigmatic column (the long fragile style of Baillon l.c., Bentham l.c., Pax 1889, Perkins and Gilg l.c., Lemée 1932, and Hutchinson 1964) terminating the vestigial subterminal styles, and the reniform-hippocrepiform* nutlets disposed around the sides of the hypanthial chamber, are unique. Like Daphnandra it rarely grows to a tree in excess of 25 m high.

It seems remarkable that the earlier revisers divined correctly the peculiar construction and orientation of the ripe nutlets from the two rather scanty fruiting collections (Vieillard 1083, Balansa 1321) available to them**. Drying has made the fruiting hypanthia in these collections difficult to dissect, and many of the nutlets have been dislodged from their position on the hypanthium wall.

Three collections of fruits*** in various stages of maturity in both fresh condition and preserved fresh in ethanol were examined in the present study. These have revealed the complete series of transformations

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* Subhippocrepiform, according to Bentham (l.c.), and Perkins and Gilg (l.c.); campylotropous, according to Baillon (1868, 1869, 1891).

** It is evident from their descriptions and other published data that their information was drawn from the various publications of Baillon.

*** McKee 18097, Schodde 5247, 5249.

the nutlet undergoes before reaching maturity. After anthesis, the carpels gradually elongate into a narrowly ellipsoid-conical acute body ca 2 mm long, terminated by an acute apiculum, the vestigial style. They at this stage are hardly different from those in any other genus of the family, except for the long filamentous stigmas that protrude through the mouth of the hypanthium instead of the styles (f.7C). As the fruiting hypanthium begins to expand towards its mature globose shape and size, the nutlets thicken, become a little dorsiventrally compressed, lengthen to nearly 3 mm, and bend in the middle with the apex becoming incurved and the stylar apiculum remaining erect and curving upwards. By the time the fruiting hypanthium has matured, the incurved nutlets have become pressed further in the same direction into a reniform or hippocrepiform shape $2\frac{1}{4}$-$2\frac{3}{4}$ mm long × 3-$3\frac{1}{2}$ mm high. Salient stages are illustrated in figure 7.

The closely packed arrangement of the ripe nutlets in the mature fruiting hypanthium indicates that the form of the nutlets and of the globose hypanthia are functionally linked. The nutlets approach, in space, a sphere fitting better into the more-or-less spherical hypanthium chamber. The form of the fruiting hypanthium itself appears to have evolved through elimination of the "neck" region found in most other genera of the family. That little or none of this region is incorporated in the fruiting hypanthium of <u>Nemuaron</u> is indicated by the attachment of nutlets anywhere over the hypanthium chamber, as far up as just below the rim.

The placenta in <u>Nemuaron</u> is also rather different from that of other genera in the family in being sub-marginal rather than quite basal, as a result of which the ovule has a more-or-less hemitropous orientation. Partial concrescence of the funicle with the ovary wall has apparently brought about this position (also Money et al. 1950). Superficially, however, the attachment and orientation of the ovule gives the impression of being sub-pendant with a superior micropyle, and therefore more-or-less orthotropous. This has confused several earlier investigators, as detailed below.

Misleading Observations Published Previously

Seriously misleading and inaccurate observations that have been made about the flowering and fruiting structures of the genus are as follows: the flowers are quoted as being hermaphrodite or polygamous by Guillaumin (1948) whereas they are always bisexual; the receptacle (= hypanthium) is recorded as flat or slightly concave in the young flower by Perkins and Gilg (1901), Perkins (1925), Lemée (1932), and Money et al. (1950), whereas it is deeply poculiform and typical of the hypanthia found in all genera of the Laurelieae with bisexual flowers; the glands ("associated staminodes") of the fertile stamens have been described as basally connate to the sides of the stamen as in <u>Laurelia</u> and <u>Doryphora</u> by Money et al. (l.c.) whereas, though sub-peltate and similar in attachment to those of <u>Laurelia</u>, they are quite different in form and attachment from those in <u>Doryphora</u>; ∞ staminodes have been said to be present in each flower (Bentham 1880, Perkins and Gilg l.c., Perkins l.c., and Hutchinson 1964) whereas there are only 4-8 staminodes in 1-2 whorls; similarly, ∞ nutlets have been quoted per fruiting hypanthium (Baillon 1868, Perkins and

Gilg l.c.) whereas there are only 5 carpels in the flower, of which often only 2 or 3 mature into nutlets; the style of the mature carpels has been described as basal by Bentham (l.c.), Perkins and Gilg (l.c.), and Perkins (l.c.) whereas it is subterminal, a position which it retains in the nutlet; the ovule has been described variously as pendulous with a superior micropyle by Baillon (1873), Perkins and Gilg (l.c., p.73), and Perkins (l.c.,p.47), though also as erect by the latter two authors (l.c., pp.14 and 15 respectively), and as erect with a superior micropyle by Lemée (l.c.), whereas it is erect with an inferior micropyle; and the fruiting receptacle has been described as fleshy by Bentham (l.c.), Pax (l.c.), Baillon (1891), Perkins and Gilg (l.c.) in part, Perkins (l.c.) in part, Lemée (l.c.) in part, and Hutchinson (l.c.), whereas it becomes quite woody in the fruit, as in all genera of the family.

Affinities

Nothwithstanding the paucity of herbarium material then available, the genus was recognised and clearly defined very early in its taxonomic history by Baillon (1873), Bentham (1880), Pax (1889), Perkins and Gilg (1901), and Perkins (1925). Even its initial union with Doryphora by Baillon (1868),when describing the first species,was made with reservation on account of "cette singulière configuration des carpelles".

Nemuaron has relatively well-marked affinities with Dryadodaphne on one side and with Laurelia on the other, a relationship consistent with the geographic distribution of the three genera. It resembles Dryadodaphne, particularly D.pterandrica, in its general branching and leaf form, and in the other characters discussed in chapter X.

Its close relationship to *Laurelia* is indicated by its general perianth structure, including the ~~associated~~ position and texture of the associated bracteoles, by the form of its androecium, including the subpeltate staminal glands, deltoid apiculate-obtuse anthers, and batilliform staminodes, by its rather irregular fruiting hypanthium rim marked with scars and persistent staminode bases, by its aromatic bark, and by its its alkaloids which are principally of the aporphine type.

Evidence that *Nemuaron* is interposed between *Dryadodaphne* and *Laurelia* is provided by the following characters. The variable position and texture of its bracteoles on the flowering hypanthium suggest an intermediate stage in a trend from herbaceous bracteoles in flower-subtending position (*Dryadodaphne*) to tepaloid bracteoles contiguous with the perianth (*Laurelia*). The transitions involved are described in chapter IV.6. The arrangement of its perianth and androecium, in series of 4 to ± 6(3+3) parts, is also intermediate between the regularly tetramerous plan in *Dryadodaphne*, and irregularly hemicyclic or subspiral arrangement in *Laurelia*. Its subpeltate staminal glands and thickened clavate to batilliform staminodes, moreover, may be regarded as respectively transitional between the wing-like glands and narrowly deltoid to lanceate staminodes of *Dryadodaphne*, and the quite peltate glands and compressed batilliform staminodes of *Laurelia*.

Nemuaron resembles *Doryphora* among the other genera of the Laurelieae in two notable characters: stipitate inflorescence buds that are strongly compressed when young in a flat obcordiform shape typical of the large mature inflorescence buds of *Doryphora*, and subterminal though not basal styles. The unenlarged inflorescence buds of *Dryadodaphne* are also similar in structure, if not so strongly compressed obcordiform. On the other hand, the pair of bracts enclosing the inflorescence bud are very early caducous in both *Nemuaron* and *Dryadodaphne*, whereas they are more persistent in *Doryphora*. Reasons for the development of inflorescence bracts of variable size and persistence in the family have been suggested and discussed in chapter IV.6.

1. Nemuaron vieillardii (Baill.)Baill

Nemuaron vieillardii (Baill.)Baill., Adansonia 10(1873)351,353 "N.Vieillardi"; Perk. & Gilg, Pflzr. 4(1901)73,74, f.20B; Guillaum., Ann.Mus.Marseilles 19(1911)8; Perk., Gattung. Monim. (1925)f.36B; Guillaum., Fl.Anal.Synopt.Nouv.-Calédonie (Phan.) (1948)123.

Doryphora vieillardii Baill., Adansonia 9(1868)128 "Doryphora? Vieillardi"; Baill., Hist.Pl. 1(1869)317 "D.? Vieillardi"; [Baill., Adansonia 10(1873)350,353 "Doryphora? Vieillardi" pro syn. Nemuaron vieillardii].

TYPE: Vieillard 1083, montagne Kanalo [= Canala] —— holotype in P, isotype in P.

Nemuaron humboldtii Baill., Adansonia 10(1873)354; Perk., Bot. Jb. 25(1898)551; Perk. & Gilg, Pflzr. 4(1901)73,74, f.20A; Guillaum., Ann.Mus.Marseilles 19(1911)8 "Nemearon Humboldtii"; Perk., Gattung.Monim. (1925)f.36A; Guillaum., Fl.Anal.Synopt.Nouv.-Calédonie (Phan.) (1948)123; Guillaum., Mém.Mus.Hist.Nat.Par. n.ser.B, 8(1957?)233.

TYPE: Balansa 1689,[Mont-Humbold] [Mt.Humboldt]——— holotype in P, isotype in A.

Figures 7, 28, 45B.

Diagnosis

See description of genus.

Detailed Description

Shrubs to usually medium-sized trees (2-)4-18(-25) m high; bole ca 15-40(-45) cm diameter breast height, ± unbuttressed, rarely coppicing; crown spreading, ± rounded corymbiform, usually short, ca. $\frac{1}{4}$ - $\frac{1}{3}$ × length of bole, with branches horizontal-ascending, and leaves ± erect on ultimate branchlets. Bark (3-)5-10 mm thick when dry, outer surface rather smooth, finely pustuled and fissured, pale brownish grey, inside pale brownish cream or pale buff-brown, drying the same colour. Wood pale brownish or yellowish cream, drying pale greyish cream or off-white, growth rings obscure. Branchlet stems ± densely, rarely openly branched, the ultimate 4-6 internodes ($\frac{3}{4}$-)1-4(-7) cm long × 1-2$\frac{1}{2}$(-3) mm thick, compressed, often ± angular tetragonous, smooth on ultimate 2-3 internodes, becoming striately wrinkled or obscurely costate, rarely pustuled below, drying blackish, less often dark grey, fawn-grey, or olive-brown, glabrous or glabrescent, with shoots and sometimes ultimate 1-2(-3) internodes sparsely to rather densely sordid stramineous to pale greyish hispidulous-strigillose, the branchlet nodes on leader stems slightly to sometimes strikingly swollen, 3-15 mm broad, smooth; shaded and sapling branchlet stems with ultimate 4-6 internodes 3-6(-8) cm long, similarly compressed. Vegetative buds narrowly conical, the enveloping pair of bract-like leaves invariably uniformly and rather densely grey-white to sordid golden strigillose, with suberect glabrous mucronate apices, expanding when buds ca 5 mm long. Petioles (3-)4-8(-10) mm long × (½-)¾-2 mm thick, shallowly impressed, infrequently planate on upper face, drying blackish, glabrous or often sparsely sordid stramineous strigillose. Leaf blades obovate or rounded cuneate, elliptic, rarely oblanceate, (1½-)2-9 cm long × (¾-)1-4(-4½) cm broad, broadly to sometimes attenuately cuneate at the base, broadly, infrequently narrowly obtuse, often retuse at the apex; margins shallowly and finely, or obscurely crenate, to faintly undulate almost entire, slightly to often markedly recurved, almost revolute towards the petiole; texture thinly to quite coriaceous, rarely almost chartaceous, the upper face rather smooth, often lined with prominulous lateral nerves anastomosing towards margins of blade; colour slightly glossy mid to dark green on upper face, duller and paler on lower, in dry leaves pale greyish to blackish olive on upper face, browner on lower; nervation on upper face as described, with midrib shallowly to deeply impressed, on lower with midrib conspicuously prominent, and (2-)6-9(-11) rather obscurely prominulous main nerves anastomosing towards margins of blade, the vein reticulum spare, often obscurely intramarginal, extending towards the midrib; glabrous or glabrescent and sparsely sordid strigose towards base of midrib, less often blade, on lower face of young leaves; leaf blades on shaded and sapling branchlets more elliptic, 4-8(-9) cm long × 2-4(-4½) cm broad, with more narrowly obtuse apices and more deeply crenulate, planate margins, thinly coriaceous to ± chartaceous, nerves and intramarginal reticulum more prominent on both faces. Bark persistently aromatic with safrol-like odour, the odour weaker in stems and leaves, evanescing in these parts when dried, ± absent in wood.

Inflorescence buds relatively broadly compressed, narrowly obcordiform, initially subsessile and complanate with stem when 1-2 mm long, the enveloping pair of bracts lanceate-navicular to ovate cymbiform, sparsely to densely pale stramineous strigillose, ultimately 2-2½(-3) mm long, with slightly diverging apices; buds subsequently elongating through the development of a compressed stipe (= base internode of primary peduncle of mature inflorescence) up to 2-3 mm long below the bracts which later diverge gradually to allow expansion of the ultimate inflorescence axes and flower buds. Mature inflorescences ± decurved, ± congested at ultimate 1-3(-4) leaf nodes among leaves, slenderly thyrsiform, (1¼-)1½-2½ (-3½) cm long, sparingly off-white to sordid stramineous strigillose, bearing 3-5(-9) flowers, the terminally central flower or solitary flowers at subterminal nodes opening first. Primary peduncles (⅓ -)¾-1¼(-1½) cm long × 1-1½ mm thick, rather broadly compressed or the distal internodes often tegragonous, ± smooth to finely costate, drying brownish black, sparsely to rather densely off-white to sordid stramineous strigillose, 1-2(-3)-noded, the subterminal nodes usually bearing solitary opposite flowers, rarely simple dichasia on secondary peduncles; bracts herbaceous, deltate navicular to ovate cymbiform, 2-3 mm long × $1\frac{1}{2}$-2 mm broad, with mucronate apices, variably strigillose abaxially, ± glabrous adaxially, ± caducous before anthesis; secondary peduncles ca 4 mm long × ca $\frac{3}{4}$ mm thick, similar in form to primary peduncle, perhaps more densely strigillose; pedicels (1-)2-4(-6) mm long × $<$ 1 mm thick, longest in terminally central or subterminal solitary flowers, terete to slightly tetragonous, not or hardly expanded under hypanthium, drying dark brownish black, often more densely off-white to sordid stramineous strigillose than peduncles, infrequently bracteolate with bracteoles subjacent to or subtending the hypanthium and caducous with bracts. Mature flower buds obtusely obovoid-clavate, 2-$3\frac{1}{2}$ mm long × $2\frac{1}{2}$-3 mm ~~broad~~ thick, sparingly sordid grey-white strigillose, the hairs longest and densest on the hypanthium and bracteoles, the bracteoles usually attached towards hypanthium rim, valvate, incompletely enclosing tepals, sometimes absent.

Open flowers small. Hypanthium poculiform, $\frac{1}{2}$-$1\frac{1}{2}$ mm long × 1 mm thick, sparsely to rather densely grey-white or sordid stramineous strigillose, bearing a pair of subtepaloid bracteoles usually towards the rim, infrequently towards the base; rim flat to slightly convex, $\frac{1}{2}$-$\frac{3}{4}$ mm broad, rather densely stramineous to off-white hispid. Perianth whitish green, 2-4-seriate in ± decussate arrangement, the outer whorl comprising usually a pair of subtepaloid bracteoles, the inner whorls 4-6 sepaloid to petaloid ± isomorphic tepals; bracteoles ovate-circular, $1\frac{3}{4}$-3 mm long ×

1-2 mm broad, with broadly obtuse mucronulate apices and entire or fimbriolate margins, herbaceous to subpetaloid, finely carinate, glabrous, or variably densely strigillose abaxially with hairs concentrated on midrib, persistent with tepals; tepals broadly to oblong elliptic, $1\frac{1}{2}$-$3\frac{1}{2}$ mm long × 1-2 mm broad, with broadly obtuse apices, and hardly thinner, entire, often undulate margins, sepaloid to petaloid, obscurely 1 or 3(or 5)-nerved, generally sparsely sordid grey-white strigillose, the hairs denser or absent adaxially, the inner tepals often slightly narrower, shorter, more petaloid, and more densely haired adaxially than the outer. Androecium* 2-3-seriate, the outer whorl comprising (4-)6(-7) stamens, rarely fewer by abortion, the inner whorl(s) 4-8 staminodes with usually 3-4 staminodes in each; stamens incurving erect, $1\frac{1}{4}$-$1\frac{3}{4}$ mm long × $\frac{2}{3}$ - 1 mm broad × $\frac{1}{4}$ - $\frac{1}{3}$ mm thick; filaments broad, rounded to dorsiventrally compressed, $\frac{2}{3}$ - 1 mm long × $\frac{1}{2}$ - $\frac{2}{3}$ mm broad, sparsely to ± densely strigillose abaxially, often glabrous adaxially; staminal glands elliptic to ovate, subpeltate, obscurely stipitate, $\frac{1}{2}$ - $\frac{2}{3}$ mm long × $\frac{1}{2}$ mm broad, attached along the sides of the filament and overlapping its adaxial face; anthers narrowly conical-cylindrical, incurved, $\frac{2}{3}$ - 1 mm long × $\frac{1}{2}$ - $\frac{3}{4}$ mm broad, with narrowly rounded truncate to obscurely apiculate apices, and ± introrsely-dehiscing narrowly elliptic valves, glabrous; staminodes slightly incurving, narrowly clavate and expanded abaxially towards the apex, or dorsiventrally compressed batilliform, ($\frac{3}{4}$-)1-2 mm long × $\frac{1}{3}$ - $\frac{2}{3}$ mm broad,

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* Colour in life unrecorded.

obtuse, sparsely to densely strigillose abaxially, sparsely strigillose to glabrous adaxially, without vestiges of staminal glands. Gynoecium of ± 5 carpels; styles vestigial, subterminal, enclosed entirely within hypanthium chamber or exserted as far as hypanthium rim; stigmatic column slenderly filamentous, sometimes branched, 1-2 mm long, exserted to near apices of staminodes or beyond.

Ripe infructescences borne at ultimate 1-4 leaf nodes among leaves on branchlets, (1-)$1\frac{1}{2}$-$2\frac{1}{2}$(-3) cm long, sparsely sordid stramineous strigillose, with 1-3(-4) hypanthia maturing per infructescence. Primary peduncles $\frac{1}{3}$ - 2 cm long × 1-2 mm thick, of the same form and colour as in inflorescence, but more sparingly strigillose almost glabrescent; pedicels 2-7 mm long × $\frac{1}{2}$-$1\frac{1}{4}$ mm thick, of the same form as in inflorescence, more sparsely strigillose. Fruiting hypanthium globulose-pyriform, 6-8 mm long × 4-7 mm thick, levigate, mid green, drying grey-brown, lignified, with walls (1-)$1\frac{1}{4}$-$1\frac{3}{4}$ mm thick, dehiscing lengthwise from the rim in 2 or 4 equal valves; rim scarred, irregular, and hispid, with staminode bases, rarely entire staminodes, persistent; hypanthium chamber spherical, uniformly sparsely pale fawn silky hirsute, with nutlets attached to the sides and base. Nutlets entirely enclosed within hypanthium chamber, 2-3(-5) maturing; bodies of ripe nutlets decurved, ultimately compressed reniform-hippocrepiform, $2\frac{1}{2}$-$2\frac{3}{4}$ mm long × 3-$3\frac{1}{2}$ mm high × 1-$1\frac{1}{2}$ mm thick, enveloped by sparse straight to curling, sordid golden-fawn or cinnamon, silky hirsute hairs, 5-10 mm long that are usually denser on the sides of and sparse or ±absent on abaxial and adaxial faces of the nutlets; styles of ripe nutlets subterminal, vestigial, persisting as fine glabrous apicula; endosperm strongly aromatic, with a safrol-like odour.

15-25-noded young plants ca 30-50 cm high, the ultimate 4-6 internodes broadly rounded compressed, hardly tetragonous, ($1\frac{1}{2}$-)2-4(-7) cm long × 1-5 mm thick on leader stems and 1-2 mm thick on lateral stems, smoothly striate, drying olive-brown to blackish, glabrous or glabrescent, the nodes on leader stems broadly compressed, 3-10 mm broad, smooth; cotyledons caducous; subsequent leaf pairs with petioles impressed on upper face, (5-)6-8(-10) mm long × $\frac{2}{3}$ - 1 mm thick, glabrous, rarely very sparsely strigillose, and leaf blades narrowly to broadly elliptic, 6-8(-9) cm long × $1\frac{3}{4}$-3(-4) cm broad, with cuneate bases, shortly acuminate mucronulate obtuse apices, closely crenulate (sub-)planate margins, chartaceous texture, glossy mid green colour, narrowly impressed midrib on upper face, 8-11 prominulous main nerves and intramarginal vein reticulum on both faces, glabrous or the midrib sparsely stramineous strigose on the lower face.

The epithet vieillardii commemorates E.Vieillard, a surgeon in the French navy who collected plants on New Caledonia at times between 1855 and 1867, including the first of this species.

Melanesian names: Nemuaro (natives of New Caledonia —— Baillon 1873, 1891, Perkins and Gilg 1901).

Vernacular names: Bois pernod (McKee 12800, field officers of the Service Forestier, New Caledonia (pers. comm.)).

Series of specimens examined: 21 collections, comprising 4 with inflorescence buds, 3 with flower buds, 3 with open flowers, 5 with young or hardly expanded fruiting hypanthia, 4 with near or fully mature fruiting hypanthia, and 1 of young plants.

Geographic Distribution (map 6)

Nemuaron vieillardii occurs throughout the mountains of New Caledonia, $20^{o}30'$- $22^{o}20'$S:

Mt. Colnett; Col des Rousettes; Katrikoin, Hte.Boghen; Table Unio; Dogny; Sentier Ciu-Koinde; mountains near Canala; Mont Humboldt; Mois de mai; Mont Mi*.

Ecology (figure 53)

Widespread and locally rather frequent, Nemuaron vieillardii is usually sub-canopy tree or shrub in montane rainforest between the altitudes of (300-)400-1300 m. Like many other members of the family, it appears to prefer the damp sheltered heads and sides of small gullies and defiles, as at Table Unio (personal observation). There it was recorded most frequently between the altitudes of 700 and 900 m. McKee (n.12800) also found it common towards the altitude of 800 m in the region of Bourail. This might suggest that the altitudinal range of 700-900 m is optimal for the occurrence of the species at the present time.

It has been recorded growing on gneissic soil at Mt.Colnett by

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* Location not known.

Hürlimann (n.1970), on serpentine at Mois de mai by Baumann-Bodenheim (n.15129), and on limestone at Table Unio by McKee (n.13429), thus indicating that it is not confined to a particular soil type and is tolerant of a wide range of soil pH.

It is still little known and collected.

Phenology

The available collections and published records, even though scanty, indicate that flowering in Nemuaron vieillardii occurs in the austral winter and spring months (May-September), and that the fruiting hypanthia mature and disseminate nutlets in mid and late summer months (December-March). Inflorescence buds for the ensuing flowering season begin to appear between August and September or later, while the fruiting hypanthia are still enlarging; they reach maturity by March to May.

There does not appear to be a close relationship between the flowering cycle and seasonal fluctuations in temperature, which are slight, or rainfall, which is heaviest between December and March. The cycle may, however, be controlled by day length responses as discussed in chapter III.

There also seems to be a time lag in flowering and fruiting in trees at higher altitudes. Trees from Katrikoin and Sentier Ciu-Koinde at 400-500 m have been recorded in open flower in June (McKee 12800), and in almost mature fruit in early December (McKee 18097). Others from Table Unio between 750 and 900 m altitude are in advanced flower bud and open flower in September (McKee 13429), and at the corresponding fruiting stage in mid January (Schodde 5247). A tree at 850 m on Table Unio (Schodde 5249), however, had slightly more advanced fruit on the same date.

Infraspecific Variation

The two species, N. vieillardii and N. humboldtii, described in the genus have been based on variations of leaf (and tree) size. The variation is correlated with altitude, higher altitude forms being smaller in tree size, with smaller but often thinner leaves. [The same variation correlation is found in Dryadodaphne.] Lower altitude forms are represented by trees ± 15(-25) m high (Robbins: CANB, from 480 m s.m.), with rather thickly coriaceous obovate-elliptic leaves up to 7-10 cm long x $3\frac{1}{2}$-$4\frac{1}{2}$ cm broad (Balansa 1321).* The extreme high altitude forms are represented by shrubs 2-5 m high, with coriaceous obovate-rounded cuneate leaves 2-4 cm long x 1-2 cm broad (Balansa 1689, from 1300 m, type of N.humboldtii).

In the small series of herbarium material seen, the extreme forms are nevertheless linked by a rather complete range of intermediates. The type collection of N. vieillardii, from mountains near Canala, is an example: it has rather thickly coriaceous obovate leaves $2\frac{1}{2}$-5 cm long. A rather absurd aspect of this is that if the type of N. vieillardii were determined according to the key characters of the two species of

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* It is assumed that the site of collection of Balansa 1321 on Mont Mi is at a relatively low altitude.

Nemuaron stated by Perkins and Gilg (1901), Guillaumin (1948), and to an extent Baillon (1873), it would be identified as *N. humboldtii*.

Taxonomic Notes and Typification

Because of the above-described continuity in the range of variability in leaf size, and the absence of any other discontinuity of variation in available material, *N. humboldtii* is here united with *N. vieillardii*.

There are two sheets of the type collection of *N. vieillardii* in herb. P. That bearing a sketch of a dissection of a nutlet and the annotation "*Doryphora? Vieillardi* H.Bn." in what is presumed to be Baillon's hand, is considered to be the holotype. The sheet of the type collection of *N. humboldtii* in P, annotated "*Nemuaron Humboldtii* H.Bn." in the same hand, is also considered to be the holotype of that name.

Chemistry

According to I.R.C.Bick (pers.comm.), the principal alkaloids of *Nemuaron vieillardii* are of the aporphine type. The species also contains a yellow alkaloid, of a type related to the aporphines, which has been isolated as a minor alkaloid of *Dryadodaphne pterandrica* and in very small amounts from *Atherosperma moschatum*.

Uses

Baillon (1873, 1891) records that the bark possesses a powerful stimulant that is used as a digestive and stomachic by the natives of New Caledonia. He mentions (1873), inter alia, that the taste of the bark is hot, "très-intense quand on la mâche".

XII. LAURELIA Juss.

Laurelia Juss., Ann.Mus.Hist.Nat.Par. 14(1809)134 [nom.cons.: nom. nov. pro *Pavonia* Ruiz]; Poir. in Lam., Encyc.meth.Bot. suppl.3, (1813)313; [R.Br. in Flinders, Voy.Terr.Austral. (1814)554 pro syn. *Pavoniae* Ruiz]; Spreng., Syst.Veg. 2(1825)470; Endl., Gen.Pl. suppl.1,(1841)1378; A.Cunn., Ann.Nat.Hist. 1(1838)380; Endl., Enchir.Bot. (1841)195,196; Meisn., Pl.vasc.gen. 1(1841) 324, 2(1841) 236; Rchb., Nomencl. (Herb.buch) (1841)69; J.B. Muell., Bot.Wörterb. (1841)246; Endl., Gen.Pl. suppl.2,(1842)35, suppl.4,2(1847,8)56; Schnizlein, Icon. 2(1849)n.105; Gay, Fl. chil. 5(1851 or 1852)353; Hook.f., Fl.N.Zel. 1(1853)218; Lindl., Veg.Kingd. ed.3,(1853)300; [Hook.f., Fl.Tasm. 1(1855)11 pro syn. *Atherospermatis*]; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)276,283, 290,414; C.Muell.in Walp., Ann.Bot. 4(1857)115; F.Muell., Pl. Colon.Vict. 1(1860)24; A.DC., Prod. 16,2(1868)642,674 p.p.; Baill., Adansonia 9(1868)116,122; Benth. in B. & H., Gen.Pl. 3(1880)139,145 p.p.; F.Phil., Cat.Pl.Vasc.Chil. (1881)265 p.p.; Hobein, Bot.Jb. 10(1888)55,71,73 p.p.; Kirk, For.Fl.N.Zeal. (1889)130; Pax, Pflzfm. 3,2(1889)95,97,102 p.p.; Bancroft, Proc.Linn.Soc.N.S.Wales 2,4(1890)1061; Perk., Bot.Jb. 25(1898) 552; Solereder, Syst.Anat.Dicot. (1899) [transl.Boodle, Fritsch, & Scott, 2(1908)699 et seq.]; Perk. & Gilg, Pflzr. 4(1901)7,8,10,11,14,76 p.p.; Cheesem., Man.N.Zeal.Fl. (1906) 599,600; Laing & Blackwell, Pl.N.Zeal. (1906)174; Dusén, Wiss.

ergeb.Schwed.Südpolar-exped. 3,3(1908)4 p.p.?; Stapf, Curtis Bot.Mag. 135(1909)t.8279 p.p.; Perk., Pflzr. 49(1911)46 p.p.; Petrie, Proc.Linn.Soc.N.S.Wales 37(1912)152; Skottsberg, Kungl. Sv.Vet.Akad.Handl. 56(1916)33 et seq. p.p.; Cheesem., Man.N. Zeal.Fl. ed.2,(1925)457,458; Perk., Gattung.Monim. (1925)9,10, 11,12,13,15,51 p.p.; Hutchinson, Fam.Fl.Pl. (1926)89,90; Allan, N.Zeal.Trees & Shrubs (1928)168; Berry, Proc.U.S.Nat. Mus. 73,22(1928)21,22; Lemée, Dict.gen.phan. 3(1931)970; Willis, Dict.Fl.Pl.Ferns ed.6,(1931)365,429; Garratt, Trop. Woods 39(1934)20 et seq. p.p.; Berry, Bot.Gaz. 96(1935)751 et seq., f.1.p.p.; Berry, Geol.Soc.Amer.spec.pap. 12(1938)5,16,23, 34 et seq., 75 et seq, f.2 p.p.; Cranwell, Rec.Auckl.Inst.Mus. 2(1942)291,293; Henry, Pl.Alkaloids ed.4,(1949)322; Metcalfe & Chalk, Anat.Dicot. 2(1950)1139 et seq.p.p.?; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)381 et seq. p.p.; Lawrence, Taxon Vasc.Pl. (1951)511 p.p.?; Croizat, Man.Phytogeogr. (1952) 18,281 et seq., f.5; Couper, N.Zeal.Geol.Surv.Bull. 22(1953)40; Core, Plant Taxon. (1955)318 p.p.; Stern, Amer.J.Bot. 42(1955) 874; Oliver, Svensk. Bot.Tidsk. 49(1955)15; Schmithüsen in Schmithüsen, Klapp, & Schwabe, Bonner Geogr.Abh. 17(1957)72; Bick, Clezy, & Crow, Austral.J.Chem. 9(1956)111; Cockayne, Veg. N.Zeal. ed.3,(1958)130,176,412,413 p.p.; Hutchinson, Fam.Fl.Pl. ed.2,1(1959)136, map; Muñoz-Pizarro, Sinops,fl.chil. (1959)155 p.p.; Zimmermann, Phylog.Pflanzen ed.2,(1959)609; Croizat, Principia Botanica 1A(1960)379; Couper, N.Zeal.Geogr.Surv. Paleont.Bull. 32(1960)31,47; Godley, Proc.Roy.Soc.Lond.B, 152(1960)459,463 p.p.; Skottsberg, ibid.p.450 p.p.; Oberdorfer, Pflzsoziol.Stud.Chile (1960)80 et seq.p.p.; Allan, Fl.N.Zeal.1 (1961)124,138,139; Müller-Stoll & Mädel, Trans.Geol.Soc.S. Africa 65(1962)f.6.; Fleming in Gressitt, Pacif.Basin Biogeogr. (1963)372,f.2; Poole & Adams, Trees & Shrubs N.Zeal. (1963)44; Buchheim in Melchior, Syllab.Pflzfm. ed.12,2(1964)122 p.p.; Good, Geogr.Fl.Pl. ed.3(1964)443; Hutchinson, Gen.Fl.Pl. 1(1964)111,112,120 p.p.; Cavaco, Webbia 19(1965)589,591, map; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7,(1966)623; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342; Wall & Allan, Bot.Names N.Zeal.Fl. (s.d.)48.

TYPE SPECIES: *Laurelia aromatica* Poir. [≡ *Laurelia sempervirens* (Ruiz & Pav.)Tul.] (typ.cons.).

Pavonia Ruiz in Ruiz & Pav., Fl.Per. & Chil.Prod. (1794)127,f.28, [nom.illeg.] [non Cav. 1786 nec Lam. 1792? [n.v.] vel Poir. in Lam. 1806], (1797)115, f.28 [n.v.]; Ruiz & Pav., Syst.Fl.per. & chil. 1(1798)253; Poir.in Lam., Encyc.meth.Bot. 8(1808)817; [Juss., Ann.Mus.Hist.Nat.Par. 14(1809)119 et seq. pro syn. *Laureliae*]; [Mol., Sagg.Chile ed.2,(1810)163,297 pro syn. *Theygae*]; R.Br. in Flinders, Voy.Terr.Austral. (1814)553; Lindl., Intr.Nat.Syst.Bot. (1830)29; Endl., Gen.Pl. (1837)315; [Hook. f., Fl.Tasm. 1(1855)11 pro syn. *Atherospermatis*]; O.Kuntze, Rev.Gen. 2(1891)568.

TYPE SPECIES: Pavonia sempervirens Ruiz & Pav., only species [≡ Laurelia sempervirens (Ruiz & Pav.)Tul.].

Theyga Mol., Sagg.Chile ed.2,(1810)163 [Thiga Mol., ibid.p.297, orth.var.]; [Spreng., Syst.Veg. 2(1825)470 "Thiga" pro syn. Laureliae]; [Endl., Gen.Pl. (1837)315 "Thiga" pro syn. Pavoniae Ruiz]; [Hook.f., Fl.Tasm. 1(1855)11 "Thiga" pro syn. Atherospermatis].

TYPE SPECIES: Theyga chilensis Mol., only species [≡ Laurelia sempervirens (Ruiz & Pav.)Tul.].

Atherosperma auctt. [non Labill.]: Hook.f., Fl.Tasm. 1(1855)11 p.p.; id., Handb.N.Zeal.Fl. 1(1864)240 p.p.; Bail., Adansonia 9(1869)134 p.p.; Baill., Hist.Pl. 1(1869)321,325,329,343 p.p.; Benth., Fl.Austral. 5(1870)284 p.p.; Baill., Dict.Bot. 1(1877) 310 p.p.; F.Muell., Nat.Pl.Vict. 1(1879)21 p.p.; Baill., Dict. Bot. 3(1891)206 p.p.; F.M.Bail., Queensl.Fl. 4(1901)1294 p.p.; Audas, The Australian Bushland (1950)92 p.p.

Atherosperma sect. Laurelia (Juss.)Baill., Adansonia 9(1868)116, 127; id., Hist.Pl. 1(1869)323; id., Dict.Bot. 3(1891)206, 521.

TYPE SPECIES: Atherosperma sempervirens (Ruiz & Pav.)Baill., only species [≡ Laurelia sempervirens (Ruiz & Pav.)Tul.].

Figures 1E, 29, 30, 45C, D.

Medium-sized to tall monoecious trees, with widespreading corymbiform to long narrow crowns; bark, wood, stems, and leaves either strongly aromatic or odourless; secondary xylem vessels predominantly solitary or up to 5% in radial multiples of 2-3, ca (50-)60-80(-100) per sq.mm, 1.3-1.7 mm long × (40-)55-75(-120)μ inner tangential diameter, the perforation plates and vessel-ray pitting exclusively scalariform*; fibres relatively thin-walled, ca 1.5 mm long × (15-)25-35(-40)μ outer tangential diameter, predominantly fibre tracheids with bordered pits with rather reduced borders, occasionally libriform wood fibres with septae in late wood; multiseriate rays (0.2-)0.3-0.8(-1.1) mm high × 2-5 cells wide, acicular crystals and marginal oil cells apparently absent; primary cortex not sclerosed, with large intercellular spaces**; ultimate branchlet stems ± markedly tetragonous, sparsely to densely hairy; petioles planate, infrequently shallowly sulcate; leaf blades large microphyllous to notophyllous, with margins variably shallowly obtuse crenate, midribs ± planate on upper face, 1-3-layered hypodermis on upper face***, oil cells confined to mesophyll****.

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* Both simple and scalariform perforation plates are recorded by Metcalfe and Chalk (1950), but the former were not found in wood examined during the present study.

** Hobein (1888), Solereder (1899), Metcalfe and Chalk (1950).

*** Hobein (1888), Solereder (1899), Money et al. (1950). Also present on lower face in <u>Laurelia sempervirens</u> (Hobein 1888, Solereder 1899).

**** Hobein (1888), Solereder (1899).

Inflorescence buds ± globose, sessile or obscurely stipitate before expansion; mature inflorescences slenderly or laxly thyrsiform, with (5-)7-17(-27) flowers, monoecious, rarely polygamous or unisexual; accessory axillary flowers usually absent; bracts small, slightly dimorphic, base node primary peduncle bracts cymbiform-navicular, ($1\frac{1}{2}$-)2-4(-5) mm long × (1-)$1\frac{1}{2}$-3 mm broad, ± lignified, and persistent during flowering, distal node bracts shallowly navicular, 2-3(-5) mm long × 1-2 mm broad, usually caducous before anthesis; bracteoles present, herbaceous to subpetaloid, ± contiguous and persistent with perianth on floral receptacle or hypanthium rim.

Flowers ± unisexual; perianth patelliform to broadly cyathiform, comprising an outer pair of sepaloid to subpetaloid perianth bracteoles, and (2-)3-8(-12) ovate-oblong-circular, obtuse, palmate-parallel-nerved tepals, 2-6(-7) mm long × ($1\frac{1}{2}$-)2-4(-5) mm broad, in 1-2(-3) obscurely trimerous or spirally arranged ± equal whorls; androecium in staminate flowers of (4-)6-11(-12) stamens arranged spirally over receptacle, the stamens (2-)$2\frac{1}{2}$-$3\frac{1}{2}$(-$4\frac{1}{2}$) mm long × ($\frac{2}{3}$ -)$\frac{3}{4}$-1(-$1\frac{1}{4}$) mm broad × $\frac{1}{4}$ - $\frac{2}{3}$ mm thick, with elliptic-circular peltate staminal glands, and obtusely apiculate, slightly introrsely-dehiscing anthers; androecium in pistilliferous flowers of (10-)12-32(-46) isomorphic to dimorphic dorsiventrally compressed batilliform to tooth-like* staminodes in 2-4(-5) subspiral whorls,

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* Laurelia sempervirens.

($\frac{1}{3}$-)$\frac{2}{3}$-2$\frac{1}{2}$(-4) mm long × ($\frac{1}{4}$-)$\frac{1}{3}$ - 1(-1$\frac{1}{2}$) mm broad, sometimes partly or fully fertile in outer whorls*; pollen grains rather ellipsoidal to near spheroidal**, sub-oblate, Lg (24-)26-32(-36) μ × long. Lt. 30-36 (-39) μ***, the colpi transversales of rather regular length, 22-29(-32) μ long, both well developed, the interstitial equatorial depressions short but well-defined, the grain walls 1-2 μ thick, the surface sculpture with lumina ± circular to irregular in outline, ($\frac{3}{4}$-)1-1$\frac{3}{4}$(-2$\frac{1}{2}$) μ long; gynoecium lacking in staminate flowers, comprising in pistilifer ~~late~~ flowers ca (7-)8-30(-45) carpels, with terminal ± hispid styles, and broadly obtuse conical or cylindrical unbranched stigmatic column; ovule narrowly ellipsoid, obtuse or apiculate at chalazal end, anatropous on basal placenta.

Fruiting hypanthium oblong- to ellipsoid-urceolate, (14-)17-20(-25) mm long × (5-)6-8(-9) mm thick, scarred with lignified protuberances towards the apex or pusticulate towards the base, sparsely haired, dehiscing into 2-3 subequal valves; perianth and androecium eventually caducous; nutlets attached superficially to hypanthium wall, ± uniformly

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* *Laurelia sempervirens*.

** The grains described and figured by Cranwell (1942,1953) for *L. novae-zelandiae* are more markedly ellipsoidal.

*** Erdtman (1952) gives dimensions of *L. sempervirens* as 27×47×36 μ and of *L. novae-zelandiae* as 20×43×37 μ. Measurements given by Cranwell (1942, 1953) for *L. novae-zelandiae* are 36-46 μ long axis or 40×24 μ.

silky hirsute, the bodies fusiform to narrowly ovoid, the styles terminal, subulate.

Additional Characters Common to Infrageneric Taxa

Average tree height range 20-30 m; wood whitish to dull grey-brown, often tinted yellowish, drying sordid greyish, growth rings faintly defined or obscure; ultimate branchlet stems drying grey to blackish brown, with cortex sometimes squashed and flattened from stele, slightly more compressed and smooth, but not swollen at branchlet and leaf nodes; vegetative buds narrowly obcordiform-conical, the enveloping pair of bract-like leaves densely sordid white to golden or greyish sericeous, with ± erect mucronate apices, expanding when buds ca 4-5 mm long; petioles drying dark-brown to black; leaf blades with midribs thickly prominent on lower face, variably persistently sparse hispid-strigose towards base and on midrib on lower face.

Inflorescence buds rather rounded obcordiform to globose, remaining sessile or sometimes becoming obscurely and thickly stipitate, the enveloping bracts ovate cymbiform, sparsely stramineous or brownish strigillose, eventually $2\frac{1}{2}$-4 mm. long × $1\frac{1}{2}$-3 mm thick, with diverging apices, the buds eventually quite globose, 3-6(-8) mm in diameter, before the densely hispid ultimate inflorescence axes and flower buds commence to expand between the gradually diverging enveloping bracts; mature inflorescences decurved, sparsely to densely hairy, borne at ultimate 1-5(-7) leaf nodes among leaves; terminal primary peduncle dichasia with central flower staminate, exceptionally pistilliferous, and lateral flowers staminate or pistilliferous, the subterminal peduncle nodes bearing usually solitary opposite pistilliferous flowers, and basal nodes either solitary opposite usually staminate flowers or secondary peduncles with 3 or 5 usually staminate flowers; staminate flowers (or inflorescences) maturing before pistilliferous flowers (or inflorescences), and those where either solitary or central in terminal dichasia opening first; peduncular bracts herbaceous, mucronate acute, those at base node of primary peduncle rather amplexicaul, prominently carinate, sparsely to densely hispidulous-strigillose or glabrescent abaxially, ± glabrous adaxially, those at distal nodes smaller, divergent, obscurely carinate, less attenuately mucronate, more densely pubescent abaxially; secondary peduncles similar in form and pubescence to primary peduncle, slenderer, the bracts similar in form to those at distal nodes on primary peduncles; bracteoles in single pairs, elliptic to ovate-deltate, rarely circular, variously cymbiform, $(2-)2\frac{1}{2}-4(-5\frac{1}{2})$ mm long × $(1\frac{1}{2}-)2-3\frac{1}{2}(-4\frac{1}{2})$ mm broad, with mucronulate acute or obtuse apices, and entire, hardly thinner margins, faintly to prominently carinate with 1 midnerve, rarely 3 obscure nerves, variably strigose-tomentose abaxially, ± glabrous adaxially; mature staminate flower buds ± globose, mature pistilliferous flower buds cylindrical to broadly ellipsoid, the bracteoles valvate, incompletely enclosing tepals.

Open staminate flowers of small or medium size; receptacle patelliform, densely hispid-strigose; perianth pale green, the tepals with entire or fimbriolate-eroded thin petaloid margins, variably hairy;

stamens pale green, with reddish purple anther valves, slender, incurving-erect, the filaments slender, dorsiventrally compressed, the staminal glands finely pitted and wrinkled, ($\frac{1}{4}$-)$\frac{2}{3}$ - $\frac{3}{4}$(-1)mm long × $\frac{1}{3}$ - $\frac{2}{3}$(-1) mm broad, attached by a slender stipe to the margins of the filament and overlapping both or particularly adaxial faces, rarely aborted, the anthers narrowly conical, narrowed into a narrowly obtuse or obscurely retuse apiculum $\frac{1}{4}$ - $\frac{1}{3}$ mm long, with narrowly elliptic valves; staminodes and carpels lacking.

Open pistilliferous flowers of small or medium-large size; hypanthium variably poculiform, densely haired; perianth of the same colour and structure as in staminate flowers, the perianth bracteoles usually smaller and more markedly acute than the tepals; functional stamens, where present, of the same form as in staminate flowers, smaller; staminodes with flat, expanded, ± obtusely deltate, ± scarious, recurved apices, the outer staminodes longer and broader than the inner, occasionally bearing vestiges of staminal glands as hyaline areas or rounded lobes on the lower margins.

Ripe infructescences borne at ultimate (1-)2-6(-10) leaf nodes among leaves on branchlets, with ± all (2-4(-6)) hypanthia maturing per infructescence, and staminate flowers and their pedicels early caducous; base node peduncle bracts sometimes persistent, often caducous; fruiting hypanthium lignified with walls averaging 1-1$\frac{1}{2}$mm thick, in dehiscence with 2-4(-6) incipient fissures developing from the rim, of which only 2-3 extend to the base; hypanthium chamber sparsely sordid stramineous to fawn silky hirsute at the base among nutlets; nutlets attached to lower sides and base of hypanthium chamber, with straight hairs sparser on adaxial face, the styles hardly expanded at the base into bodies of nutlets, with hairs becoming gradually shorter towards the ultimately hispidulous or glabrous apex.

The name *Laurelia* is taken from "Laurel", the name given to *Laurelia sempervirens* by the Spanish colonists of Chile because of its resemblance in aromatic properties and uses to the sweet bay or laurel (*Laurus nobilis*) (de Jussieu 1809, J.B.Mueller 1841, Tulasne 1855, C. Mueller in Walpers 1857, Wall and Allan s.d.).

Species, Geographic Distribution, and Ecology

The genus *Laurelia* comprises two species, one in New Zealand (both islands) between 35° and 46°S, and one in southern Chile between 33° and 42°S. (maps 2, 7, 8).

The species occur in primary cool subtropical rainforest between sea-level and 2400 m altitude in Chile and from sea-level to 600(-1600) m in New Zealand. In Chile, its optimal occurrence is in the laurel valley forest of *Persea lingue* and *Nothofagus obliqua*, below the altitudes and north of the latitudes of occurrence of most species of *Nothofagus* in the region. Likewise in New Zealand, it is associated with mixed rainforest, often with *Podocarpus* in semi-swamp sites, at lower altitudes and more northerly latitudes than Nothofagus forest.

According to data available for *L. novae-zelandiae*, germination of seeds occurs in the litter and soil of the forest floor during the austral spring between August and December or January, shortly after nutlet dissemination (Moore: CHR 87542, Oliver: WELT 17926, Schodde 5305). In that species, regeneration by suckering and root grafts from the base of the trunks and lateral roots has also been noted.

Flowering is strictly seasonal and takes place in the late austral spring from September to November in both species, under prevailing seasonal conditions of relatively uniform rainfall and warmer summer and colder winter temperatures. Fruit is set in late summer and autumn months (January-May), and the inflorescence buds for the following season appear between February and May, before fruiting hypanthium dehiscence.

Notes on Generic Characters

Despite the extensive differences between its two species, Laurelia is a well-defined genus in the tribe Laurelieae. It is distinguished from other members of the tribe by its relatively narrow, 2-5 cells-wide multiseriate xylem rays, the presence of large intercellular spaces in its primary bark and cortex* (Hobein 1888, Solereder 1899), its ± sessile globose inflorescence buds, its pubescent thyrsiform monoecious inflorescences, its tepaloid bracteoles that are hardly distinguishable from and ± contiguous with perianth tepals, its often cyathiform perianth

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* This may account for the peculiar flattening or squashing of bark or cortex from ultimate branchlets that is found occasionally in herbarium specimens of both species.

with an irregular number of obtuse tepals with palmate-parallel nerving, its stamens, irregular in number in staminate flowers, with peltate staminal glands and conical anthers, its irregular number of recurving batilliform staminodes in pistilliferous flowers, and its oblong-urceolate fruiting hypanthium with caducous perianth and androecium and a smooth or scarred but never ribbed neck. Aspects of these and other morphological peculiarities of *Laurelia* are discussed below.

Whereas the inflorescence buds in other genera of the family become markedly stipitate before expanding, they remain almost sessile and globose in *Laurelia*, as described in chapter IV.3. Their form in *Laurelia* appears to be related to the greater amount of protection that they need in the temperate, seasonally variable latitudes in which the genus occurs. The inflorescence buds enlarge and expand during the austral winter months, and the outer enveloping pair of bracts, which are the bracts of the base node of the primary peduncle, are apparently retained to protect the bud during this period.

The base node bracts differ from those of the nodes above in their thick, somewhat lignified texture, deeper cymbiform shape, usual lack of dense indumentum, and persistence. They are smaller in *Laurelia novae-zelandiae* than in *L. sempervirens*, and do not enclose the inflorescence primordia to such an extent. They appear to be comparable in their function with those enclosing the flower buds in *Doryphora*, which they resemble in form, if not size, and with which they may be homologous (cf. chapter IV.6).

Bracts of similar form occur regularly at the base of lateral leafy branchlets in *Laurelia sempervirens*, but in no other species in the family.

From all herbarium material studied, it appears that trees of both species of *Laurelia* are invariably monoecious, never dioecious as has been recorded in many cases (Cunningham 1838 p.p., J.D.Hooker 1853, 1864*, Tulasne 1855*, A. de Candolle 1868*, Baillon 1869*, Bentham 1880*, Pax 1889*, Perkins and Gilg 1901*, Cheeseman 1906*, 1925*, Perkins 1925*, Richards 1947, Hinds and Reid 1957, Allan 1961, Hutchinson 1964*)*. The inflorescences themselves are usually monoecious, infrequently polygamous or staminate. Sampson (1967) has also observed this to be the case in all trees of *L. novae-zelandiae* he examined.

Undoubtedly because of their tepal-like form and proximity to the perianth on the hypanthium, the outer pair of "perianth parts" in the flowers of both sexes in *Laurelia* have never been recognised as bracteoles. That they are bracteoles is indicated by their position opposite to each other in the transverse plane, their essentially herbaceous texture, prominent abaxial midribs, and mucronulate apices. These features are

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* Though the authors asterisked refer specifically to "flowers dioecious or polygamous" or "flowers ....polygamo-dioecious, in axillary racemes", the contexts of their descriptions imply that the trees or inflorescences are dioecious.

found in the peduncular bracts but not the inner perianth tepals. Moreover, the venation of the bracteoles in *Laurelia novae-zelandiae*, in comprising a prominent, ± solitary midnerve, resembles the pattern in the peduncular bracts rather than the inner tepals (Sampson 1967). Whether the bracteoles are homologous with those in *Nemuaron* and *Dryadodaphne* is uncertain but perhaps not unlikely in view of the close relationship between the three genera.

The inner tepals in one collection of *L. novae-zelandiae* (Petrie: NSW 67911) from Te Akatea are constricted at the base and there bear paired peltate glands similar to those in fertile stamens. Except for their lack of pollen sacs, they resemble the form of the outer stamens in *Gomortega* (Gomortegaceae), and parallel the occurrence of petaloid stamens in *Doryphora* (*D. aromatica*).

The occasional presence of apparently functional stamens in the pistilliferous flowers of both species* of the genus has already been inferred by Gay (1851 or 1852), Tulasne (1855), Perkins and Gilg (1901), Perkins (1925), Hutchinson (1964), and others by their references to "polygamous" flowers (= inflorescences). Sampson (1967) has suggested that the presence of apparently fertile stamens in pistilliferous flowers is linked not with pollen production but with the maintenance of the associated glands that function as nectaries to attract insect pollinators. If this is correct, functional stamens appear to have been retained because the staminal glands would otherwise have been aborted concomitantly with the anthers in the development of staminodes. Thus

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* Fewer and more irregular in occurrence in *L. sempervirens* than in *L. novae-zelandiae*.

the occurrence of occasional stamens in the pistilliferous flowers of *Laurelia* species may not represent the result of atavism, as would appear at first sight.

Variations in the form of the fruiting hypanthia of both species of the genus have been reviewed in chapter IV.16. The hypanthium of *Laurelia sempervirens* is uniquely scarred with lignified protuberances which, representing the bases of caducous bracteoles, tepals, and androecium parts, are dispersed over the upper half of the hypanthium. In the flower of that species, the whorls of perianth and androecium parts are closely contiguous on the rather ill-defined rim, showing that, as the hypanthium enlarges during fruiting, elongation of the hypanthium wall occurs partly by intercalary growth between these whorls or their remnants. Growth in this region of the hypanthium in the family is apparently confined to this species, and to *Daphnandra* where it is much less marked.

Affinities

Although it has been thought to be closely related to *Athersperma* (Brown 1814, Bancroft 1890, and Cheeseman 1925), and was even united with that genus by J.D.Hooker (1855), Baillon (1868,1869,1877,1891) (who treated it as a section of *Atherosperma*), Bentham (1870), F.v. Mueller (1879), and others, *Laurelia* is as distinct from *Atherosperma* as any genus in the family. The only features common to the two are unisexual flowers, and a rather cyathiform perianth of obtuse, conspicuously pubescent tepals with palmate-parallel venation. Both features are in the specialised condition for the family (table IV), and are likely to have evolved in parallel. All revisers after Bentham (1880) have accepted *Laurelia* as distinct.

Laurelia is more closely allied to *Nemuaron*, and through it to *Dryadodaphne*, than to any other genus in the tribe. As well as in having very occasional libriform wood fibres with septae in late wood, it resembles *Nemuaron* also in the form of its perianth and androecium parts, as discussed in chapter XI, irrespective of their occurrence in flowers of different sexes. Its alkaloids, which are apparently exclusively of the aporphine type*, bear out this relationship.

Laurelia also approaches *Dryadodaphne*, and to lesser extent *Daphnandra*, in its more conventional fruiting structures, notably in the general form of its cylindrical-urceolate fruiting hypanthium, and its nutlets which retain the long hirsute terminal style. Its similarity to *Doryphora* in the basal inflorescence bracts has been mentioned.

Certain characters of its secondary xylem, such as the predominantly solitary pores of medium diameter, resemble those of *Doryphora* more closely than those of any other genus. In view of the many other fundamental differences between the two genera, it is not unlikely that such similarities have developed wholly or partly in parallel for the reasons discussed in chapter IX. Moreover, the occasional prevalence of

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* Data for *Laurelia novae-zelandiae* only.

very large pores in the secondary xylem of Laurelia novae-zelandiae, as in sample Z.10, may reflect the swampy environment in which the species grows rather than indicate a necessarily close affinity with Dryadodaphne and Nemuaron.

Interspecific Relationships

Laurelia sempervirens and L. novae-zelandiae are vicarious species. They are separated geographically in Chile and New Zealand (cf. Cavaco 1965). If their distribution results from former land connections, as seems likely for the reasons pointed out by Dansereau (1963), they indicate either that there have been historically recent land connections between Chile and New Zealand (which nevertheless appear to antedate Cretaceous times, cf. Adie in Gressitt 1963), or that their rate of evolution has been slow according to the assessment of rates given by Stebbins (1950, chpt. XIV) for woody plants.

Both species, nevertheless, are more different from each other than are those in any other genus of the family. Except for the more sepaloid obscurely-nerved tepals and greater frequency of stamens in the pistilliferous flowers in L. novae-zelandiae, the floral and fruit characters by which they differ appear to be at a less specialised level of organisation in L. sempervirens. In L. sempervirens, the inflorescences are more loosely branched; the base internodes of the primary peduncles are more contrastingly flattened, the counter-parts of basal primary peduncle bracts occur at the base of leafy axillary branchlets; the bracteoles are more bract-like and are frequently inserted well below the perianth on the hypanthium in pistilliferous flowers; the tepals, androecium parts, and carpels are greater in number per flower; the staminodes are dimorphic; and the vestiges of bracteole, perianth, and androecium parts persist as lignified protuberances on the outer wall of the fruiting hypanthium.

The two species apparently differ significantly also in the size and frequency of their secondary xylem pores, the greater size of the flowers of *L. sempervirens*, and in patterns of floral pubescence. The xylem pores average 56 μ in inner diameter and 80 per sq. mm in transection in *L. sempervirens*, and larger, with an average inner diameter of 72 μ and a frequency of 62 per sq. mm, in *L. novae-zelandiae*. These characters are usually much more constant between the species in other genera of the family (tableII). Whether they have been induced by the rather different ecological sites occupied by the two species - relatively well-drained in the case of *L. sempervirens*, and semi-swamp in *L. novae-zelandiae* - has not been investigated, but may not be unlikely in view of how the frequency and size of pores may vary between species depending on whether the species grow in wet or dry situations (Brazier 1968).

As far as can be judged from the limited number of pollen samples examined, the grain reticulum is slightly coarser in *L. sempervirens* (lumina 1-2(-2$\frac{1}{2}$) μ longest axis) than in *L. novae-zelandiae* (lumina $\frac{3}{4}$-1$\frac{1}{4}$(-2) μ diameter) (f.45C, D).

The presence of less specialised morphological features in the Chileah rather than New Zealand species appears to be inconsistent from a geographic point of view. It might be expected that *L. novae-zelandiae*, geographically nearer to *Nemuaron* in New Caledonia and *Dryadodaphne* in New Guinea, would possess the greater number of unspecialised or linking characters because *Laurelia* is more specialised than either of these two genera in most homologous features (cf. table IV).

A distinction needs to be drawn here between unspecialised or "primitive" characters per se which may be retained, and those which link taxa because of common origin. In this case, those characters which are less specialised in *L. sempervirens* than in the New Zealand species do not occur in similarly unspecialised form in either *Nemuaron* or *Dryadodaphne*. Many characters of *Laurelia novae-zelandiae*, on the other hand, approach their counterparts in *Nemuaron* and *Dryadodaphne* more closely than do those of the Chilean species. Examples are the pattern of pubescence (or lack of it) on stems, leaves, and nutlets, the form of the leaves, the lack of odour (aromatic oils), the form of the base node primary peduncle bracts, the texture and nerving of the tepals, and the structure of the fruiting hypanthium. Some of these characters, such as pubescence and leaf form, may be fortuitously similar because of environmental influences. Even so, the complexity of these similarities, and differences between the species of *Laurelia* and the genera *Nemuaron* and *Dryadodaphne*, illustrates the reticulate nature of relationships in the tribe Laurelieae, and the difficulty of aligning the taxa in an unequivocal phylogenetic sequence.

Key to the Species of Laurelia

1a Fruiting hypanthium scarred with lignified protuberances towards the apex, levigate below; all parts strongly and persistently aromatic; perianth of ♂ and ♀ flowers (6-)8-10(-14)-partite, of medium size; leaves ± elliptic, with shallowly crenate to undulate margins; staminodes densely pubescent towards the base .... 1. L. sempervirens (Ruiz & Pav.)Tul.

1b Fruiting hypanthium levigate towards the apex, pusticulate towards the base; all parts ± odourless; perianth of ♂ and ♀ flowers 4-5(-7)-partite, small; leaves obovate-spathulate, with rather deeply crenate-dentate margins; staminodes usually entirely glabrous .... 2. L. novae-zelandiae A. Cunn.

1. *Laurelia sempervirens* (Ruiz & Pav.)Tul.

Laurelia sempervirens (Ruiz & Pav.)Tul., Arch.Mus.Hist.Nat.Par. 8(1855)416; C.Muell.in Walp., Ann.Bot. 4(1857)116; A.DC., Prod. 16,2(1868)675 p.p.; [Baill., Adansonia 9(1868)116 pro syn. *Atherospermatis sempervirentis*]; [F.Phil., Cat.Pl.Vasc. Chil. (1881)265 p.p. pro syn. *Laureliae aromaticae* et *L. serratae* R.Phil. non Bert.]; Hobein, Bot.Jb. 10(1888)71; Pax, Pflzfm. 3,2(1889)103 p.p., f.67A-C; [O. Kuntze, Rev.Gen. 2(1891)568 pro syn. *Pavoniae sempervirentis*]; Solereder, Syst.Anat.Dicot. (1899) [transl.Boodle, Fritsch, & Scott, 2(1908)700]; Perk. & Gilg, Pflzr. 4(1901)4,11,77 p.p., f.21 A-K; Dusén, Wiss.ergeb.Schwed.Südpolar-exped. 3,3(1908)4,24; Stapf, Curtis Bot.Mag. 135(1909)t.8279; Perk., Pflzr. 49(1911)46; Skottsberg, Kungl.Sv.Vet.Akad.Handl. 56(1916)44, 226; Perk., Gattung Monim. (1925)7,12,13,51, f.39 A-K; Warming, Oecol.Pl. [Engl.ed.]ed.1,impr.2,(1925)339; Garratt, Trop.Woods 39(1934)21; Looser, Rev.Asoc.Chil.Quim.y Farm. 21(1934)9; Berry, Bot.Gaz. 96(1935)754; Macbride, Field Mus.Bot. 13,2 (1938)784; Berry, Geol.Soc.Amer.spec.pap. 12(1938)75; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)389,392, f.III.38; Muñoz-Pizarro, Sinops.fl.chil. (1959)155,244, f.137; Oberdorfer, Pflzsoziol.Stud.Chile (1960)86 et seq.; Buchheim in Melchior, Syllab.Pflzfm. ed.12,2(1964)122; Hutchinson, Gen.Fl.

Pl. 1(1964)120.

Pavonia sempervirens Ruiz & Pav., Syst.Fl.per.et chil. 1(1798)253; [A.Cunn., Ann.Nat.Hist. 1(1838)381 pro syn. Laureliae chilensis]; [Gay, Fl.chil. 5(1851 or 1852)355 pro syn. Laureliae aromaticae]; [Tul., Arch.Mus.Hist.Nat.Par. 8(1855)416 pro syn. Laureliae sempervirentis]; [Baill., Hist.Pl. 1(1869)323 pro syn. Atherospermatis sempervirentis]; F.Phil., Cat.Pl.Vasc.Chil. (1881)265 pro syn. Laureliae aromaticae only]; O.Kuntze, Rev.Gen. 2(1891)568, 3(1898)276.

TYPE: Dombey, [Chile] [Concepcion] [Conceptione] [Pérou]* —— lectotype in BM (♂ and ♀ flowers), syntypes in BM, K, L, MA, MEL, P, US (photograph).

Atherosperma sempervirens (Ruiz & Pav.)Baill., Adansonia 9(1868)116; Baill., Hist.Pl. 1(1869)323,336, f.369,370; Baill., Dict.Bot. 1(1877)310, f.

Laurelia aromatica Poir.in Lam., Encyc.meth.Bot.suppl. 3,(1813)313 [nom.superfl.]; Spreng., Syst.Veg. 2(1825)470**; Bert., Merc. Chil. 15(1829)685 [n.v.] [transl. Ruschenberger, Amer.J.Sc. 23(1833)89]; [A.Cunn., Ann.Nat.Hist. 1(1838)381** pro syn.

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* In error.

** Authors incorrectly citing de Jussieu as the author of Laurelia aromatica.

Laureliae chilensis]; Gay, Fl.chil. 5(1851 or 1852)355*; [Tul., Arch.Mus.Hist.Nat.Par. 8(1855)416,417 pro syn. *Laureliae sempervirentis*]; R.Phil., Bot.Zeit. 15(1857)401; [Baill., Hist.Pl. 1(1869)323 pro syn. *Atherospermatis sempervirentis*]; F.Phil., Cat.Pl.Vasc.Chil. (1881)265*; [Hobein, Bot.Jb. 10(1888)71, pro f. *Laureliae sempervirentis* sine comb.]; Lesquereux, U.S.Geol.Surv.Monogr. 17(1892)108; Reiche, Bot.Jb. 21(1895)17 et seq.; Schenk, Deutsche Tiefsee Exped. 2,1(1905)127 [in errore pro *Laureliopse philippiana*?]; Berry, Proc. U.S.Nat.Mus. 7B,22(1928)21; Willis, Dict.Fl.Pl.Ferns ed.6,(1931)365**; Garratt, Trop.Woods 39(1934)19 et seq.p.p., f.III,2**; Schimper & v. Faber, Pflzgeogr. ed.3,2(1935)683 p.p.?; Metcalfe & Chalk, Anat.Dicot. 2(1950)1144**; Erdtman, Pollen Morph.& Pl.Taxon. (1952)271; Core, Plant Taxon. (1955)318; Schmithüsen in Schmithüsen, Klapp, & Schwabe, Bonner Geogr.Abh. 17(1957)35; Cockayne, Veg.N.Zeal. ed.3,(1958)413; Good, Geogr.Fl.Pl. ed.3,(1964)218; Hutchinson, Gen.Fl.Pl. 1(1964) 112**; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7,(1966)623**.

Laurelia chilensis A.Cunn., Ann.Nat.Hist. 1(1838)381 [nom. superfl.].

Theyga chilensis Mol., Sagg.Chile ed.2,(1810)163 [*Thiga chilensis* Mol., ibid. p.297, orth.var.]; [Spreng., Syst.Veg. 2(1825)470

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* Authors incorrectly citing Sprengel as the author of *Laurelia aromatica*.

** Authors incorrectly citing de Jussieu as the author of *Laurelia aromatica*.

"Thiga chilensis" pro syn. *Laureliae aromaticae*]; [A.Cunn., Ann.Nat.Hist. 1(1838)381 "Thiga chilensis" pro syn. *Laureliae chilensis*]; [Tul., Arch.Mus.Hist.Nat.Par. 8(1855)417 "Thiga chilensis" pro syn. *Laureliae sempervirentis*].

TYPE: lost.

Laurelia serrata Bert., Merc.Chil. 15(1829)685 [n.v.] [transl. Ruschenberger, Amer.J.Sc. 23(1833)89] [non R.Phil. 1857]; [Tul., Arch.Mus.Hist.Nat.Par. 8(1855)416 pro syn. *Laureliae sempervirentis*]; [Baill., Hist.Pl. 1(1869)323 pro syn. *Atherospermatis sempervirentis*]; [F.Phil., Cat.Pl.Vasc.Chil (1881)265 pro syn. *Laureliae aromaticae*].

TYPE: Bertero 361, Taguatagua —— isotype in P.

[*Laurelia crenata* Pöpp. ex Tul., Arch.Mus.Hist.Nat.Par. 8(1855)416, nom.nud. pro syn. *Laureliae sempervirentis*; A.DC., Prod. 16,2(1868)675 pro syn. *Laureliae sempervirentis*; Baill., Hist. Pl. 1(1869)323 pro syn. *Atherospermatis sempervirentis*; F.Phil., Cat.Pl.Vasc.Chil. (1881)265 pro syn. *Laureliae aromaticae*; Hobein, Bot.Jb.10(1888)81, pro f. *Laureliae sempervirentis* sine comb.; Perk. & Gilg, Pflzr. 4(1901)77 pro syn. *Laureliae sempervirentis*. —— not validly published as not accepted by any author: I.C.B.N. 1966, art.34.]

[*Laurelia odorata* Schmithüsen in Schmithüsen, Klapp, & Schwabe, Bonner Geogr.Abh. 17(1957)42, nom.nud.]

The following illustrations referred to as Atherosperma sempervirens Baill., Laurelia aromatica Poir., and L. sempervirens Tul. respectively in Index Londinensis have not been seen but are likely to refer to this species: Baillon, Traité Bot.Méd.Phan. 1(1883)531; Warburg, Muskatnuss (1897)506; Castillo & Dey, Jeogr.Vej.Rio Valdivia ed.2,1(1908)51; Beille, Bot.Pharm. 2(1909)326.

Figures 1E, 8, 29, 45C.

Diagnosis

Trees (15-)20-30 m high; bark pale grey-brown; ultimate branchlet stems ± densely stramineous to brownish hispid-strigose, with a pair of bracts often present at base of lateral branchlets; leaf blades ±

elliptic or rather obovate, ± narrowly obtuse, (2-)3-7$\frac{1}{2}$(-11) cm long × (1-)1$\frac{1}{2}$-3$\frac{1}{2}$(-5) cm broad, with shallowly and distantly crenate to ± undulate margins, and faintly prominulous vein reticulum confined to blade margin on lower face; all parts strongly aromatic.

Mature inflorescences divergently branched, (2-)3-5(-6) cm long, stramineous-golden hispid-strigose; base internode of primary peduncle markedly shorter, more broadly compressed, and more sparsely haired than distal internodes; pedicels (3-)4-10(-20) mm long × $\frac{1}{4}$-$\frac{1}{2}$(-$\frac{3}{4}$) mm thick in staminate flowers, (4-)7-15(-25) mm long × ($\frac{1}{3}$ -)$\frac{2}{3}$ - $\frac{3}{4}$(-1) mm thick in pistilliferous flowers.

Open staminate flowers of medium size; receptacle hispid among stamens; perianth (6-)8(-12)-partite, the inner tepals (2$\frac{1}{2}$-)3-5(-6) mm long × (1$\frac{1}{2}$-)2-3(-4) mm broad, ± petaloid, ± sparingly haired; stamens (2$\frac{1}{2}$-)3-3$\frac{1}{2}$(-4$\frac{1}{2}$) mm long, with filaments ± densely haired on both faces. Open pistilliferous flowers of medium-large size; hypanthium (1-)2$\frac{1}{2}$-3$\frac{1}{2}$ (-5) mm long × (2-)3-4$\frac{1}{2}$(-6) mm thick, the rim obliquely erect, hispid; perianth (8-)± 10(-14)-partite, the perianth bracteoles deltate, mucronate acute, herbaceous, (2$\frac{1}{2}$-)3-4(-5$\frac{1}{2}$) mm long × (1$\frac{1}{2}$-)2$\frac{1}{2}$-3$\frac{1}{2}$(-4$\frac{1}{2}$) mm broad, usually inserted below tepals, the inner tepals (3-)4-6(-7) mm long × (1$\frac{1}{2}$-)2-4(-5) mm broad, ± petaloid, ± sparingly haired; androecium ± entirely sterile, comprising 2-3 outer whorls of (12-)16-24(-36) batilliform, basally strigillose staminodes, and 1 inner whorl of (6-)±8(-10) tooth-like, densely hispid staminodes inserted on rim; gynoecium of (15-)20-30(-45) carpels, the stigmatic column broadly obtusely conical, (1-)2(-3) mm long.

Ripe infructescences with pedicels (10)12-20(-25) mm long; fruiting hypanthium ± cylindrical-ovoid, scarred towards the apex with lignified protuberances, levigate towards the base; bodies of ripe nutlets fusiform, rarely narrowly ellipsoid, (3-)5-6(-8) mm long × ($\frac{2}{3}$ -)$\frac{3}{4}$-1(-1$\frac{1}{2}$) mm thick.

Detailed Description

Medium-sized to tall trees (15-)20-30 or more m high; bole ca 20 or more cm diameter breast height*, buttresses and suckering unrecorded; crown rather widespreading**, apparently shorter than the bole, with branches obliquely horizontal***. Bark ca 10-15 mm thick*** when dry, outer surface rather smooth or finely fissured, pale grey-brown, inside drying dull brown. Wood whitish, tinted yellowish green****, drying sordid greyish, the duramen often lined blackish*. Branchlet stems openly branched, the ultimate 4-6(-8) internodes ($\frac{1}{2}$-)1-3$\frac{1}{2}$(-6) cm long × (1-)1$\frac{1}{2}$-3(-4) mm thick, variably angular tetragonous on ultimate 2-4 internodes and more rounded compressed below, smooth, drying brownish black, less often dark grey or brown, sparsely to densely sordid stramine-

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* Bertero (1829).

** Perkins and Gilg (1901).

*** Muñoz-Pizarro (1959).

**** Tulasne (1855).

ous to dirty brown curly hispid or somewhat strigose, glabrescent below; shaded and sapling branchlet stems with ultimate 4-6 internodes (1-)2-4(-7) cm long, drying olive-grey or brown, more sparsely pubescent; an early caducous pair of bracts often present at base of lateral branchlet stems. Petioles broad, (3-)5-10(-15) mm long × (⅔-)1¼-2(-2½) mm thick, shallowly impressed or planate on upper face, sometimes with narrow marginal flanges, persistently sparse sordid curly hispidulous-strigillose, eventually glabrescent, particularly on shaded and sapling branchlets. Leaf blades narrowly to broadly elliptic, or rather obovate, (2-)3-7½(-11) cm long × (1-)1½-3½(-5) cm broad, obtuse to broadly, rarely narrowly cuneate at the base, narrowly, less often broadly obtuse, or slightly acuminate, very rarely mucronate acute at the apex; margins shallowly and distantly, less often deeply crenate, or almost undulate, slightly to markedly recurved; texture coriaceous to thickly coriaceous, the upper face ± smooth, often conspicuously lined with prominulous nerves; colour glossy dark green*, in dry leaves pale olive-grey to dark olive-brown on both faces, sometimes with a characteristic sub-glossy golden or yellowish tone; nervation on upper face as described, with midrib ± planate, on lower with (4-)5-8(-9) main nerves hardly more prominulous than on upper face, anastomosing obscurely towards blade margin, the vein reticulum faintly prominulous, confined to blade margin; glabrescent with very sparse sordid stramineous curly strigose hairs, occasionally bearing small

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* Comber 592.

pale brown glandular pits; leaf blades on shaded and sapling branchlets 5-9(-11) cm long × 2-3$\frac{1}{2}$(-5) cm broad, with narrower apices, and more deeply closely crenate planate margins, thinly coriaceous to almost chartaceous, nerves and vein reticulum more extensively prominent on both faces, ± glabrous. Bark, wood, stems, and leaves strongly and persistently aromatic with a sweet safrol- or camphor-like odour, the odour sometimes evanescing in dry wood.

Mature inflorescences rather divergently branched thyrsiform, monoecious, rarely unisexual with either staminate or pistilliferous flowers, very rarely polygamous, (2-)3-5(-6) cm long, sordid stramineous to golden hispid-strigose, bearing (5-)7-17(-27) flowers. Primary peduncles (1-)1$\frac{1}{2}$-4(-5$\frac{1}{2}$) cm long, the base internodes ($\frac{1}{2}$-)1$\frac{1}{2}$-2$\frac{1}{2}$(-3) mm thick, short, rather broadly compressed, ± sparsely brownish strigose, the distal internodes slenderer often tegragonous, more densely pale sordid stramineous to tawny-golden hispid-strigose, (2-)3-5(-7)-noded, the subterminal nodes single-flowered, or often bearing secondary peduncles at basal 1-2 nodes; base node bracts of primary peduncle ovate-deltate, cymbiform, (1$\frac{1}{2}$-)2-4(-5) mm long × (1-)2-3 mm broad; distal node bracts ovate-deltate, more shallowly cymbiform, 2-3 mm long ×1-2 mm broad; secondary peduncles ($\frac{1}{3}$ -)$\frac{1}{2}$-1$\frac{1}{2}$(-2) cm long, 1-2 noded; pedicels in staminate flowers slender, (3-)4-10(-20) mm long × $\frac{1}{4}$-$\frac{1}{2}$(-$\frac{3}{4}$) mm thick, in pistilliferous flowers longer and thicker, (4-)7-15(-25) mm long × ($\frac{1}{3}$ -)$\frac{2}{3}$ - $\frac{3}{4}$(-1) mm thick, terete hardly compressed, densely sordid stramineous to tawny curly hispid or hispid-strigose, the terminally central and lower subterminal pedicels occasionally bracteolate. Mature staminate flower buds (2-)2½-3½(-4) mm long × (2-)2½-3½(-4) mm thick, sparsely sordid tawny hispid-strigose, the hairs markedly denser on receptacle; mature pistilliferous flower buds broadly ellipsoid, sometimes obovoid, (3-)4-5(-6) mm long × (2-)3-4 mm thick, rather more densely and uniformly paler hispid-strigose than in staminate flower buds.

Open staminate flowers of medium size. Receptacle (¼-)½-1½(-2) mm long × (½-)1½-2½(-3) mm broad, ± densely, rarely sparsely stramineous-tawny hispid-strigose outside, hispid inside among stamens. Perianth shallowly patelliform to almost rotatiform, (6-)8(-12)-partite in 3(-4) whorls; outer pair of perianth bracteoles broadly ovate-deltate, rarely oblong or circular, often shallowly cymbiform, (2-)2½-3½(-4) mm long × (1¾-)2-3(-3½) mm broad, with acute, infrequently obtuse mucronulate apices, herbaceous to sub-petaloid, 1- or 3-nerved with only mid nerve conspicuous, sparsely to rather densely sordid stramineous-tawny strigillose-tomentose abaxially, with hairs denser along a median keel, glabrous adaxially; tepals (4-)6(-10), narrowly to broadly to oblong-elliptic, rarely ovate or circular or obovate, planate, (2½-)3-5(-6) mm long × (1½-)2-3(-4) mm broad, with broadly to narrowly obtuse apices, and entire to irregularly undulate, or fimbriately-eroded margins, sub-petaloid to petaloid, ± conspicuously (1 or) 3 or 5(or 7)-nerved from the base, sparsely, rarely rather densely pale sordid strigose on the median region of both faces, rarely almost glabrous, the inner tepals longer and narrower, more petaloid, with more deeply and irregularly eroded margins, more conspicuously mid-nerved, and usually more sparsely haired than the outer. Androecium comprising 6-11(-12) stamens $(2\frac{1}{2}-)3-3\frac{1}{2}(-4\frac{1}{2})$ mm long × $(\frac{2}{3}-)\frac{3}{4}-1$ mm broad × $\frac{1}{3}-\frac{2}{3}$ mm thick; filaments $1-1\frac{1}{2}(-2)$ mm long × $(\frac{2}{3}-)\frac{3}{4}-1\frac{1}{4}$ mm broad, rather densely sordid whitish to stramineous hispid-strigose or strigillose on both faces; staminal glands elliptic-circular, rarely depressed elliptic, $(\frac{1}{4}-)\frac{2}{3}-\frac{3}{4}(-1)$ mm long × $\frac{1}{2}-\frac{2}{3}(-1)$ mm broad; anthers $(1\frac{1}{4}-)1\frac{3}{4}-2(-2\frac{1}{4})$ mm long × $(\frac{2}{3}-)\frac{3}{4}-1$ mm broad, glabrous or the connective sparsely strigillose at the base.

Open pistilliferous flowers of medium-large size. Hypanthium broadly poculiform, $(1-)2\frac{1}{2}-3\frac{1}{2}(-5)$ mm long × $(2-)3-4\frac{1}{2}(-6)$ mm thick, densely pale tawny to sordid pale grey hispid-tomentose or silky strigose, the bracteoles occasionally borne below the perianth on the sides of the hypanthium; rim ill-defined, obliquely erect, ca 1 mm high, stramineous to off-white hispid, at the apex densely long brownish hispid, dentate. Perianth shallowly patelliform, (8-)± 10(-14)-partite in 2-3 whorls, of the same form as in staminate flowers; perianth bracteoles as in staminate flowers, but usually more deltate mucronate acute, larger, $(2\frac{1}{2}-)3-4(-5\frac{1}{2})$ mm long × $(1\frac{1}{2}-)2\frac{1}{2}-3\frac{1}{2}(-4\frac{1}{2})$ mm broad, more thickly herbaceous, sometimes densely pubescent, often inserted conspicuously below tepals on hypanthium; tepals as in staminate flowers, but larger, (3-)4-6(-7) mm long × $(1\frac{1}{2}-)2-4$ (-5) mm broad, more petaloid towards the margins, conspicuously (1 or) 3 or 5(or 9)-nerved from the base, the inner tepals longer, narrower, and more petaloid than the outer as in staminate flowers. Androecium ± entirely sterile, 3-4-seriate, the whorls unequal, the outer 2-3 comprising

(12-)16-24(-36) variably batilliform staminodes, the inner whorl (6-)± 8 (-10) tooth-like staminodes inserted on the apex of the rim; functional stamens, when present, $2\frac{1}{2}$-3(-4) mm long; staminodes of outer whorls recurving to reflexed towards the apex, the outermost staminodes batilliform, ($1\frac{1}{2}$-)2-$2\frac{1}{2}$(-4) mm long × ($\frac{3}{4}$-)1mm broad, the superjacent staminodes smaller, more broadly batilliform almost trullate, rarely linear, ($\frac{3}{4}$-) $1\frac{1}{4}$-$1\frac{3}{4}$(-2) mm long × ($\frac{1}{3}$ -)$\frac{2}{3}$ - $\frac{3}{4}$(-$1\frac{1}{2}$) mm broad, closely sordid stramineous strigillose on both faces at the base; staminodes of inner whorl erect, narrowly to broadly deltate or dorsiventrally compressed conical, ($\frac{1}{3}$ -)$\frac{2}{3}$ - 1 mm long × $\frac{1}{3}$ -$\frac{3}{4}$(-1) mm broad, ± densely enveloped by long dark stramineous to brownish hispid hairs extending to 1 mm beyond staminode apices. Gynoecium of ca (15-)20-30(-45) carpels; styles rarely exserted beyond hypanthium rim in a thick cylindrical column; stigmatic column broadly ± obtusely conical, (1-)2(-3) mm long × 1(-3) mm broad, exserted up to 2 mm beyond apices of inner staminodes.

Ripe infructescences (3-)4-5(-7) cm long, persistently sordid stramineous to golden hispid-strigose. Primary peduncles ($\frac{3}{4}$-)$1\frac{1}{2}$-3(-4) cm long × ($1\frac{1}{4}$-)$1\frac{1}{2}$-$2\frac{1}{2}$(-3) mm thick, of the same form as in inflorescence, sometimes more sparingly pubescent with the base internode frequently glabrescent; pedicels (10-)12-20(-25) mm long × ($\frac{2}{3}$ -)$\frac{3}{4}$-1(-$1\frac{1}{3}$) mm thick, often widely divaricate, longer, thicker, and more lignified than in inflorescence, often slightly expanded under hypanthium, sometimes more sparsely hispid. Fruiting hypanthium cylindrical-ovoid to narrowly ellipsoid-ovoid, hardly narrowed into a neck, (14-)17-20(-25) mm long × (5-)6-8(-9) mm thick, scarred towards the apex with lignified protuberances developed from the bases of caducous, rarely persistent perianth bracteoles, tepals, and staminodes, levigate towards the base, drying fawn to reddish brown, rarely blackish, sparsely hispidulous-strigillose, the hairs denser towards the apex, and densest and longest in the axils of the scars and lignified protuberances, the walls $(\frac{3}{4}-)1\frac{1}{4}-1\frac{1}{2}(-2)$ mm thick; rim elongated and obliquely erect, usually densely hispid, irregularly obscurely denticulate, with the innermost staminodes usually persistent; hypanthium chamber narrowly rounded at the base, densely short pale stramineous hispid towards the rim. Nutlets elongating in maturing hypanthium to increase the exsertion of the style tips to 1-2(-3) mm beyond the hypanthium rim; bodies of ripe nutlets fusiform, rarely narrowly ellipsoid, (3-)5-6(-8) mm long × $(\frac{2}{3}-)\frac{3}{4}-1(-1\frac{1}{2})$ mm thick, sordid dark stramineous to brownish silky hirsute, the hairs 7-11 mm long; styles of ripe nutlets (6-)8-13(-17) mm long, densely fine hispid at the apex.

The epithet *sempervirens* refers to the evergreen character of this species which apparently renders it distinct at a distance in forests of otherwise predominantly deciduous trees of *Nothofagus* (cf. Ruiz and Pavón 1798).

Indian names: Hague (herb. Bridges 668), Theygue (Molina 1810), Thihue (Molina 1810, Gay 1851 or 1852, Tulasne 1855, Perkins 1911, herb. Krause: US 1690278), Tihue (Muñoz-Pizarro 1959). These are apparently variations of the one name "Tihue" given to the species by the Araucanian Indians.

Vernacular name: Laurel (Ruiz and Pavón 1798, Bertero 1829, Gay 1851 or 1852, Tulasne 1855, R. Philippi 1857, C.Mueller in Walpers 1857, Perkins and Gilg 1901, Stapf 1909, Perkins 1911, 1925, Garratt 1934, Muñoz-Pizarro 1959, herb. Dombey, herb. Krause: US 1690278, herb. R.Morton Middleton: BM, leg. F.Philippi and Borchers 1885, R. Philippi 280).

Series of specimens examined: 39 collections, comprising 3 with expanding inflorescence buds, 13 with staminate flower buds, 17 with open staminate flowers, 10 with pistilliferous flower buds, 17 with open pistilliferous flowers, and 17 with near or fully mature fruiting hypanthia.

Several collections have been sometimes mixed on the one herbarium sheet, for example those of Dombey which include the lectotype of the species, and may comprise flowering and fruiting material together. Where they have identical data they are cited under one collection in Index I.

Geographic Distribution (map 7)

Laurelia sempervirens is confined to southern Chile, from the coast to the west scarp of the Andes, between 33° and ca 42°S:

Prov. Concepción. Tomé; Talcahuano ad Antuco; Concepción; environs of Concepción; Lota.

Prov. Arauco. Nahuelbuta Chacras Buenas.

Prov. Malleco. Capitan Pastenes, Alrededores.

Prov. Cautin. Maquehue; Temuco; Llolli?

Prov. Valdivia. Pangüipúlli; Calle-Calle; Valdivia;

Riñihue; Corral; colony Arique.

Prov. Osorno. Centinela; Osorno.

Prov. Llanquihue. Puerto Varas.

Chiloé? Sancta Carola*?

Perkins (1911), citing Dusén, records it from the coastal cordillera above Angol, Kuntze (1898) from Ercilla and southwards, and Skottsberg (1916) from near Ancud, Chiloé, and from Puella am Lago, Todos los Santos, and Perez Rosales Gap in prov. Llanquihue. Northwards, it has also been recorded at Puchacay, Itata, Rere, and Cauquenes (Ruiz and Pavón 1798). Looser (1934) considers it to have its northern limit in the San Fernando range at ca 34°S, but Oberdorfer (1960) implies that it may extend northward of Valparaiso (33°S) in confined areas where pockets of south Chilean or Valdivian laurel forest occur. Several earlier reviewers - Tulasne (1855), C.Mueller in Walpers (1857), A. de Candolle (1868), Perkins and Gilg (1901), and Perkins (1925) - quote its distribution as defined by Gay (1851 or 1852), i.e. Chile between 34° and 42°S (Chiloé). Pax (1889) gives it as Chile 34°- 32°S, the 32°S probably being a misprint for 42°S.

The species has also been recorded beyond Chile in Peru (Perkins 1911), and in the Patagonian Andes (Skottsberg 1916, Berry 1935, 1938). Its

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* One collection of the species is mixed with a collection of *Laureliopsis philippiana* on a sheet bearing the single locality "ex Sancto Carolo chiloensi" in herb. MA.

occurrence in both these regions is doubtful. Perkins' record was based on what she presumed to be a Pavón collection, and apparently part of the syntype series of Pavonia sempervirens. As is pointed out below, many of these specimens are labelled incorrectly with the printed locality "Pérou"; all of them came from Chile (cf. Macbride 1938).

Skottsberg's and Berry's records are from Lago Nahuelhuapi and Puerto Blest. They are not confirmed by herbarium collections seen, although there are several collections of the distantly related Laureliopsis philippiana available from these localities. Even though Skottsberg was aware of some of the differences between the species (cf. Perkins 1911), the possibility that he may have confused or mistaken them must be considered. The present environment of the region appears to be unsuitable for Laurelia sempervirens.

Schenk's (1905) record of the species from the "Feuerländischen Wald" is also doubtful for the same reasons and probably refers to Laureliopsis philippiana (chapter VII).

Ecology

Usually a tree of the forest canopy, rarely a tall shrub, Laurelia sempervirens is a prominent element of the "Valdivian" rainforest* or South Chilean laurel valley forest** with a subtropical aspect***.

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* Skottsberg (1910,1916,1960), Schimper & v. Faber (1935), Godley (1960), Kuschel (1960).

** Oberdorfer (1960).

*** Warming (1925).

It occurs mainly in mountains up to 2400 m altitude in the northern parts of its range (cf. Pöppig coll. 3, n.135), more extensively in the valleys and lowlands in the central parts, and to near sea-level in the south (Skottsberg 1916, Oberdorfer 1960). It is found frequently or usually in well-drained sites (cf. L. novae-zelandiae).

It is most frequent and sometimes a co-dominant in the laurel forest associations of Nothofagus obliqua - Persea lingue, and tique forest associations of Lapageria rosea - Aextoxicon punctatum. These range altitudinally between 400 and 800 m at 36°S near the centre of its geographic range, and down to sea-level between 38°-41°S. It is also occasional or rare in the Alstroemeria aurea - Aristotelia chilensis association, the Rhaphithamnus spinosum - Aristotelia chilensis association with Nothofagus obliqua, N. dombeyi, Drimys winteri, and Eucryphia cordifolia, and the Fuchsia magellanica-Aristotelia chilensis association with Nothofagus obliqua and Caldcluvia paniculata at higher altitudes (800-1700 m, at 36°S) and more southern latitudes (42°-43°S, at sea-level) (from Schmithüsen 1957, Oberdorfer l.c.).

According to R. Morton Middleton (coll. in herb.BM), Laurelia sempervirens was very abundant before the turn of the present century but has since become gradually scarcer, undoubtedly because of forestry operations and forest clearing.

Laureliopsis philippiana, the only other Chilean member of the family, occurs in cooler temperate rainforest at more southern latitudes. Where the ranges of the two species overlap, it is confined to higher altitudes (chapter VII, Looser 1934). [This relationship is comparable to that between Doryphora sassafras and Atherosperma moschatum in south-eastern Australia (figures 49, 50).]

Phenology

Flowering is seasonally regular, and occurs from September to November. One collection (Montaldo 1145, from prov. Arauco) has opening flowers in February. The fruit ripens between January and April, during which period the inflorescence buds for the ensuing season appear in the uppermost leaf axils.

Inflorescence elongation and flower bud enlargement do not commence until a month or so before flowering, so that the inflorescence and flower bud primordia remain enclosed by the base primary peduncle node bracts during the austral autumn and winter months in the same manner as those in Atherosperma and Doryphora.

Infraspecific Variation

No well-marked or consistent variation in the vegetative characters of the ultimate branchlets, or in the characters of the flowers and fruit, was apparent in the series of specimens examined.

It may be significant that those collections from the northern part of the geographic range of the species (coll. Dombey, Claude-Joseph 4842, from Temuco) have generally larger and broader leaves than those from farther south. Collections from Riñihue, originally, (Kausel 38), and Puerto Varas (Hicken: SI) at the southern limit of its range have the smallest and narrowest leaves of any seen. But it is uncertain how much these characters are affected by altitude or the position in the tree crown, whether exposed or shaded, from which the specimens were taken. Altitudes have been rarely recorded on the specimen labels and are not given on any of the above collections. The flowering collection with the largest and broadest leaves seen (Buchtien 25.XI.1896: GH, L, US, from Calle-Calle) is from near the southern geographic limit of the species and appears, from its sub-coriaceous leaf texture and general lack of pubescence, to have come from shaded rather than exposed branches.

Taxonomic Notes and Typification

So tangled is the taxonomic and nomenclatural history of *Laurelia sempervirens* that a detailed account is given below.

The species was first described under the name *Pavonia sempervirens* by Ruiz and Pavón (1798) from observations and material collected in Chile in 1782-3 by the great botanical exploring expedition to Peru and Chile fostered by the Spanish Crown. Because the collection of type material has been attributed to Pavón (and Ruiz) (Perkins 1911, collections in herb. K), it is necessary to point out that of the Chilean specimens collected by the expedition's three botanists, Ruiz, Pavón, and Dombey, only those of Dombey reached Europe safely. The Ruiz and Pavón collections were lost at sea with the foundering of the San Pedro de Alcántara (vide Steele 1964). Herbarium sheets on which Ruiz and Pavón or Pavón are indicated as the collectors are probably from the poorer duplicate set Dombey had to leave in Spain before being allowed to take his collections to France. Three sheets loaned by herb. MA for study bore no collectors' names.

Because *Pavonia sempervirens* was described from a range of flowering and fruiting material gathered obviously over several months, it may be typified by Dombey's entire collections of the species. A number of these bear the incorrect locality "Peróu" printed on the label. The error may be explained by the fact Dombey's and the expedition's collecting was centred in that country. Macbride (1938) quotes a type collection in herb. MA labelled with the locality Concepción. But as there are at least three different collections of the syntype series there and two bear the locality Conception or Conceptione, he cannot be held to have indicated a lectotype. A lectotype, therefore, has been chosen here, in accordance with the provisions of the Guide for the Determination of Types, I.C.B.N. 1966.

De Jussieu proposed the name *Laurelia* in 1809 to replace *Pavonia* Ruiz & Pav. (1794), a later homonym of *Pavonia* Cav. (1786). He considered the genus only, ignoring the species involved, and it was not until 1855 that Tulasne made the correct combination *Laurelia sempervirens*.

Meanwhile Poiret (1813), adopting de Jussieu's name for the genus, published the species under a new name, *Laurelia aromatica*. Based on *Laurelia* Juss. and in turn *Pavonia* Ruiz & Pav. without the inclusion of any new material, it is a nomenclatural synonym of *Pavonia sempervirens* Ruiz & Pav. The combination *Laurelia aromatica* has been attributed wrongly to de Jussieu (1809) by Sprengel (1825), A. Cunningham (1838), Willis (1931), Garratt (1934), Metcalfe and Chalk (1950), Hutchinson (1964), and Airy Shaw (1966). Gay (1851 or 1852) and F. Philippi (1881), moreover, have attributed it to Sprengel (1825).

The monographic treatments of Tulasne (1855), de Candolle (1868), Baillon (1869), Perkins and Gilg (1901), and Perkins (1911) and the comments by Stapf (1909) have shown clearly that Laurelia sempervirens is the correct name for the species and that Laurelia aromatica is superfluous. It is regrettable, then, that the latter name has been used persistently in a number of modern general texts in the fields of ecology (Schimper and von Faber 1935), anatomy (Metcalfe and Chalk 1950), palynology (Erdtman 1952), taxonomy (Core 1955), plant geography (Good 1964), as well as in revisions (Hutchinson 1964), and dictionaries (Airy Shaw 1966).

Laurelia chilensis A.Cunn. (1838) is also a nomenclatural synonym of L. sempervirens. Without mentioning any new material, Cunningham proposed it as a new name for the species to which the names Pavonia sempervirens, Laurelia aromatica, and Theyga chilensis had already been given. It is doubtful whether Theyga chilensis is the basionym because Cunningham, although citing it with the other above names in synonymy, does not indicate it as such. Laurelia chilensis has not been taken up by any subsequent author and is not listed in Index Kewensis.

There are three taxonomic synonyms of Laurelia sempervirens. The first described is Theyga chilensis Mol. (1810). No type has been located and, according to Professor F. Bertossi (pers. comm.), Molina's collections were lost about 1770 in transit from Santiago to Bologna. Nevertheless, there is little doubt that Molina's species is the same as *Laurelia sempervirens*. Not only are its two descriptions on pages 163 and 297 respectively of the second edition of his Saggio Chile compatible with *Laurelia sempervirens*, but also the Indian name "Thihue" quoted for it (p.297) is the same (see Indian names).

Tulasne (1955) and de Candolle (1868), however, were misled to believe that *Theyga chilensis* Mol. in the second edition of the Saggio was synonymous with *Salix chilensis* Mol. in the first edition (1782, p. 169) [p.140 in the French translation by Gruvel (1789)], undoubtedly on account of the similarity in the Indian name, "Thiege", given for *Salix chilensis*. The issue is further complicated by Molina who used two names in the second edition for the genus: *Theyga chilensis* (p.163) and *Thiga chilensis* (p. 297). Most subsequent authors have cited the generic name as *Thiga*. De Candolle (l.c.), incidentally, quotes Sprengel as its author.

The second is *Laurelia serrata* Bert. (1829). The only type specimen seen is sterile and falls within the range of *L. sempervirens*. Looser (1934) has already poihted out that it is not distinct from *L. sempervirens*.

The third, *Laurelia crenata* Pöpp.ex Tul. (1855), is without nomenclatural status. It is based on Pöppig coll.3 pl. Chil. n.135, of which one sheet in herb. BM has been seen. A branchlet with staminate ~~flower~~

buds, it falls within the range of variation of *Laurelia sempervirens*. The name has always been cited in synonymy with *L. sempervirens* and is therefore not validly published (I.C.B.N.1966, Art.34); it also lacks a description.

Two further names appear in the literature. One, *Atherosperma sempervirens* (Ruiz & Pav.)Baill. (1868) is the formal combination made by Baillon when uniting the genus *Laurelia* with *Atherosperma*. The other, *Laurelia odorata* Schmithüsen (1957), is a nomen nudum apparently printed in error for *L. aromatica* Poir.

Laurelia sempervirens has also been confused taxonomically with *Laureliopsis philippiana*, the other Chilean member of the family, by A. de Candolle (1868), Pax (1889), Perkins and Gilg (1901), and others. The two are remarkably similar in gross leaf and inflorescence form, as has been mentioned in chapter VII. In both, for example, the ultimate branchlet internodes are relatively densely curly hispid-strigose, the leaf blades have planate midribs on the upper face, and the inflorescences are thyrsiform and hairy.

Laurelia sempervirens may be readily distinguished, nevertheless, by its simple if sometimes tufted strigose leaf hairs, its more elaborate inflorescences, its usually unisexual flowers, its apiculate anthers with peltate glands in staminate flowers, and its elongate ellipsoid fruiting hypanthia with scarred apices and ultimately caducous perianth. Diagnostic field characters are its more obtusely or broadly elliptic or obovate leaves with more bluntly crenate margins, and its sweet, almost sickly, safrol-like or camphoraceous odour in the bark and leaves.

It is the only species in the family in which a hypodermal layer has been recorded on the underside of the leaf blade (Hobein 1888, Solereder 1899).

Chemistry

No information traced.

Uses

The pleasantly aromatic leaves and bark are used locally in Chile for preparing tea-like infusions and as cooking or pickling spices (Ruiz and Pavón 1798, Gay 1851 or 1852, Tulasne 1855, Pax 1889, Perkins and Gilg 1901, Perkins 1925, Willis 1931, Garratt 1934, Buchheim 1964). The fruiting hypanthia, known as Peruvian nutmegs, have also been used for this purpose (Willis 1931, Metcalfe and Chalk 1950, Core 1955, Hutchinson 1964, Airy Shaw 1966). Ruiz and Pavón (1798) add that the crushed leaves may be employed as an inhalant for curing catarrh and clearing the nose. Bertero (fide Ruschenberger 1833) gives an engaging account of its uses, recording, inter alia, that beverages and fumigations from the leaves are respectively antivenereal and useful for convulsions and paralytic diseases. Baillon (1877) mentions the value of the bark as a stimulant and digestive.

The wood, being easily cut and worked, is used widely in the making of furniture, and also as poles, stakes, and timber beams in building and general construction work (Ruiz and Pavón l.c., Gay l.c., herb. R. Morton Middleton: BM).

2. *Laurelia novae-zelandiae* A.Cunn.

Laurelia novae-zelandiae A.Cunn., Ann.Nat.Hist. 1(1838)381 "L. Novae Zelandiae"; Raoul, Choix Pl.N.-Zél. (1846)42 "Laurelia Novae Zelandiae"; Hook.f., Fl.N.Zel. 1(1853)218, f.51 "Laurelia Novae-Zelandiae"; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)291 "Laurelia Novo-Zeelandiae", 417 "Laurelia Novae-Zeelandiae"; C.Muell.in Walp., Ann.Bot. 4(1857)116 "Laurelia Novae Zeelandiae"; [Hook.f., Handb.N.Zeal.Fl. 1(1864)240 pro syn. *Atherospermatis novae-zelandiae*]; A.DC., Prod. 16,2(1868) 675; Hobein, Bot.Jb. 10(1888)71; Kirk, For.Fl.N.Zeal. (1889) 33,130, pl. 71; Pax, Pflzfm. 3,2(1889)103, f.67D "Laurelia Novae-Zeelandiae"; Bancroft, Proc.Linn.Soc.N.S.Wales 2,4(1890) 1061; [O. Kuntze, Rev.Gen. 2(1891)568 pro syn. *Pavoniae novae-zelandiae*]; Perk. & Gilg, Pflzr. 4(1901)11,77, f.21L-M; Cheesem., Man.N.Zeal.Fl. (1906)600 "Laurelia novae-zealandiae"; Laing & Blackwell, Pl.N.Zeal. (1906)174; Dusén, Wiss.ergeb. Schwed.Südpolar-exped. 3,3(1908)4; Malcolm, Ann.Rep.Dept.Agric. N.Zeal. (1908) [n.v.]; Aston, J.Chem.Soc. 97(1910)1381; Kirk, N.Zeal.Pl. (1910)41; Perk., Pflzr. 49(1911)46; Petrie, Proc Linn.Soc.N.S.Wales 37(1912)152 "Laurelia Novae-Zealandeae"; Cheesem., Man.N.Zeal.Fl. ed.2,(1925)458 "Laurelia novae-zealandiae"; Perk., Gattung.Monim. (1925)13,51, f.39L-M; Allan, N.Zeal.Trees Shrubs (1928)117,168; Barger & Girardet, Helv.Chim.Acta 14(1931)481 [n.v.]; Girardet, ibid. (1931)504 [n.v.]; Willis, Dict.Fl.Pl.Ferns ed.6,(1931)365" Laurelia Novae-Zealandiae"; Barger & Schlittler, Helv.Chim.Acta 15(1932) 381 [n.v.]; Schlittler, ibid. (1932)394 [n.v.]; Garratt, Trop.Woods 39(1934)19 et seq.; Richards, N.Zeal.Trees Flowers (1947)15, f.; Henry, Pl.Alkaloids ed.4,(1949)322; Metcalfe & Chalk, Anat.Dicot. 2(1950)1139 et seq., f.276B "Laurelia novae-zeylandiae"; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)383 et seq., text f.15, f.II.25, IV.42; Erdtman, Pollen Morph. & Pl.Taxon. (1952)271; Cranwell, Bull.Auckl.Inst.Mus. 3(1953)73, text.f.2,f.I.12,VIII.20; Couper, N.Zeal.Geol.Surv.Bull. 22(1953)13,40, f.V.44,45 "Laurelia cf. novae-zealandiae"?; Manske in Manske & Holmes, Alkaloids 4(1954)134,137 "Laurelia novae-zelandae"; Core, Plant Taxon. (1955)318 "L. novae-zealandiae"; Davies, N.Zeal.Nat.Pl.Stud. (1956)99, f.35; Hinds & Reid, For.Trees & Timb.N.Zeal. (1957)103, map; Cockayne, Veg.N.Zeal. ed.3,(1958)121 et seq.; Cockayne & Turner, Trees N.Zeal. ed.4,(1958)20,71,161, f.49; Hair & Beuzenberg, N.Zeal.J.Sci. 2(1959)150, f.21 "Laurelia novae-zealandiae"; Couper, N.Zeal.Geol.Surv.Paleontol.Bull. 32(1960) 36,47?; Allan, Fl.N.Zeal. 1(1961)139; Dansereau in Gressitt, Pacif.Basin Biogeogr. (1963)295; Poole & Adams, Trees & Shrubs N.Zeal. (1963)41 (f.),44; Good, Geogr.Fl.Pl.ed.3,(1964)222 "Laurelia novae-zealandiae"; Hutchinson, Gen.Fl.Pl. 1(1964)121; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7,(1966)623; Salmon, N.Zeal.Fl.Pl. (1963)68, pl.180-182; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342 "L. novae-zealandiae".

TYPE: A.Cunningham (79), near the Keri Keri river [Bay of Islands], Oct.1826 —— holotype in K, isotypes in A(?), BM (Allan 1961), K,MEL,SING.

Atherosperma novae-zelandiae (A.Cunn.)Hook.f., Handb.N.Zeal.Fl. 1(1864)240 "Atherosperma novae-Zelandiae"; Baill., Hist.Pl. 1(1869)323,336, f.366-368; Baill., Dict.Bot. 1(1877)310, f.; [Kirk, For.Fl.N.Zeal. (1889)130 pro syn. *Laureliae novae-zelandiae*].

Pavonia novae-zelandiae (A.Cunn.)O.Kuntze, Rev.Gen. 2(1891)568 "P. Novozelandiae"; [Perk. & Gilg, Pflzr. 4(1901)77 pro syn. *Laureliae novae-zelandiae*].

The following illustrations referred to as this species in Index Londinensis have not been seen: Baillon, Traité Bot. Méd.Phan. 1(1883) 531 (*Atherosperma novae-zelandiae*); Cockayne, N.Zeal.Pl. ed.2,(1919)137.

Figures 30, 45D.

Diagnosis

Trees 25-30(-40) m high; bark pale cream-grey to whitish; ultimate branchlet stems ± sparsely off-white to greyish or golden hispidulous-strigillose, without bracts at base of lateral branchlets; leaf blades obovate to spathulate, rarely elliptic or ovate, ± broadly obtuse, (2-)3-5$\frac{1}{2}$(-7) cm long × (1$\frac{1}{4}$-)2-3$\frac{1}{2}$(-4$\frac{1}{4}$) cm broad, with deeply ± closely crenate-dentate margins, and clearly prominulous vein reticulum extensive on lower face; all parts ± non-aromatic.

Mature inflorescences slenderly raceme-like, (1-)1$\frac{3}{4}$-3(-4$\frac{1}{2}$) cm long, pale grey-stramineous hispid-strigose; base internode of primary peduncle hardly different from distal internodes in dimensions and pubescence; pedicels 2-4(-5) mm long × ± $\frac{1}{3}$(- $\frac{2}{3}$) mm thick in staminate flowers, ($\frac{2}{3}$ -)1$\frac{1}{2}$-3$\frac{1}{2}$(-7) mm long × ($\frac{1}{3}$ -)$\frac{1}{2}$-$\frac{3}{4}$(-1) mm thick in pistilliferous flowers.

Open staminate flowers small; receptacle glabrous among stamens; perianth 4-5(-6)-partite, the inner tepals (2-)2$\frac{1}{2}$-3$\frac{1}{2}$(-4) mm long × 2-3 mm broad, sepaloid to sub-petaloid, densely strigose-tomentose; stamens (2-)2$\frac{1}{2}$-3(-3$\frac{1}{4}$) mm long, with filaments ± glabrous adaxially. Open pistilliferous flowers small; hypanthium (1$\frac{1}{4}$-)1$\frac{1}{2}$-2$\frac{1}{2}$(-3$\frac{1}{2}$) mm long × 1$\frac{1}{2}$-2 (-2$\frac{1}{2}$) mm thick, the rim flat or convex, glabrous; perianth (4-)5(-7)-partite, the perianth bracteoles elliptic-ovate, obscurely mucronulate obtuse, tepal-like, (2-)2$\frac{1}{2}$-3(-3$\frac{1}{2}$) mm long × 2-2$\frac{1}{2}$(-3) mm broad, contiguous with tepals, the inner tepals 2-3(-4) mm long ×(1$\frac{1}{2}$-)± 2(-3) mm broad, sepaloid to sub-petaloid, densely strigose-tomentose; androecium often partly fertile, comprising 1 outer whorl of 4(-5) fully or partly functional stamens, and 2-3(-4) inner whorls of (10-)12-15(-18) batilliform, ± entirely glabrous staminodes; gynoecium of (7-)8-12(-15) carpels, the stigmatic column slenderly conical, $\frac{1}{4}$-$\frac{1}{2}$ mm long.

Ripe infructescences with pedicels (2-)3-5(-7) mm long; fruiting hypanthium ± urceolate, levigate towards the apex, pusticulate towards the base; bodies of ripe nutlets narrowly ellipsoid to ovoid, (5-)6-8 (-9) mm long × (1$\frac{1}{2}$-)2-2$\frac{1}{2}$ mm thick.

Detailed Description

Tall trees ca 25-30(-40) m high; bole ca 60-100(-150) cm diameter above buttresses, extensively buttressed with plank buttresses; root root grafting and suckering from lateral roots frequent, often developing slender compressed, lenticellate, dichotomously branched aerial roots ca 1$\frac{3}{4}$-2$\frac{1}{4}$ mm in diameter, and upright, broad, or conical pneumatophores ca 12 mm high*; crown rather narrow, ca as long as or longer than bole, with many separate corymbiform heads of foliage on large sub-erect branches. Bark 8-12(-15) mm thick when dry, outer surface rather smooth, pale cream-grey to almost white, inside very pale buff-brown, drying pale brown. Wood pale cream to dull grey-brown, drying with yellowish or greenish tints, the duramen darker, often prettily streaked and clouded dark brown**. Branchlet stems relatively closely branched, ultimate

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* Cockayne (1958).

** Kirk (1889), Cheeseman (1906, 1925), Laing and Blackwell (1906), Cockayne and Turner (1958).

4-6(-8) internodes (¾-)1-3(-4½) cm long × (1-)1½-2½(-3) mm thick, compressed angular tetragonous, smooth, drying dark grey-fawn to blackish brown or grey, sparsely, rarely densely off-white to sordid grey or golden brown hispidulous-strigillose, glabrescent below; shaded and sapling branchlet stems with ultimate 4-6 internodes (1-)2-5(-7) cm long, more markedly angular tetragonous, marone-purple tinted, drying grey- to olive-brown, more sparsely pubescent, sometimes entirely glabrescent; bracts at base of lateral branchlet stems lacking. Petioles slender, (3-)5-9(-12) mm long × 1-1½ mm thick, shallowly and narrowly impressed or planate on upper face, sparsely sordid stramineous to grey-white hispidulous or glabrescent. Leaf blades obovate to spathulate, rarely rather elliptic, circular, or ovate, (2-)3-5½(-7) cm long × (1¼-)2-3½ (-4¼) cm broad, narrowly to broadly ± cuneate at the base, broadly, less often narrowly obtuse at the apex; margins usually deeply and rather closely crenate-dentate, rarely shallowly crenate, slightly to markedly recurved; texture thinly to quite coriaceous, rarely thick, the upper face smooth, obscurely lined with prominulous nerves, rarely vein reticulum; colour rather glossy mid to dark green on upper face, paler but glossy on lower, in dry leaves pale grey-brown to dull-brown on both faces; nervation on upper face as described, with midrib planate or sometimes shallowly impressed towards the petiole, on lower with (5-)6-8 (-10) ± prominent nerves anastomosing conspicuously, the vein reticulum clearly prominulous, extending between the nerves towards the midrib; glabrescent, or persistently and obscurely sparse sordid stramineous hispid-strigose; leaf blades on shaded and sapling branchlets (3½-)5-7 (-10) cm long × (1¾-)3-4(-5) cm broad, with more deeply crenate-dentate, planate margins, subcoriaceous to chartaceous, nerves and vein reticulum more, often equally prominent on both faces, ± glabrous. Bark, wood, and stems ± odourless, fresh leaves very weakly fragrant*.

Mature inflorescences slender, raceme-like thyrsiform, rarely divergently branched from the base, monoecious or polygamous, sometimes staminate, the monoecious-polygamous inflorescences borne at ultimate 1-3 leaf nodes on branchlets, (1-)1¾-3(-4½) cm long, the staminate inflorescences at nodes below, (1-)1¼-2¼(-3) cm long, when both occur on the same stem, sordid pale grey-stramineous hispid-strigose, monoecious-polygamous inflorescences bearing 7-11(-23) flowers, and staminate inflorescences (5-)7-9(-11) flowers. Primary peduncles (1¼-)1½-2½(-3½) cm long × (½-)¾-1½(-1¾) mm thick in monoecious-polygamous inflorescences, (½-)1-1¾ (-2½) cm long × ± 1 mm thick in staminate inflorescences, the base internode hardly more broadly compressed than the slenderly tetragonous distal internodes, ± uniformly and usually rather densely sordid stramineous to sordid pale grey-green hispid-strigose, with hairs rarely darker or sparse on the base internode, (1-)3-4(-5)-noded, the subterminal nodes usually single-flowered, rarely bearing secondary peduncles at basal 1-2 nodes; base node bracts of primary peduncle narrowly to broadly

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* Cheeseman's comment (1906, 1925) that the fresh stems and leaves are strongly aromatic when bruised seems to be an exaggeration.

ovate-deltate, shallowly cymbiform-navicular, (1½-)2-4(-5) mm long × (1-)1½-2½(-3) mm broad; distal node bracts narrower ovate-deltate, shallowly navicular, (2-)2½-3(-5) mm long × 1-2 mm broad; secondary peduncles ½-1¼ cm long, 1-2-noded; pedicels in staminate flowers 2-4(-5) mm long × ± ⅓(- ⅔) mm thick, in pistilliferous flowers (⅔ -)1½-3½(-7) mm long × (⅓ -)½-¾(-1) mm thick, terete or somewhat tetragonous where terminally central, usually densely sordid off-white to golden stramineous or pale greenish grey hispid-strigose, the terminally central pedicels frequently bracteolate. Mature staminate flower buds (2-)2½-3 mm long × (2-)2½-3 mm thick, uniformly densely sordid off-white to golden stramineous strigose-tomentose, almost hirsute; mature pistilliferous flower buds cylindrical-ellipsoid, 3½-4 mm long × 3 mm thick, pubescent as in staminate flower buds.

Open staminate flowers small. Receptacle (¼-)½(-¾) mm long × (¼-)¾-1(-1½) mm broad, ± densely pale stramineous to pale grey-green hispid-strigose outside, glabrous inside among stamens. Perianth broadly cyathiform to shallowly patelliform, 4-5(-6)-partite in 2 whorls; outer pair of perianth bracteoles elliptic to broadly ovate, shallowly cymbiform, (2-)2½-3½(-4) mm long × (2-)2½-2¾(-3) mm broad, with obtuse obscurely mucronate apices, herbaceous, obscurely 1-nerved, densely sordid stramineous to pale grey-green strigose-tomentose abaxially, with hairs denser and longer along a median keel, sparingly haired, almost glabrous adaxially, with hairs confined towards the base of median nerve; tepals 2-3(-4), broad oblong to ovate, obovate, or almost circular, planate to slightly cymbiform, (2-)2½-3½(-4) mm long × 2-3 mm broad, with broadly obtuse apices, and entire, sometimes hair-fringed margins, sepaloid or sub-petaloid, ± obscurely 3(or 5)-nerved from the base with midnerve obscurely prominent, pubescent as in perianth bracteoles. Androecium comprising (4-)6-10(-11) stamens (2-)$2\frac{1}{2}$-3(-$3\frac{1}{4}$) mm long × $\frac{3}{4}$-1 mm broad × $\frac{1}{4}$-$\frac{1}{2}$ mm thick; filaments ($\frac{3}{4}$-)1-$1\frac{1}{2}$(-$1\frac{3}{4}$) mm long × ± $\frac{1}{2}$ mm broad, sparsely, rarely densely pale stramineous strigillose abaxially, usually glabrous adaxially; staminal glands elliptic-circular, $\frac{2}{3}$ - $\frac{3}{4}$(-1) mm long × $\frac{1}{3}$ - $\frac{2}{3}$ mm broad; anthers (1-)$1\frac{1}{4}$-$1\frac{1}{2}$(-$1\frac{3}{4}$) mm long × $\frac{3}{4}$-1 mm broad, glabrous.

Open pistilliferous flowers small. Hypanthium poculiform to poculiform-urceolate, ($1\frac{1}{4}$-)$1\frac{1}{2}$-$2\frac{1}{2}$(-$3\frac{1}{2}$) mm long × $1\frac{1}{2}$-2(-$2\frac{1}{2}$) mm thick, densely sordid stramineous to greyish hispid- or silky-strigose, the bracteoles contiguous with perianth, very rarely borne slightly below on the sides of the hypanthium; rim narrow, rather flat or convex, ca $\frac{1}{3}$ - $\frac{1}{2}$ mm wide, glabrous. Perianth broadly cyathiform to shallowly patelliform, usually spreading less than in staminate flowers, (4-)5(-7)-partite in 2[*] whorls of the same form and pubescence as in staminate flowers; perianth bracteoles as in staminate flowers, but often more shallowly cymbiform, smaller, (2-)$2\frac{1}{2}$-3(-$3\frac{1}{2}$) mm long × 2-$2\frac{1}{2}$(-3) mm broad; tepals as in staminate flowers, but often more planate and smaller, 2-3(-4) mm long × ($1\frac{1}{2}$-) ± 2(-3) mm broad, with more obscure nerves. Androecium partly, rarely entirely, sterile, 2-4(-5)-seriate, the whorls subequal, the outer

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[*] 9-10 perianth parts in 3 whorls of 2, 3, and 4-5 in some pistilliferous flowers of one collection, Mathews: WELT 17918.

whorl comprising 4(-5) fully or partly fertile stamens and staminodes, rarely entirely sterile, the inner whorls (10-)12-15(-18) variably batilliform staminodes; fully or partly functional stamens $2-2\frac{1}{2}$ mm long, with filaments more sparsely strigillose abaxially, and staminal glands smaller and attached more towards base of filament than in staminate flowers, the anther thecae often partly aborted; staminodes erect to rather reflexed towards the apex, the outer staminodes stamen-like to batilliform, $(1\frac{1}{2}-)1\frac{3}{4}-2(-2\frac{1}{3})$ mm long × $\frac{1}{2}-1$ mm broad, the inner staminodes narrower batilliform, $(\frac{3}{4}-)1-1\frac{1}{2}$ mm long × $(\frac{1}{4}-)\frac{1}{3}-\frac{1}{2}(-\frac{2}{3})$ mm broad, glabrous, or the outer staminodes occasionally sparsely strigillose abaxially. Gynoecium of (7-)8-12(-15) carpels; styles exserted ca $1-1\frac{1}{2}(-2)$ mm beyond hypanthium rim in a slenderly cylindrical or narrowly conical column; stigmatic column slenderly curling conical, $\frac{1}{4}-\frac{1}{2}$ mm long, exserted to apices of outer staminodes and stamens.

Ripe infructescences $(2-)3\frac{1}{2}-4\frac{1}{2}(-6)$ cm long, ± sparsely sordid stramineous to pale grey or brownish hispidulous-strigillose, ultimately glabrescent. Primary peduncles $(1-)1\frac{1}{2}-2\frac{1}{2}(-3)$ cm long × $1-1\frac{1}{2}$ mm thick, of the same form as in inflorescence, more sparingly pubescent to occasionally glabrescent; pedicels (2-)3-5(-7) mm long × $(\frac{1}{2}-)1(-1\frac{1}{2})$ mm thick, longer, thicker, and more lignified than in inflorescence, hardly at all expanded under hypanthium, sparsely haired to glabrescent. Fruiting hypanthium slenderly urceolate to cylindrical-urceolate, (15-)17-20(-25) mm long × 6-8 thick, narrowed into a long neck ca $\frac{1}{2}-\frac{2}{3}$ × length of hypanthium, levigate towards the apex and sparsely ± conspicuously pusticulate towards the base, rather glossy mid green, drying pale to mid greyish brown, uniformly sparsely hispidulous-strigillose to glabrescent, the walls ($\frac{3}{4}$-)1-1$\frac{1}{2}$ mm thick; rim unenlarged, flat, glabrous, irregular with variably persistent lignified bases of perianth parts and staminodes; hypanthium chamber spherical at the base, glabrous towards the rim. Nutlets elongating in maturing hypanthium to maintain the exsertion of the style tips 1-2 mm beyond the hypanthium rim; bodies of ripe nutlets narrowly ellipsoid to narrowly ovoid, (5-)6-8(-9) mm long × (1$\frac{1}{2}$-)2-2$\frac{1}{2}$ mm thick, sordid grey-white to fawn or brown silky hirsute, the hairs (8-)9-11(-12) mm long; styles of ripe nutlets (8-)9-14(-16) mm long, finely hispidulous to glabrous at the apex.

2-4-noded seedlings ca 6-13 cm high, the stem internodes tetragonous, 5-20 mm long, smooth, glabrous; terminal buds sparsely golden grey hispid; cotyledons with petioles 2-4(-5) mm long, and blades elliptic to ovate, 12-14(-16) mm long × 6-10 mm broad, with obtuse bases, broadly obtuse apices, entire planate margins, chartaceous texture, obscurely reticulate venation, with or without occasional whitish hispid hairs on both faces; first leaf pair with petioles 4-5 mm long, and blades more broadly orbicular to obovate or spathulate, 9-15 mm long × 9-10 mm broad, with somewhat cuneate bases, broadly obtuse apices, deeply crenate-dentate margins, ± chartaceous texture, without hairs; successive leaf pairs progressively larger and approaching the form and pubescence of leaves of adult trees.

Maori names: Pukatea (Hooker 1853, Tulasne 1855, Kirk 1889, Bancroft 1890, Cheeseman 1906, 1925, Laing and Blackwell 1906, Kirk 1910, Allan 1928, 1961, Richards 1947, Henry 1949, Davies 1956, Hinds and Reid 1957, Cockayne 1958, Cockayne and Turner 1958, Allan 1961, Poole and Adams 1963, Salmon 1963), or apparently incorrectly Bukatea (Laing and Blackwell l.c.), Puketea (Allan 1961), and Pucatea (C.Mueller 1857). [The names Tawairo (Tulasne l.c.) or Towairo (C.Mueller l.c.), have been cited possibly in error for *Beilschmiedia tawa*, *B. tararai*, or *Weinmannia sylvicola*.]

Series of specimens examined: 63 collections, comprising 3 with expanding inflorescence buds, 17 with staminate flower buds, 29 with open staminate flowers, 10 with pistilliferous flower buds, 22 with open pistilliferous flowers, 13 with near or fully mature fruiting hypanthia, 3 of seedlings, and 1 with aerial roots.

Geographic Distribution (map 8)

Laurelia novae-zelandiae occurs throughout the North Island of New Zealand except the central plateau about Lake Taupo, 35°-41°30′S, and the northern and western coast of the South Island of New Zealand, south to 42°S in the north-east and 46°S in the south-west:

North Island. Fairburn; Kaitaia; Kaiaka; Kerikeri river; Kohukohunui; Whangarei; Waipoua; Paparoa Kaipara; Kaipara; Little Barrier island; Huia, southern end of Waitakere range; Titirangi; Auckland, Ellerslie Racecourse; Manukau Harbour; Mauku; Papakira; Nguruawahia; Dunphail farm, Te Akatea; Glen Massey, Te Akatea; Pukeamaru; Mt. Hikurangi; Egmont National Park; Foxton; Otaki Forks-

Waitatapia; Waikanae; Kaitoke Water Reserve; Porirua; Horokiwi; Wairarapa; Lake Ponui; Makara; Wainuiomata valley; Mt. Mathews.

South Island. Catherine's Cove, D'Urville island; Nelson; Ngakuta inlet; Kenepuru; Marlborough Sounds; Greymouth (introduction?).

In the North Island, the species is most abundant in two areas, between Raglan Harbour and the Mokau river adjacent to the west coast, and between Te Aroha and Rotorua adjacent to the Bay of Plenty (Hinds and Reid 1957). In the South Island, it has been recorded from Nelson and Marlborough provinces no farther south than ca 42°S by Laing and Blackwell (1906), Allan (1928), Davies (1956), Hinds and Reid (1957), Cockayne (1958), Cockayne and Turner (1958), and Poole and Adams (1963). Kirk (1889), Cheeseman (1906, 1925), Richards (1947), Allan (1961), and Salmon (1963), however, indicate that it is also rare and local in west coast areas southwards in the Westland and Southland provinces to 46°S (Preservation Inlet). No specimens have been seen from these southern localities.

Ecology (figure 54)

Laurelia novae-zelandiae is a tree of the forest canopy or subcanopy of primary subtropical rainforest in general, and of lowland "semi-swamp" forest communities in particular (Hinds and Reid 1957, Cockayne 1958*, Cockayne and Turner 1958*, Allan 1961, Poole and Adams 1963, Salmon 1963). It occurs from sea-level to 600 m altitude, rarely to ca 1600 m as at Mt. Hikurangi (Petrie: WELT 17917) in the North Island, and to 150 m in the South Island (Hinds and Reid 1957).

It is confined mainly to swampy land or damp shaded banks of streams and gullies, is intolerant of drought, and has been termed a "semi-obligate" swamp species by Cockayne (1958). Aerial roots and pneumatophores have been undoubtedly developed in response to the habitat. Nevertheless, the species occasionally occurs in drier situations, though always where rainfall is well distributed through the year (Hinds and Reid 1957, Cockayne and Turner 1958). Shunning frost and snow, it is found at its southern limits only in sheltered sites with a sunny aspect (Hinds and Reid 1957).

It has been recorded on deep fertile soils that are persistently wet or inclined to bogginess, irrespective of whether they are derived from limestone or pumice (Hinds and Reid 1957); it is therefore tolerant of ~~a wide~~ some range of soil pH. The latter rock forms soil with greater

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* Richards (1952) refers to the rainforest in New Zealand (and southern Chile) as temperate or antarctic, because it is dominated by temperate-latitude species such as *Nothofagus*, and has a flora which is not tropical. Cockayne (l.c.) and Cockayne and Turner (l.c.) nevertheless distinguish between the subtropical rainforest and temperate or sub-antarctic (*Nothofagus*) forest of higher altitudes and latitudes in New Zealand.

moisture retentivity.

Laurelia novae-zelandiae usually occurs in forests of mixed tree species, but is frequently associated with *Podocarpus dacrydioides* as a sub-dominant in what has been termed Kahikatea semi-swamp forest (Cockayne 1958). At Waipoua forest, south of Hokianga, it is also co-dominant with *Rhopalostylis sapida* (Nikau palm) (Cockayne 1958). Other trees with which it is frequently associated are *Beilschmiedia tarairi*, *Dysoxylum spectabile*, *Vitex lucens*, and *Weinmannia sylvicola* in the north part of the North Island, 35°-38°S, and *Beilschmiedia tawa*, *Dacrydium cupressinum*, *Dysoxylum spectabile* (cf. Walker 5167), *Podocarpus ferrugineus*, *P. spicatus*, and *P. totara* over the southern part of the North Island. *Laurelia novae-zelandiae* is a host tree to many epiphytes, particularly *Freycinetia banksii* and *Metrosideros robusta* (Hinds and Reid 1957).

Phenology

Flowering is seasonally regular, and occurs from late September to November. Aberrant specimens have been recorded in flower in February (Thomas: SING, from Titirangi) and March (Petrie: WELT 17919, from Te Akatea). The fruit ripens and dehisces between February and May, rarely persisting until July (or November, cf. Sampson 1967). The inflorescence buds for the ensuing season begin to appear between March and May, usually before the ± mature ~~fruit has~~ nutlets have been disseminated. The flowering and fruiting periods recorded by Allan (1961) are not consistent with those indicated by the series of herbarium collections seen.

A detailed account of the annual cycle of initiation and maturation of organs and spores in the inflorescence and infructescence in trees at New Plymouth has been given by Sampson (1967).

Infraspecific Variation

Laurelia novae-zelandiae appears to be a rather monomorphic species. In the series of specimens examined, no well-defined or consistent variation in vegetative, floral, or fruit characters could be related to geographic or altitudinal position.

Taxonomic Notes and Typification

Since its description in 1838, the species has been accepted by all revisers. No forms have been distinguished.

The chromosome number, n = 22, has been reported by Hair and Beuzenberg (1959).

That the staminal glands function as nectaries has been demonstrated by Sampson (1967). The sugars sucrose and perhaps raffinose are secreted (see chapters IV.8 and IX). Pollen has been observed to fill the lobes and wrinkles in the glands in at least one collection (Wood: US 2038724).

The morphology, ontogeny, sporogenesis, and embryology of the inflorescences, flowers, and fruits have been examined in detail by Sampson (1967). Relevant aspects of his investigation are referred to in appropriate sections in chapter IV.

In typifying Laurelia novae-zelandiae, it is necessary to distinguish between A. Cunningham's 1826 and 1838 collections of the species, because the latter have been treated as type material in several herbaria. In the original publication, Cunningham clearly indicated the collection from which he described the species with a locality, "Keri-Keri river", and a date, 1826. His collections are not so precisely labelled, and often lack this locality or date or both. Authentic material, however, can be recognised by its relatively thick, insect-eaten leaves, and mature inflorescences. The only other collections of the species made by Cunningham, in 1838, have relatively thin leaves, and expanding globose inflorescence buds.

Specimens on a sheet in herb.K, numbered 79, and labelled with the date "Octr.1826" and locality "margins of running streams near the Bay of Islands" [= Keri Keri river, cf. original type citation], have been treated as the holotype because the label bears other annotations on the characters and relationships of the specimens in Cunningham's hand. They are mixed on the sheet with one sterile branchlet of the 1838 collection, and two labels numbered 354 and 600 respectively, neither of which apply to the type. The sheet has been seen from a photograph.

It is noteworthy that although Cunningham in the original description says that female flowers were unknown to him, flowers of both sexes are present on the type collection.

Chemistry

All alkaloids isolated so far from this species are of the aporphine type (Aston 1910, Barger and Girardet 1931, Girardet 1931, Barger and Schlittler 1932, Schlittler 1932). They comprise pukateine, ($C_{18}H_{17}O_3N$), a feeble base with a melting point of 200°C, comprising one phenolic hydroxy-group, one N-methyl-group, and a methylenedioxy-group; laureline, ($C_{19}H_{19}O_3N$), which crystallises in tablets, is feebly basic, has a melting point of 97°C, and comprises one methoxy-group, one N-methyl -group, and a methylenedioxy-group; and laurepukine, ($C_{18}H_{17}O_4N$), which crystallises in colourless needles or hexagonal plates with a melting point of ca 230°C, and comprises two phenolic hydroxy-groups, one N-methyl-group, and one methylenedioxy-group. Their structures and properties are summarised by Petrie (1912), Henry (1949), and Manske in Manske and Holmes (1954).

Uses

The alkaloids have potential use as drugs: they have the physiological action of promoting excitability, followed quickly by loss of power and paralysis (Bancroft 1890, Malcolm 1908).

The timber, although soft, is strong, tough, and not readily split or burnt, and has been used principally in boat building, despite its tendency to become water-logged (J.D.Hooker 1853, 1864, Tulasne 1855, Kirk 1889, 1910, Cheeseman 1906, 1925, Laing and Blackwell 1906, Garratt 1934, Richards 1947, and Hinds and Reid 1957). To a lesser extent, it has been employed in furniture making, cabinet work, and turnery (Kirk 1889, Perkins and Gilg 1901, Cheeseman l.c., Perkins 1925, Garratt l.c., Metcalfe and Chalk 1950, Hinds and Reid l.c.). It has also been used occasionally for weatherboards (Kirk 1889, Garratt l.c., Hinds and Reid l.c.), and for posts in sandy soil (Garratt l.c.), although it reputedly lacks durability when in contact with the ground (Kirk 1889, Hinds and Reid l.c.). A recent account of the silvicultural features of the species and the economics and properties of its timber has been published by Hinds and Reid (l.c.). They record, in addition to the above-stated uses, its value in the building of motor bodies, trellis laths, bottle stoppers, wedge heels, clogs, mining sluices, verandah floors, wall frames, and fence battens.

XIII. DORYPHORA Endl.

Doryphora Endl., Gen.Pl. 1(1837)315 [non Kütz. 1840* [n.v.] nec Rchb. 1841**], suppl. 1,(1841)1378; id., Enchir.Bot. (1841)195, 196; Meisn., Pl.vasc.gen. 1(1841)324, 2(1841)236; [Rchb., Nomencl. (Herb.buch) (1841)69, pro nom.illeg. sub syn. Learosae]; Schnizlein, Icon. 2(1849) n.105; Lindl., Veg.Kingd. ed.3,(1853) 300; [Hook.f., Fl.Tasm. 1(1855)11 pro syn. Atherospermatis]; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)294,422; C.Muell. in Walp., Ann.Bot. 4(1857)83,119; A.DC., Prod. 16,2(1868)642,676; Baill., Adansonia 9(1868)127, (1869)129,134 p.p.; Baill., Hist.Pl. 1(1869)317,319,335,342 p.p.; Benth., Fl.Austral. 5(1870)283,284; Baill., Adansonia 10(1873)350,351; Baill., Dict.Bot. 1(1877)310; Benth.in B. & H., Gen.Pl. 3(1880)138,139,145; Woolls, Pl.Indig. Neighbour, Sydney (1880)9; F.Muell., Syst.Cens.Austral.Pl. 1(1882)3; F.M.Bail., Synops.Queensl.Fl. (1883)421; Moore, Cens. Pl.N.S.Wales (1884)58; Baill., Dict.Bot. 2(1886)468; Hobein, Bot.Jb. 10(1888)53,71,73; F.Muell., Sec.Syst.Cens.Austral.Pl. 1(1889)5; Pax, Pflzfm. 3,2(1889)96,103,104; F.M.Bail., Cat. Pl. Queensl. (1890)39; Moore & Betche, Handb.Fl.N.S.Wales (1893)

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* fide Baillon (1886) and Pax (1889).

** Doryphora Rchb., Nomencl. (Herb.buch) (1841) 56 = Dorycheile Rchb., l.c. (Orchidaceae). Doryphora Rchb. is not validly published as it was not accepted by the author (I.C.B.N. 1966, art.34).

14,15; Perk., Bot.Jb. 25(1898)552; Solereder, Syst.Anat.Dicot. (1899) [transl. Boodle, Fritsch, & Scott 2(1908)699,701]; F.M. Bail., Queensl.Fl. 4(1901)1288,1295; Perk. & Gilg, Pflzr. 4(1901) 2,4,8,11,14,79; Deane, Rec.Geol.Surv.Vict. 1(1902)26; Maiden, For.Fl.N.S.Wales 1(1903)42; Petrie, Proc.Linn.Soc.N.S.Wales 37(1912)139,146,151 et seq.; F.M.Bail., Compr.Cat.Queensl.Pl. (1913)419; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80; Perk., Gattung.Monim. (1925)5,6,9,10,13,16,52; McLuckie & Petrie, Proc. Linn.Soc.N.S.Wales 52(1927)175,184; Francis, Austral.Rain-For. Trees (1929)94,95; Welch, J.Proc.Roy.Soc.N.S.Wales 62(1929)362 et seq.; Lemée, Dict.gen.phan. 2(1930)726; Willis, Dict.Fl.Pl. Ferns ed.6,(1931)227; Garratt, Trop.Woods 39(1934)19 et seq.; Berry, Bot.Gaz. 96(1935) f.1,n.18; Berry, Geol.Soc.Amer.spec. pap. 12(1938) f.2,n.18; Lemée, Dict.gen.phan. 7(1939)235; Metcalfe & Chalk, Anat.Dicot. 2(1950)1139 et seq.; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)381 et seq., text-f.16; Francis, Austral.Rain-For.Trees ed.2,(1951)109,110; Croizat, Man. Phytogeogr. (1952)281, f.5,n.18; Stern, Amer.J.Bot. 42(1955)874, 881; Anderson, Trees N.S.Wales ed.3,(1956)369; Bick, Clezy, & Crow, Austral.J.Chem. 9(1956)111; Baur, Austral.J.Bot. 5(1957)205 et seq.; L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)48,49; Croizat, Principia Botanica 1A(1960)379, f.144C p.p.; Müller-Stoll & Mädel, Trans.Geol.Soc.S.Africa 65(1962) f.6; Burbidge, Dict.Austral.Pl.Gen. (1963)104; Evans in Beadle, Evans, & Carolin, Handb. Vasc.Pl. Sydney & Blue Mts. (1963)130; Buchheim in Melchior, Syllab.Pflzfm. ed.12,2(1964)122; Good, Geogr.Fl.Pl. ed.3,(1964)150; Hutchinson, Gen.Fl.Pl. 1(1964)111,112,122; Rüffle, Geol. Jahrg. 1(1965)83; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7,(1966) 377; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342, 343.

TYPE SPECIES: *Doryphora sassafras* Endl., only species.

Learosa Rchb., Nomencl.(Herb.buch) (1841)69 [nom.nov. pro *Doryphora* Endl.]; id., synon.reduct. 40; Endl., Gen.Pl. suppl.2,(1842)35; id., suppl.4,2(1847,8)56; [Tul., Arch.Mus.Hist.Nat.Par. 8(1855) 422 pro syn. *Doryphorae* Endl.]; F.Muell., Pl.Colon.Vict. 1(1860) 24.

Doratophora Lem.in Orbigny, Dict.hist.nat. 5(1845)119 [n.v.] [in errore pro *Doryphora* Endl.?]; [Baill., Dict.Bot. 2(1886)466 pro syn. *Doryphorae* Endl.].

Atherosperma auct. [non Labill.]: Hook.f., Fl.Tasm. 1(1855)11 p.p.; Hook.f., Handb.N.Zeal.Fl. 1(1864)240 p.p.

Daphnandra auctt. [non Benth.]: F.M.Bail., Queensl.Woods (1886)64 p.p., (1888)95 p.p.; F.Muell., Sec.Syst.Cens.Austral.Pl. 1(1889) 5 p.p.; Pax, Pflzfm. 3,2(1889)103 p.p.?; F.M.Bail., Cat.Pl. Queensl. (1890)39 p.p.; F.M.Bail., Queensl.Fl. 4(1901)1288,1295 p.p.; Perk., Pflzr. 49(1911)44 p.p.; F.M.Bail., Compr.Cat. Queensl.Pl. (1913)430 p.p.; Maiden, For.Fl.N.S.Wales 7(1921)368 et seq. p.p.; Domin, Bibl.Bot. 89,2(1925)674 p.p.; Perk., Gattung.Monim. (1925)47 p.p.; Welch, J.Proc.Roy.Soc.N.S.Wales 62(1929)362 et seq. p.p.; Lemée, Dict.gen.phan. 2(1930)501 p.p.?; Willis, Dict.Fl.Pl.Ferns ed.6,(1931)206 p.p.?; Croizat, Man. Phytogeogr. (1952)281, f.5,n.17 p.p.?; Bick, Clezy, & Vernengo, J.Chem.Soc. n.950(1960)4928 p.p.; Hutchinson, Gen.Fl.Pl. 1(1964) 120 p.p.; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed. 7,(1966)330 p.p.

[Atherospermatis A.Cunn.ex Tul., Arch.Mus.Hist.Nat.Par. 8(1855)422, nom.nud. pro Atherosperma p.p. pro syn. Doryphorae Endl. —— not validly published as not accepted by the author: I.C.B.N. 1966, art.34].

Figures 1F-G, 17, 18, 31, 32, 37A, 46A.

Tall bisexual trees, with slender, compactly cylindrical crowns; bark, wood, and leaves strongly, sweetly aromatic; secondary xylem vessels predominantly solitary, rarely up to 5% in radial multiples of 2-3, ca (40-)50-75(-85) per sq. mm, (1.3-)1.5-1.7(-2.0) mm long × (30-)60-80 (-150) μ inner tangential diameter, the perforation plates and vessel-ray pitting exclusively scalariform or occasionally replaced by pitted areas*; fibres relatively thin-walled, (1.9-)2.3-2.4(-2.6) mm long × (20-)25-35 (-50) μ outer tangential diameter, ± exclusively fibre tracheids with distinctly bordered pits; multiseriate rays (0.2-)0.4-0.8(-1.3) mm high

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* Recorded by Garratt (1934), but not observed in specimens examined in the present study.

× (2-)3-5(-7)* cells wide, acicular crystals and marginal oil cells absent or rare**; primary cortex sclerosed, without large intercellular air spaces***, ultimate branchlet stems compressed rounded tetragonous, glabrous or very sparsely strigillose; petioles shallowly to deeply sulcate; leaf blades large microphyllous to notophyllous, with margins deeply crenate(-serrate) to undulate or subentire, midribs sulcate on upper face, 1-3-layered hypodermis on upper face ****, oil cells confined to mesophyll*****.

Inflorescence buds ± broadly compressed, stipitate before expansion; mature inflorescences (false) simple dichasia; accessory axillary flowers absent; bracts large, dimorphic, the bracts of the first peduncle node (outer bracts) deeply navicular to cymbiform, herbaceous, (3-)5-8(-10) mm long × 2-5 mm broad, ± enclosing all mature flower buds, caducous ± at anthesis, the bracts of the second peduncle node (inner bracts) elliptic to oblanceate-obovate, ± tepaloid, 3-8(-10) mm long × 1-3 mm broad, subtending terminal flower, caducous ± with outer bracts; bracteoles absent.

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* Garratt (1934) records rays up to 8 cells wide.

** Oil cells observed as occasional in occurrence by Garratt (1934), but not confirmed by the present study.

*** Hobein (1888), Solereder (1899), Metcalfe and Chalk (1950).

**** Hobein (1888), Solereder (1899), McLuckie and Petrie (1927), Money et al. 1950.

***** Hobein (1888), Solereder (1899).

Flowers bisexual; perianth rotatiform, obscurely trimerous or dimerous, comprising (3-)4 or 6(-8) lanceate, acute, penninerved tepals, (4-)5-13(-18) mm long × ($1\frac{1}{2}$-)$2\frac{1}{2}$-4(-7) mm broad, in ± 2 whorls; androecium 3-4-seriate, the outer whorl* comprising (4-) 5 or 6, exceptionally more stamens, 5-10(-13) mm long × $\frac{3}{4}$-$2\frac{1}{4}$(-$2\frac{1}{2}$) mm broad × $\frac{1}{3}$ - $\frac{1}{2}$ mm thick, with lanceate to ovate-deltate planate staminal glands, and flexuously aristate latrorsely-slightly introrsely-dehiscing anthers, the inner whorls unequal, the outer comprising 3-6(-8) stamen-like staminodes, ($2\frac{1}{2}$-)$3\frac{1}{2}$-7(-8) mm long, with reduced, rarely vestigial staminal glands, the inner 1-2 whorls of 3-12(-14) style-like staminodes, ($\frac{3}{4}$-)1-2(-$2\frac{1}{2}$) mm long; pollen grains ellipsoidal, rarely subspheroidal, oblate to suboblate, Lg (25-)26-32(-34) μ × long. Lt. (27-)30-44(-46)** μ, the colpi transversales of ± regular length, 20-32 μ long, one frequently rather longer and broader than the other, the interstitial equatorial depressions rather short but distinct, the grain walls ($1\frac{1}{3}$ -)$1\frac{1}{2}$-$1\frac{3}{4}$(-2) μ thick, the surface sculpture with lumina ± regularly circular in outline, $\frac{1}{2}$(-1) μ in diameter; gynoecium of 6-12(-15) carpels, the styles lateral, hispid, the stigmatic column stellately branched, very rarely entirely

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* Sampson (1967) correctly points out that the 6 stamens of D. sassafras, like the tepals, are in two whorls of 3 each. These two whorls are macroscopically obscure, more of ontogenetic interest, and are not described in detail here.

** Erdtman (1952) gives the longest grain axis of D. sassafras as 50 μ.

connate; ovule ellipsoid, obtuse at chalazal end, anatropous on basal placenta.

Fruiting hypanthium urceolate, rarely ± cylindrical, (10-)13-23(-25) mm long × (3-)5-8(-10) mm thick, 4-6-ribbed from tepal decurrences, sparsely and ± uniformly strigillose, dehiscing ± irregularly into 2(-4) equal or subequal valves; perianth and androecium early caducous*; nutlets attached superficially to hypanthium wall, the bodies ovoid to ellipsoid, glabrous, the styles sub-basal, filiform, silky hirsute.

Additional Characters Common to Infrageneric Taxa

Average tree height range 20-50 m; bole often coppicing; crown branches ± horizontal, usually short and close; branchlet stems ± closely branched, the ultimate 2-5 internodes ± smooth, often striately wrinkled and pustuled below, drying greyish brownish, glabrescent, usually very sordid white to tawny brownish strigillose, with hairs often densest about nodes and/or stem faces adjacent to the petiole decurrences, the branchlet nodes broadened, often slightly swollen; vegetative buds narrowly conical or obcordiform, variably compressed, the enveloping pair of bract-like leaves densely off-white to pale grey-green or dirty golden brown strigose, with ± erect glabrous mucronate apices, expanding when buds 7-9 mm long; petioles shallowly to deeply impressed on upper face, drying dark olive-grey to blackish brown, rarely pale brown; leaf blades with upper face smooth, often faintly

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* Innermost style-like staminodes variably persistent.

lined with prominulous nerves, rarely vein reticulum, midribs shallowly to deeply impressed on upper face, conspicuously prominent on lower, generally glabrous, with usually a few short sordid whitish to stramineous strigose hairs towards the base of the midrib on the lower face, particularly on younger leaves; anticlinal walls in leaf blade epidermal cells undulate*, or straight**; bark, wood, and stems strongly and sweetly aromatic with the odour of safrol, the leaves equally aromatic but with a more citronella-like odour, the odour weaker in saplings and shaded branchlets, and persistent, rarely completely evanescent in all parts when dried.

Inflorescence buds **slightly** to broadly compressed, obcordiform, initially subsessile and complanate with stem when 1-2 mm long, the enveloping pair of bracts ovate to lanceate, cymbiform to navicular, sparsely sordid pale grey to tawny strigilloso, ultimately (3-)5-8(-10) mm long, with erect apices; buds subsequently elongating through the development of a broadly compressed stipe (= base internode of peduncle of mature inflorescence) up to (2-)4-9(-11) mm long below the bracts which enclose the ultimate inflorescence parts until the flower buds are almost mature or ready to burst; mature inflorescences decurved, generally strigillose, borne at ultimate 1-4(-6) leaf nodes among leaves; peduncles essentially 2-noded, the base internode well-developed, broadly compressed, the first

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*Hobein (1888), Solereder (1899).

**Money et al. (1950), by inference.

node bearing solitary opposite flowers, the distal internode ± suppressed or slenderly tetragonous, bearing a solitary terminal flower which opens first; outer pair of bracts drying thinly ligneous, dark brown to blackish, sparsely sordid pale grey to tawny strigillose abaxially, often more densely and finely silkier strigose adaxially; inner pair of bracts with obscurely mucronate acute apices, and slightly incurving margins; pedicels not or hardly expanded under hypanthium; mature flower buds usually attenuately ovoid acute, the outer tepals imbricate, partly or almost entirely enclosing inner tepals.

Open flowers large; hypanthium poculiform, densely strigillose, the rim flat to sloping slightly upwards, glabrous towards outer margin, hispidulous on inner margin among staminodes; perianth white, the tepals petaloid, with entire, rarely eroded or undulate margins, conspicuously nerved with lateral nerves and vein reticulum, densely grey-white or sordid pale grey-green strigillose abaxially with hairs longer and denser along midnerve, more sparsely and uniformly strigillose adaxially; androecium white, with yellowish cream anther valves, inner staminode whorls sometimes appearing disposed in a close spiral, with occasional members transitional in form between outer stamen-like staminodes and inner style-like staminodes; stamens erect, the filaments broadly dorsiventrally compressed, glabrous or strigillose abaxially, the staminal glands broadly sessile along the margins of the filament towards its base and compressed in the same plane, the anthers glabrous, with circular valves and infrequently partly aborted pollen sacs; stamen-like staminodes erect, dorsiventrally compressed at the base, with paired subsessile glands on the margins, rarely with partly developed pollen sacs; style-like staminodes with recurving, caudate-subulate, glabrous apices, and erect, thickened almost ventricose, densely brownish stramineous hispid-strigose bases, usually eglandular; gynoecium with stigmatic column exserted beyond and slightly overhanging inner staminodes.

Ripe infructescences borne at ultimate 1-4(-8) leaf nodes among, rarely below leaves on branchlets, unevenly and sparsely fine pubescent, sometimes entirely glabrescent; pedicels of the same thickness and form as in inflorescence, not expanded under fruiting hypanthia, slightly more sparsely haired than in inflorescence, those of lateral hypanthia usually longer than those of terminal hypanthia; fruiting hypanthium contracted into a ribbed neck $\frac{1}{3} - \frac{2}{3}(-\frac{3}{4})$ × length of hypanthium, lignified with walls $\frac{1}{2}$-$\frac{3}{4}$(-1) mm thick, in dehiscence with (1-)2-4(-6) incipient fissures developing between the neck ribs from the rim, of which only 2 opposite, rarely 1, 3, or 4 extend towards the base; hypanthium rim of the same form as in flower, glabrescent and scarred, the inner margin fihely hispid, irregular, with innermost style-like staminodes and sometimes broken bases of stamen-like staminodes variably persistent, rarely completely caducous; hypanthium chamber rounded at the base, densely sordid or golden brown silky hirsute, shorter paler hispid-hirsute on neck towards rim; nutlets attached to sides and base of hypanthium chamber, the bodies dorsiventrally flattened when infertile, pale to dark or greyish brown, the styles attached to adaxial face of nutlet, unexpanded and easily broken at the base from nutlet body, uniformly silky hirsute with straight hairs, the hairs gradually shorter towards the sordid off-white to pale grey-green hispidulous, infrequently ultimately glabrous apex; endosperm strongly aromatic with a safrol-like odour.

The name *Doryphora* is formed from δορυ , a spear, and φορος , carrying or bearing, probably in allusion to the flexuosely aristate stamens and outer staminodes (Tulasne 1855, C.Mueller 1857, F.M.Bailey 1883, 1901, Perkins and Gilg 1901, Maiden 1903, Francis 1929, 1951).

Species, Geographic Distribution, and Ecology

The genus *Doryphora* comprises two species in coastal eastern Australia, one in north-east Queensland, and the other in south-east Queensland and eastern New South Wales, between 16° and 37°S (maps 2, 9).

The species occur in primary cool subtropical and/or submontane rainforests between sea-level and 1500 m altitude, and enter temperate rainforests up to 1500 m in the southern region. In northern and central regions, they are a frequent though inconspicuous element of floristically rich rainforests, while in southern areas, one species becomes a co-dominant with *Ceratopetalum apetalum* south of about 30°-31°S, and ultimately a single dominant element of the rainforest south of about 33-34°S, along the sea board of New South Wales.

Germination of seeds occurs freely in the leaf litter and soil of the forest floor (personal observations of both species, and seedlings and saplings collected of *D. sassafras*: Schodde 3476, 3493). Regeneration by coppicing is of frequent occurrence; suckering has not been recorded.

Flowering is strictly seasonal, occurring at about the same time for both species, from mid or late May until late August or early September over the austral winter and early spring, notwithstanding that one species is confined to tropical latitudes under relatively slight seasonal fluctuations in climate, while the other occurs in more temperate latitudes with more marked climatic variation. Fruiting hypanthia mature and dehisce between late spring and early autumn (September-May). Inflorescence buds for the following season usually appear before the maturation of the fruiting hypanthia in the southern species (*D. sassafras*), **and usually after** in the tropical-latitude species (*D. aromatica*). The flowering and fruiting period of the latter is apparently much shorter (about five months) than that of the former (about seven months).

Notes of Generic Characters

Doryphora is distinct among the genera of the Laurelieae in its secondary xylem in which large multiseriate rays (2-)3-5(-7) cells wide are associated with a ground mass of ± exclusively fibre tracheids with large and very frequent bordered pits, and in its essentially three-flowered inflorescence, the flower buds of which are enclosed in a pair of large cymbiform or deeply navicular bracts and lack bracteoles or their homologues, its large penninerved tepals and flexuosely aristate androecium parts, its relatively high frequency of androecium parts transitional in form between tepal, stamen, and staminode, its lanceate-deltate staminal glands that are compressed in the same plane as the filament, its carpels with glabrous bodies and slender lateral styles, its stellately branched stigmatic columns, and its ribbed fruiting hypanthia. Further aspects of these morphological features are considered below.

It is apparent, from a comparison of inflorescence structures in the family (chapter IV.6), that the inflorescence of Doryphora is a three-flowered "dichasium" through reduction of a more elaborate inflorescence of the type found in Dryadodaphne and Laurelia. The homologies and differences in the inflorescence buds and bracts at the base (= first) peduncle nodes between Doryphora, and Daphnandra, Dryadodaphne, Laurelia, and Nemuaron have been discussed in chapter IV.3,6.

Other indications of inflorescence reduction are to be found in differences in inflorescence structure between the two species of Doryphora (f.1 F,G). In D. aromatica, the primary peduncle has two distinct internodes (f.9 B,J). At its terminal node it bears a solitary flower which is flanked not by a pair of flowers from the same node to form a simple dichasium as is usual in the family, but by opposite solitary flowers from the subterminal node. Though the distal internode may resemble the pedicels in its slenderness and pubescence, evidence that it is none-the-less part of the primary peduncle is provided by a second pair of large, densely haired bracts at its terminal node, by its tetragonous form, and by the occasional development of solitary aborted flower buds in the axils of the second bracts.

In Doryphora sassafras, the distal internode of the primary peduncle is almost completely suppressed, as indicated by the second pair of bracts which are attached more-or-less at the top of the subterminal node, contiguous with the base pair of bracts. It needs to be emphasised that, despite superficial appearances, particularly in D. sassafras, the inflorescence of Doryphora is a false simple dichasium in which the solitary terminal and two flanking flowers arise from different nodes.

The regularly hexamerous flower of Doryphora sassafras is unique in the family. Its derivation may be envisaged through the reduction of parts in a tetramerous flower with biseriate perianth and stamens as described in chapter IV.10. An intermediate stage in its development may be represented by the flower of D. aromatica, which comprises a basically but not regularly 4-partite perianth with sometimes 3, 5, or 6 tepals, and an androecium with usually 5 but occasionally 4 or 6 stamens (see following section).

Transitional structures between tepals, stamens, and staminodes are rather frequent in flowers of the genus. Examples are stamens with either tepal-like expansions to their filaments and apices, or aborted pollen sacs and reduced staminal glands. Staminodes intermediate in form, pubescence, and vestigial glands between stamen-like and style-like staminodes also occur. These transitional structures appear to indicate an unstable or imperfectly settled floral phyllotaxis (see following section).

Laterally attached styles are peculiar to the genus. In carpels in the unopened flowers, the styles are sub-terminal in position on the adaxial face of the carpel body. As the flower matures and the young fruiting hypanthium commences to enlarge, the apex of the carpel body elongates so that the style becomes attached relatively further and further down the side of the nutlet until, at nutlet maturity, it is sub-basal. This development may be either concerned with facilitating ~~shortening~~ the path of the pollen tube to the micropyle of the basal anatropous ovule, or result from a dissociation of tissues in response to modifications of patterns of vascularisation of the type occurring in other genera of the family (Money et al. 1950). Carpel vascularisation in *Doryphora* has not been studied. In *Atherosperma* and *Laurelia* (Money et al. l.c., Sampson 1967), the style is vascularised by an abaxial strand, and this may be the usual condition in the family. Because the style in *Doryphora* becomes dissociated from the adaxial face of the ovuliferous section of the carpel, marked modification of this system may be expected.

The ribs on the fruiting hypanthia are aligned with the scars of the fallen tepals on the hypanthium rim which, in the case of *D. aromatica*, are sometimes a little below the rim proper on the outer hypanthium wall. The three obscure ribs on the floral hypanthium of *D. sassafras*, decurrent from the outer three tepals, may well indicate that the entire hypanthium, not just the neck of the fruiting hypanthium, is derived from floral parts rather than axial tissue.

Affinities

Since its description, and even before (cf. R.Brown 1814), *Doryphora* has been recognised as a genus distinct from all others in the family, except by J.D.Hooker (1855, 1864) who united all genera known in the family at the time under the one genus, Atherosperma. Doryphora is as distinct from Atherosperma as any member of the tribe Laurelieae, notwithstanding that the two genera have been associated for the reasons described in chapter VIII and evaluated in chapter IX. It also stands apart from other genera of the Laurelieae and is only related to them through Dryadodaphne, in the way discussed in chapter X.

Chemistry

Despite their close morphological similarities, the two species of Doryphora have remarkably different alkaloids. Those of D. aromatica are of the bisbenzylisoquinoline type, and the two major alkaloids present, daphnoline and aromoline, are found also in species of Daphnandra. Those of D. sassafras comprise both bisbenzylisoquinoline and aporphine types. While none of them have been found in either Doryphora aromatica or species of Daphnandra, at least one, liriodenine, occurs in Atherosperma moschatum and the Magnoliaceae. It is difficult to assess the significance of these differences, especially as neither species has yet been examined in great detail with modern methods (Bick, pers.comm.).

Interspecific Relationships

The two species of Doryphora are vicarious, and resemble each other closely in most features. They differ essentially in the degree of reduction of the inflorescence and concomitant increase in the size of the outer flower bud-enclosing bracts, in the structure of the inner bracts, in flower size and number of flower parts, and in the number of ribs per fruiting hypanthium, as well as by minor differences in the shape, texture, and venation of the leaves, and surface of the bark. The pollen grains of *D. aromatica* (Hyland 3131) also average smaller in dimensions (Lg. (25-)28-30μx long. Lt.(27-)35-40μ) than those examined in *D. sassafras*, but the differences, coming from a single collection, cannot be conclusive.

Except perhaps for the number of style-like inner staminodes, the features which distinguish the species appear to be at a less specialised level in the tropical-latitude species, *D. aromatica*, and approach more closely the form of these characters in other genera of the family. *D. aromatica* has, for example, smaller flowers. Its number of tepals and stamens not only approaches the basic tetramerous arrangement of floral parts but also varies from flower to flower and suggests, as mentioned before, an intermediate stage in the development of the regularly hexamerous flower represented by *D. sassafras*. Its proportion of androecium parts transitional in form between tepals and stamens (and staminodes) further emphasises the state of flux in the differentiation of its flower parts. Its inflorescence is less reduced, the second or distal node of which occasionally bears aborted lateral flowers flanking the terminal flower in a true simple dichasium. Its outer (= lower) inflorescence bracts, moreover, which are only slightly enlarged to envelop the flower buds, resemble the bracts at the base (= first) node of the primary peduncles in *Daphnandra*, *Dryadodaphne*, and *Laurelia* much more closely than those of *Doryphora sassafras*.

The rather larger, less coriaceous, and more openly veined leaves of

D. aromatica apparently reflect the more uniform environment in which the species grows. Its smooth bark may also be viewed as the end point of a well-marked cline in the roughness of bark on the trunks of *D. sassafras*. In that species, the bark is roughest and most deeply furrowed in southern forms and smoother in northern forms.

Excluded Species

Doryphora austro-caledonica Seem., Fl.Viti. (1867)206

"Doryphora (?) Austro-Caledonicus".

The leaves and habit of the type of this name in herb. BM, seen from photographs and several leaves, are unlike those of any living member of the Atherospermataceae, but appear to resemble those of an *Ascarina*. Dr.H.S.McKee (pers.comm.) shares this opinion. The collection is sterile.

Key to the Species and Infraspecific Taxa of *Doryphora*

1a. Peduncles with 1 internode; perianth of 6 tepals, exceptionally more or less, (6-)7-13(-18) mm long; inner style-like staminodes (4-)8-12(-14), in usually two whorls; mature fruiting hypanthia 6-ribbed; leaf blades deeply to shallowly crenate-serrate, with ± close prominent vein reticulum on lower face 2

  2a. Crown leaf blades (3-)6-9(-13) cm long; mature inflorescences (1½-)2-3 cm long; mature fruiting hypanthia (13-)16-22(-25) mm long .... 2a. *D. sassafras* Endl.var. *sassafras*

2b. Crown leaf blades (1-)3-6(-9) cm long; mature inflorescences $(1\frac{1}{4}-)1\frac{1}{2}-2(-2\frac{1}{2})$ cm long; mature fruiting hypanthia (12-)13-16 (-19) mm long .... 2b. *D. sassafras* var. *microphylla* Schodde

1b. Peduncles with 2 internodes (distal internode pedicel-like); perianth of (3-)4(-6) tepals (4-)5-7(-10) mm long; inner style-like staminodes 3-6, in ± one whorl; mature fruiting hypanthia 4(-6)-ribbed; leaf blades shallowly crenate to undulate almost entire, with ± spare obscure vein reticulum on lower face. .... 1. *D. aromatica* (F.M. Bail.)L.S. Smith

1. *Doryphora aromatica* (F.M.Bail.)L.S.Smith

Doryphora aromatica (F.M.Bail.)L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)48.

Daphnandra aromatica F.M.Bail., Synops.Queensl.Fl. suppl.1,(1886) 46; F.M.Bail., Queensl.Woods (1886)64; Bancroft, J.Proc.Roy. Soc.N.S.Wales 20(1887)70; F.M.Bail., Queensl.Woods (1888)95; Maiden, Useful Nat.Pl.Austral. (1889)414; F.Muell., Sec.Syst. Cens.Austral.Pl. 1(1889)5; F.M.Bail., Cat.Pl.Queensl. (1890)39; J.F.Bail., Queensl.Ag.J. 5(1899)401; F.M.Bail., Queensl.Fl. 4(1901)1295,1296; [Perk., Pflzr. 49(1911)44 pro syn. *Daphnandrae repandulae*]; Petrie, Proc.Linn.Soc.N.S.Wales 37(1912)152; F.M.Bail., Compr.Cat.Queensl.Pl. (1913)430, f.415; Maiden, For. Fl.N.S.Wales 7(1921)369,371; Jones & Smith, Proc.Roy.Soc. Queensl. 35(1924)61,133; Domin, Bibl.Bot. 89,2(1925)674; Perk., Gattung.Monim. (1925)50; Francis, Austral.Rain-For.Trees (1929)20; Welch, J.

Proc.Roy.Soc.N.S.Wales 62(1929)357,364, f.5; Garratt, Trop. Woods 39(1934)19; Hurst, Poison Pl.N.S.Wales (1942)123 "Daphnandra aromatic"; Bick & Whalley, Univ.Queensl.Pap. I,28(1946)1, I,33(1948)1; Bick & Todd, J.Chem.Soc. (1948)2170; Webb, C.S.I.R.Bull. n.232(1948)109; Bick, Ewen, & Todd, J.Chem. Soc. (1949)2767; Francis, Austral.Rain-For.Trees ed.2,(1951)24, 401, f.244; Kulka in Manske & Holmes, Alkaloids 4(1954)221; Bick, Clezy, & Vernengo, J.Chem.Soc. (1960)4928; Kulka in Manske, Alkaloids 7(1960)443.

TYPE: Bancroft, Johnstone River, 1885 —— holotype in BRI (lost?), isotype in MEL, NSW.

Daphnandra repandula auctt. [non F.Muell.]: Perk., Pflzr. 49(1911) 44 p.p.; C.T.White, Contrib.Arn.Arbor. 4(1933)32.

Figures 1F, 9, 17, 31.

Diagnosis

Bark smooth or occasionally striate and sparsely pustuled, pale to mid grey or pale grey-brown, often tinted pink; ultimate branchlet stems often somewhat angular tetragonous; crown leaf blades elliptic to obovate, (2-)4-11(-14) cm long × ($1\frac{1}{2}$-)2-$2\frac{3}{4}$(-$5\frac{1}{2}$) cm broad, with shallowly crenate to undulate or almost entire margins, and rather inconspicuous, loose, spare vein reticulum on lower face.

Mature inflorescence buds slightly compressed obcordiform; peduncles of mature inflorescence 2-noded, the base internode rather compressed,

($\frac{2}{3}$ -)$\frac{3}{4}$(-1$\frac{1}{4}$) mm broad, the distal internode pedicel-like, slenderly tetragonous, $\frac{1}{4}$ - $\frac{1}{3}$(-$\frac{1}{2}$) cm long × ($\frac{1}{3}$ -)$\frac{1}{2}$ - $\frac{2}{3}$(-$\frac{3}{4}$) mm thick, densely greyish hispidulous-strigillose; outer bracts slenderly navicular-cymbiform, (3-)5-6 mm long × ± 2 mm broad; inner bracts slightly navicular, ± herbaceous, 3-4 mm long × 1-1$\frac{1}{4}$ mm broad; mature flower buds (3-)4-6(-7) mm long × (1-)1$\frac{1}{3}$ - 2(-2$\frac{1}{2}$) mm thick, often slenderly clavate when terminal in inflorescence.

Open flowers with perianth comprising (3-)4(-6) broadly lanceate to ovate tepals,(4-)5-7(-10) mm long × (1$\frac{1}{2}$-)2$\frac{1}{2}$-3$\frac{1}{2}$(-4) mm broad, in 2 ± decussate whorls; androecium 3-seriate, comprising an outer whorl of (4-)5(-6) stamens 5-6(-7$\frac{1}{2}$) mm long × $\frac{3}{4}$-1$\frac{1}{4}$ mm broad, an inner whorl of 3-5 stamen-like staminodes 4-7 mm long × $\frac{1}{3}$ - $\frac{1}{2}$ mm broad, and 1 innermost whorl of 3-6 style-like staminodes ($\frac{3}{4}$-)1-1$\frac{1}{4}$(-1$\frac{1}{2}$) mm long × $\frac{1}{4}$ - $\frac{1}{3}$ mm thick; gynoecium of 6-8(-10) carpels.

Ripe infructescences with peduncles ($\frac{3}{4}$-)1$\frac{1}{4}$-1$\frac{3}{4}$(-2$\frac{1}{4}$)cm long, 2-noded, the distal internode pedicel-like, tetragonous; fruiting hypanthium with 4(-6)-ribbed neck, the ribs short, sometimes obscure; bodies of ripe nutlets (2$\frac{1}{2}$-)3-4$\frac{1}{2}$(-5) mm long × (1-)2(-2$\frac{1}{2}$) mm thick, the hairs at the base of the styles (8-)10-15(-16) mm long.

Detailed Description

Slender trees 25-35(-40) m high; bole 45-60 cm diameter breast height, not or slightly buttressed; crown usually short, ca $\frac{1}{5}$ - $\frac{1}{3}$(-$\frac{1}{2}$) × length of bole. Bark up to 10 mm thick when dry, outer surface smooth or occasionally striate and sparsely pustuled*, variously pale to mid grey or pale grey-brown, often tinted pink, inside pale pink-cream to pale yellowish, drying pale brownish. Wood yellow-cream to pink-cream, deepest in heartwood, drying greyer or browner off-white. Branchlet stems with ultimate 2-5 internodes (½-)1-3½(-7) cm long × (½-)1¼-1¾(-2) mm thick, compressed, often somewhat angular tegragonous, drying greyish to rather dark olive-brown, sometimes blackish, glabrescent, the ultimate 1-3 internodes often very sparsely strigillose; shaded and sapling branchlets with ultimate 2-4 internodes 3-7(-9½) cm long × 1½-2½ mm thick, more rounded compressed. Petioles (4-)5-8(-11) mm long × (¾-)1-1⅓(-1½) mm thick, glabrescent, the younger leaves very sparsely strigillose. Leaf blades variously elliptic to obovate, rarely ovate, (2-)4-11(-14) cm long × (1½-)2-3¾(-5½) cm broad, variously cuneate or rather obtuse at the base, narrowly to ± acuminately mucronulate obtuse, rarely broadly obtuse or rather acute at the apex; margins shallowly and distantly crenate to undulate or almost entire, obscurely recurved, sometimes almost planate; texture thinly to quite coriaceous; colour dull to ± glossy rather dark green on upper face, duller and paler on lower, in dry leaves olive(-brown -)grey on upper face, more brownish grey on lower; nervation on lower face with 5-8(-11) prominulous, sometimes prominent main nerves, the vein reticulum more finely prominulous, often rather obscure, loose and spare, rarely close, extending between the nerves towards the midrib; generally glabrous;

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* Bick and Whalley (1948), Francis (1951), L.S.Smith (1958).

leaf blades on shaded and sapling branchlets (5½-)8-14(-16) cm long × (2½-)3-6(-7½) cm broad, with more deeply crenate-serrate margins, more thinly coriaceous to chartaceous, nerves and vein reticulum more prominent on upper face.

Mature inflorescence buds and stipe 1-1¼ cm long, the buds ± compressed obcordiform, 3-5mm long × ± 3 mm broad. Mature inflorescences 3-flowered, exceptionally 5-flowered false dichasia, usually congested on ultimate branchlets, with 1, often 2 per leaf axil, ca (1-)1½-2½(-3) cm long, generally pale grey to sordid golden grey strigillose. Peduncles 2-noded; base internode peduncle-like, (⅓ -) ½-1(-1¼) cm long × (⅔ -)¾(-1¼) mm broad, broadly, sometimes angularly compressed towards the apex, drying blackish brown, very sparsely grey-white to sordid tawny strigillose; outer bracts lanceate to narrowly ovate, navicular-cymbiform, weakly bilaterally compressed, (3-)5-6 mm long × ± 2 mm broad, with mucronate acute apices, and less prominent abaxial midribs than in *D. sassafras*, abaxial hairs usually distributed uniformly, slightly enlarged to enclose the expanding inflorescence, caducous at or just before flower opening; distal internode pedicel-like, ¼ - ⅓(-½) cm long × (⅓ -)½ - ⅔(-¾) mm thick, slenderly tetragonous, densely pale greyish, rarely tawny hispidulous-strigillose; inner bracts narrowly oblanceate to narrowly elliptic, slightly navicular, 3-4 mm long × 1-1¼ mm broad, with a ± prominent abaxial midrib, ± herbaceous, ± uniformly dense greyish to sordid pale tawny loose strigose, caducous with outer bracts; pedicels (1-)2-4(-7) mm long × (⅓ -)½ - ⅔(-¾) mm thick, ± terete, rarely markedly compressed, densely sordid grey-white or pale grey, rarely tawny strigose. Mature flower buds attenuately ovoid acute to fusiform-clavate when terminal, attenuately ovoid acute when lateral, (3-)4-6(-7) mm long × (1-)$1\frac{1}{3}$ - 2(-$2\frac{1}{2}$) mm thick, densely pale grey strigose.

Open flowers. Hypanthium ($\frac{3}{4}$-)1-$1\frac{3}{4}$(-2) mm long × ($\frac{3}{4}$-)1-$1\frac{3}{4}$(-2) mm thick, pale grey to rather sordid tawny coarse strigillose; rim $\frac{1}{3}$ - $\frac{2}{3}$ (-$\frac{3}{4}$) mm broad. Perianth comprising (3-)4(-6) tepals in 2 ± decussate subequal whorls; tepals broadly lanceate to ovate, (4-)5-7(-10) mm long × ($1\frac{1}{2}$-)$2\frac{1}{2}$-$3\frac{1}{2}$(-4) mm broad, with attenuately acute to narrowly obtuse apices, coarsely strigillose abaxially, inner tepals usually narrower than the outer. Androecium 3-seriate, stamens (4-)5(-6) in an outer whorl, 5-6(-$7\frac{1}{2}$) mm long × $\frac{3}{4}$-$1\frac{1}{4}$ mm broad × ± $\frac{1}{3}$ mm thick at the pollen sacs, one occasionally tepal-like with expanded apices; filaments $\frac{2}{3}$ - $1\frac{1}{2}$ mm long × ($\frac{1}{2}$-)$\frac{2}{3}$ - 1 mm broad, rarely up to $\frac{1}{4}$ mm thick; staminal glands lanceate- to ovate-deltate, obtuse, $\frac{2}{3}$ - 1 mm long, or ellipsoid-cylindrical, obtuse, $\frac{1}{2}$-$\frac{3}{4}$ mm long, very rarely aborted and vestigial; anthers with flexuosely aristate apices 4-6 mm long, usually slightly expanded or compressed towards the tip, and pollen sacs ($\frac{2}{3}$ -)$\frac{3}{4}$ mm long; stamen-like staminodes 3-5 in an inner whorl, flexuosely aristate, 4-7 mm long, $\frac{1}{3}$ - $\frac{1}{2}$ mm broad at the base, glabrous, sometimes sparsely strigillose, the glands cylindrical-ellipsoid to oblong-elliptic obtuse, $\frac{1}{3}$ - $\frac{2}{3}$ mm long, hardly stipitate; style-like staminodes 3-6 in innermost whorl, ($\frac{3}{4}$-)1-$1\frac{1}{4}$(-$1\frac{1}{2}$) mm long × $\frac{1}{4}$ - $\frac{1}{3}$ mm thick, eglandular. Gynoecium of

6-8(-10) carpels; styles lateral, exserted $(\frac{1}{2}-)\frac{2}{3} - 1\frac{1}{4}(-1\frac{1}{2})$ mm beyond hypanthium rim in a slender cylindrical column ± $\frac{1}{2}$ mm thick; stigmatic column connate at the base, stellately branched at the apex, ca $\frac{2}{3} - \frac{3}{4}$ (-1) mm long.

Ripe infructescences often appearing congested on branchlets where two infructescences occur per leaf axil, $(2\frac{1}{2}-)3\frac{1}{2}-4(-4\frac{1}{2})$ cm long, (2-)3 hypanthia maturing per infructescence. Peduncles $(\frac{3}{4}-)1\frac{1}{4}-1\frac{3}{4}(-2\frac{1}{4})$ cm long × $1-1\frac{1}{2}(-2)$ mm broad at the base internode, and $(\frac{1}{3}-)\frac{2}{3} - \frac{3}{4}(-1)$ mm thick at the distal internode, of the same form and colour as in inflorescence, more thickly lignified, rather more sparsely haired to glabrescent, the distal internode remaining pedicel-like, tetragonous, and more densely greyer hispidulous-strigillose than the base internode; pedicels (2-)3-8(-9) mm long. Fruiting hypanthium slenderly urceolate, (10-)15-23(-25) mm long × (3-)5-8(-10) mm thick at the base, $1\frac{1}{2}-3(-4)$ mm thick at the neck, with 4(-6) obscure to prominent short ribs rarely extending over hypanthium base from the neck, rather glossy mid green, drying dark grey-brown to blackish, glabrescent, or very sparsely unevenly sordid grey-white strigillose, the hairs denser on young hypanthia; rim $(\frac{2}{3}-)\frac{3}{4}-1\frac{1}{4}(-1\frac{1}{2})$ mm broad, the outer pair of tepal scars often up to $\frac{1}{2}$ mm below the inner. Nutlets elongating in maturing hypanthium to maintain the exsertion of the style apices beyond the hypanthium rim as in flower; bodies of ripe nutlets ovoid to ellipsoid, $(2\frac{1}{2}-)3-4\frac{1}{2}(-5)$ mm long × $(1-)2(-2\frac{1}{2})$ mm thick, entirely glabrous; sub-basal styles of ripe nutlets (10-)14-18(-20) mm long, the basal hairs (8-)10-15(-16) mm long, mid to dark brown.

The epithet aromatica refers to the aromatic fragrance of the bark and leaves (F.M.Bailey 1886a,1901).

Aboriginal names: Cheedingnan (Barron river —— J.F.Bailey 1899, F.M.Bailey 1901, 1913, Maiden 1921).

Vernacular names: Cairns sassafras (Maiden 1921), Grey sassafras (Welch 1929, Francis 1951), Net sassafras (Francis 1951), Northern sassafras (Bick and Whalley 1948, Webb 1948), Northern grey sassafras (Francis 1951), Sassafras(J.F.Bailey 1899, Welch 1929), Satin wood (Fitzalan: MEL 3226).

Series of specimens examined: 16 collections, comprising 3 with inflorescence buds, 3 with mature flower buds, 4 with open flowers, 5 with young (unelongated) fruiting hypanthia, 8 with near or quite mature (fully elongated) fruiting hypanthia, and 2 of sapling and coppice branchlets. Many of the eighteen collections cited by L.S.Smith (1958) were unavailable for study.

Geographic Distribution (map 9)

Doryphora aromatica is confined to coastal ranges and adjacent areas in north-east Queensland, from the Bloomfield river, Alexandra Bay, and Mt.Spurgeon-Mt.Lewis range south to the Atherton and Evelyn Tablelands, and Rockingham Bay, 16°-18°S:

Ayton road, north of Bloomfield river; Daintree river; Mossman river; Churchill creek, ca 12 miles north of Mt.Molloy; Atherton

Tableland; Gadgarra; Forest Reserve 310, Gadgarra; Forest Reserve 194, Herberton range; Johnstone river; Palmerston Highway; Mt. Koolmoon Forest Reserve, 7 miles south of Ravenshoe; Innisfail; Rockingham Bay.

L.S.Smith (1958) quotes its geographic distribution from the Big Tableland (south of Cooktown?) in the Cook District south to Murray Upper and the Kirrama range near Kennedy at 18°30′S in the North Kennedy District. The species probably extends northwards along the coast range at least as far as Mt. Finnigan.

Ecology (figure 52)

A frequent or occasional tree of the forest canopy, D. aromatica occurs in primary, less often disturbed, ± subtropical rainforest between the altitudes of 15-1100 m. Its optimal occurrence is between 600 and 900 m s.m., slightly above that for Daphnandra repandula, with which it is sympatric. It has a marked preference for sheltered and shallowly sloping sides and heads of gullies; it is less frequent on alluvial flats on the margins of streams and rare on mountain ridges. It grows on a variety of soil types, including deep red soils at Mt. Koolmoon Forest Reserve (Schodde 3283).

Phenology

The few available dated collections when correlated with those cited by L.S.Smith (1958) indicate that inflorescence bud and flower bud expansion occur during austral autumn months (May-June), flowering during winter months between late May and September, and fruit maturation in spring between August and November, or occasionally in January

(C.T.White: Mazlin's creek) and even May (Kajewski 1005). Francis (1951) records mature fruit in October and January. Such variation suggests either that flowering times differ between individual trees or that there are two flowering seasons per year. The latter possibility seems to be remote in view of the seasonal regularity in flowering in D. sassafras and other members of the family.

The duration of the flowering and fruiting period, from inflorescence expansion* to fruiting hypanthium dehiscence, is usually about five months. Inflorescence buds do not usually appear in the upper leaf axils before the dehiscence of the fruiting hypanthia of the previous season, and have been recorded only in Kajewski 1005 (May), and by L.S.Smith (1958) in Smith and Webb 4855 (November). Trees which bore young and elongating fruiting hypanthia during August in the Herberton and Mt.Lewis ranges, moreover, were observed to be without fruit, presumably dehisced and fallen, in October (personal observations).

Infraspecific Variation

Differences between the limited number of specimens examined are small and difficult to assess, partly because of the diversity of altitudes and habitat between the collection localities and partly because **the specimens have** been gathered from different positions (on either exposed or shaded branchlets) on the trees of collection.

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* Defined by the falling of the outer flower bud-enveloping peduncular bracts.

Taxonomic Notes and Typification

Having fruiting material only, F.M.Bailey originally described the species in the genus *Daphnandra*. It was maintained there by all later authors, despite Bailey's stated reservations (Queensland Woods, 1886), until L.S.Smith (1958) transferred it to *Doryphora* on the basis of characteristics of both its flower and fruit. It is noteworthy that flowering material of the species was not available in herbaria until after 1948, the first collection being that of L.S.Smith and Webb 4045 (L.S.Smith 1958).

Perkins (1911) treated the species as a synonym of *Daphnandra repandula*. Domin (1925) subsequently pointed out differences in vegetative characters between the two, and in the same year, Perkins (1925) re-distinguished them. C.T.White's (1933) use of the name *Daphnandra repandula* for Kajewski 1005 results from misidentification.

As pointed out by L.S.Smith (1958), *Doryphora aromatica* has all the peculiar characteristics of *Doryphora*, notably the essentially 3-flowered inflorescences, flexuosely aristate staminal apices, lateral styles, and safrol-like odour in all vegetative parts. The latter two characters are quite obvious in fruiting specimens. As such material was available to early investigators, it is difficult to understand how they failed to refer the species to *Doryphora*. Even the morphological features of its secondary xylem are almost identical with those of *D. sassafras* and quite different from those in *Daphnandra*, as is apparent from the photomicrograph of a transverse section of its wood published by

Welch in 1929.

F.M.Bailey (1886) described *Daphnandra aromatica* from specimens collected by T. Bancroft on the Johnstone river, apparently in the year 1885 judging from Bancroft's (1887b)own reference to the species. The type collection (holotype) in BRI referred to by L.S.Smith (1958) was not available for examination and may be lost. The only other specimens traced that are consistent with the protologue are single sheets in herb. MEL (3227) and herb. NSW (67938).

The NSW sheet carries fruiting specimens agreeing in detail with the original description, a piece of bark, and the relevant annotation "Hab. Johnstone River". The collector and date of collection are not given. But there can be little doubt that Bancroft was the collector because, first, the sheet is the only one examined bearing the locality Johnstone river, second, the annotation repeats exactly the locality reference in the original description, and third, the bark specimen included is likely to be consistent with Bancroft's collecting practice.

The MEL sheet bears specimens agreeing in all details with the NSW material but carries the label "North Ql.Timber Collect.1885 Bailey" in F. von Mueller's hand. A field note on the collection also mentions bark and probably refers to a large piece of bark of this species in herb. MEL labelled *Daphnandra repandula* by Mueller. As Bailey was not in north Queensland in the year 1885(C.T.White 1950), it is more than likely that these specimens were from the series collected by Bancroft on the Johnstone river subsequently sent to Mueller by Bailey, hence the reference to the latter.

Chemistry

The essential and volatile oils of Doryphora aromatica have been investigated by Jones and F. Smith (1924 a, b). They found that both bark and leaves yeilded ca 0.3% essential oils. Oil from the bark was dark amber in colour and, possessing the characteristic odour of sassafras, comprised 95% safrol. The lower fraction indicated a terpene with the general characteristics of laevo-rotary pinene. Total oil from the leaves (yield 0.5%) was light greenish yellow in colour, possessed an agreeable cinnamon-like odour, and appeared to comprise approximately 30-40% sesquiterpene, 20-25% d-phellandrine, 10-15% cineol, 5-10% d-pinene, and 5-10% sesquiterpene alcohol, with minor aldehydic, phenolic, and ester constituents.

The alkaloids of this species were first examined by Bancroft (1887b), who claimed to have isolated three alkaloids with the same poisonous properties as those of Daphnandra apatela and D. repandula.

Subsequent investigations by Bick and Whalley (1948), and Bick, Ewen, and Todd (1949), reviewed by Kulka in Manske (and Holmes)(1954, 1960), have revealed that the total alkaloid content of air-dried bark is over 6%, an amount comparable to that found in species of Daphnandra (Bancroft l.c., Pyman 1914, Bick et al., l.c.), and that at least two major alkaloids are present. Both are colourless, phenolic, and have two diphenyl ether linkages and high positive specific rotations.

The alkaloid present in larger quantity, daphnoline, has the formula

$C_{35}H_{36}O_6N_2$ (or possibly $C_{34}H_{34}O_6N_4$ cf. Pyman 1914), comprises two phenolic-groups, two methoxy-groups, and one methylimino-group, and melts between 194°-195°C. It is related to trilobamine of the oxyacanthine-berbamine group, and occurs also in Daphnandra apatela.

The alkaloid in smaller quantity, aromoline, has the formala $C_{36}H_{38}O_6N_2$, and comprises two phenolic-groups, two methoxy-groups, and one methylimino-group. It forms colourless, flat, plate-like crystals which melt at 174°-175°C. It has also been recorded in very small amounts in Daphnandra tenuipes but no other species so far investigated in the family.

One major alkaloid has apparently not been isolated yet (Bick, pers. comm.).

Uses

The alkaloids have potential use as drugs. Alkaloid extracts of the bark were found by Bancroft (1887) to contain respiratory and cardiac poisons similar in physiological action to those of Daphnandra repandula (see also F.M.Bailey 1901, Bick and Whalley 1948). No instances of their having poisoned stock appears to be known.

The timber, which is sometimes milled, is light in colour, without grain, and rather soft with an average lateral hardness of 255 kg (Welch 1929). It resembles "pine-wood", and may serve as a substitute for "pine" in many circumstances (F.M.Bailey 1886, 1888, 1901, 1913, Maiden 1889, 1921, J.F.Bailey 1899). According to Welch (l.c.) and Garratt (1934), it may be used for the same purposes as the timber of Daphnandra apatela and Doryphora sassafras, in turned articles and interior work.

2. Doryphora sassafras Endl.

Doryphora sassafras Endl., Icon.Gen.Pl. 1(1837)10, pl.10; Schnizlein, Icon. 2(1849)n.105, f.17-26; Lindl., Veg.Kingd. ed.3,(1853)300, f.208; Hook.f., Fl.Tasm. 1(1855)11,12; Tul., Arch.Mus.Hist.Nat. Par. 8(1855)424; C.Muell.in Walp., Ann.Bot. 4(1857)119,120; Seem., Fl.Viti. (1867)205; Woolls, Contrib.Fl.Austral. (1867) 111,176; A.DC., Prod. 16,2(1868)676; Baill., Hist.Pl. 1(1869)319, 335, f.357-9; Bentham, Fl.Austral. 5(1870)283; Woolls,Pl.Indig. Neighbour.Sydney (1880)9; F.Muell., Syst.Cens.Austral.Pl. 1(1882) 3; F.M.Bail., Synops.Queensl.Fl. (1883)422; Moore, Cens.Pl.N.S. Wales (1884)58; Baill., Dict.Bot. 2(1886)468, f.; Woolls, Vict. Nat. 4(1887)104; Hobein, Bot.Jb. 10(1888)71; Maiden, Useful Nat.Pl.Austral. (1889)168,418; Maiden, Proc.Linn.Soc.N.S.Wales 4(1889)107; F.Muell., Sec.Syst.Cens.Austral.Pl. 1(1889)5; Pax, Pflzfm. 3,2(1889)104, f.68 F-H; F.M.Bail., Cat.Pl.Queensl. (1890)39; Moore & Betche, Handb.Fl.N.S.Wales (1893)15; "M.T.M.", Gard.Chron. 3,18(1895)34, f.6; Lauterer, Proc.Roy.Soc.Queensl. 11(1895)21; Solereder, Syst.Anat.Dicot. (1899) [transl.Boodle, Fritsch, & Scott, 2(1908)701]; Nicholson, "1900" Suppl.Dict.Gard 1(1900)329 [n.v.]; F.M.Bail., Queensl.Fl. 4(1901)1295; Deane, Proc.Linn.Soc.N.S.Wales 25(1901)587, f.1; Perk.& Gilg, Pflzr. 4(1901)79, f.22 K-M; Deane, Rec.Geol.Surv.Vict. 1(1902)26;

Maiden, For.Fl.N.S.Wales 1(1903)42, f.7, 2(1906)187; Dixon, Pl. N.S.Wales (1906)31; Maiden, For.Fl.N.S.Wales 4(1910)158, pl.; Guilfoyle, Austral.Pl. (1911)145,384 (pl.), 462; Perk., Pflzr. 49(1911)47; Petrie, Proc.Linn.Soc.N.S.Wales 37(1912)139; F.M. Bail., Compr.Cat.Queensl.Pl. (1913)419;Maiden & Betche, Cens. N.S.Wales Pl. (1916)80; Maiden, Some Princip.Comm.Trees N.S.Wales (Forest.Handb.2)(1917)209, pl.7; Baker, Hardwoods Austral. (1919) 332; Penfold, J.Proc.Roy.Soc.N.S.Wales 55(1921)270 et seq.; Brough, McLuckie, & Petrie, Proc.Linn.Soc.N.S.Wales 49(1924)475 et seq.; Perk., Gattung.Monim. (1925)4,52, f.40 K-N; Chisholm, Proc.Linn.Soc.N.S.Wales 50(1925)288,296; McLuckie & Petrie, Proc. Linn.Soc.N.S.Wales 52(1927)175, text-f.7; Francis, Austral. Rain-For.Trees (1929)4,20,23,26,95, f.57,58; Welch, J.Proc.Roy. Soc.N.S.Wales 62(1929)350,354 et seq., f.1; Lemée, Dict.gen. phan. 2(1930)727; Garratt, Trop.Woods 39(1934)19 et seq.; Fraser & Vickery, Proc.Linn.Soc.N.S.Wales 63(1938)148 et seq., table 1; Davis, Proc.Linn.Soc.N.S.Wales 66(1941)12,16,23; Hurst, Poison Pl.N.S.Wales (1942)122,123; Bick & Whalley, Univ.Queensl.Pap. I,28(1946)1; de Beuzeville, Austral.Trees Austral.Planting (1947) 110,153; Webb, C.S.I.R. Bull. n.232(1948)110; Turrill, Curtis Bot.Mag 165(1948)t.30; Henry, Pl. Alkaloids ed.4,(1949)320; Metcalfe & Chalk, Anat.Dicot. 2(1950)1139 et seq., f.275E, 276A, F; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950)390,392, f.II.29-32, IV.43; Francis, Austral.Rain-For.Trees ed.2,(1951)5,24,28,31,49, 112, f.58,59; Erdtman, Pollen Morph.& Pl.Taxon. (1952)271; Burges & Johnston, J.Ecol. 41(1953)72 et seq.; Anderson, Trees N.S.Wales ed.3,(1956)140,223; Baur, Austral.J.Bot. 5(1957)194 et seq.; L.S.Smith, Proc.Roy.Soc.Queensl. 69(1958)48; Baur, Forest.Comm. N.S.Wales Research Note 9(1962)49 et seq., f.2,5; Evans in Beadle, Evans, & Carolin, Handb.Vasc.Pl.Sydney & Blue Mts. (1963) 130; Florence, Proc.Linn.Soc.N.S.Wales 88(1963)176; Buchheim in Melchior, Syllab.Pflzfm. ed.12,2(1964) f.42H; Hutchinson, Gen. Fl.Pl. 1(1964)112, 122*; Gharbo, Beal, Schlessinger, Cava, & Svoboda, Lloydia 28(1965)237; Rüffle, Geol.Jahrg. 1(1965) f.V.2; Deulofeu, Comin, & Vernengo in Manske, Alkaloids 10(1968)452; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342*; Manske in Manske, Alkaloids 10(1968)559 "Doryphora sassafras".

TYPE: A. Cunningham 6, Illawarra, Aug.1824 —— holotype in W (lost), lectotype in K, isolectotypes in A (with locality Blue Mountains), K, SING; A. Cunningham 179, Five Islands, Nov.1818 —— syntypes in BM, K.

[*Atherosperma sassafras* A.Cunn.ex Endl., Gen.Pl. 1(1837)315 pro syn. *Doryphorae*; Meisn., Pl.vasc.gen. 2(1841)236 pro syn. *Doryphorae*; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)276,422 "Atherospermatis sassafras", 424 "Atherosperma sassafras" pro syn. *Doryphorae sassa-*

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* The author citation "Engl." (= Engler) given by these authors is a misprint for "Endl." (= Endlicher).

fras; A.DC., Prod. 16,2(1868)676 pro syn. Doryphorae sassafras;
TURRILL, CURT. BOT. MAG. 165(1948)t. pro syn. Doryphorae sassafras
Baill., Hist.Pl. 1(1869)317 pro syn. Doryphorae sassafras?;
not validly published as not accepted by any author: I.C.B.N. 1966, art.34.]

The following illustrations of this species cited in Index Londinensis have not been seen: Ettingshausen, Denkschr.Akad.Wiss.Wien 15(1858) f.XXVIII.5-7; Ettingshausen, Blatt-Skel.Dikot. (1861)f.16,17; Baill., Traité Bot.Méd.Phan. 1(1883)527.

Figures 1G, 18-20, 32, 37A, 46A.

Diagnosis

Bark rather rough, longitudinally cracked or furrowed, mid grey-brown to mid grey; ultimate branchlet stems rounded, infrequently angular tetragonous; crown leaf blades elliptic to lanceate-ovate, (1-)3-9(-13) cm long × ($\frac{3}{4}$-)1$\frac{1}{4}$-3$\frac{1}{2}$(-5) cm broad, with shallowly to deeply crenate-serrate margins, and conspicuously prominent rather close vein reticulum on lower face.

Mature inflorescence buds broadly compressed obcordiform; peduncles compressed, (1-)1$\frac{1}{4}$-2(-2$\frac{1}{2}$) mm broad, the distal internode ± suppressed, with inner bracts inserted adjacent to or on the first node, ± contiguous with outer bracts; outer bracts deeply ovate cymbiform, (4-)5-8(-10) mm long × 3-5 mm broad; inner bracts planate, tepaloid, (4-)6-8(-10) mm long × (2-)2$\frac{1}{2}$-3 mm broad; mature flower buds (5-)6-8(-9) mm long × (2-)2$\frac{1}{2}$-3(-3$\frac{1}{2}$) mm thick, invariably attenuately ovoid acute when terminal in inflorescence.

Open flowers with perianth comprising 6, exceptionally more or less, lanceate to narrowly elliptic tepals, (6-)7-13(-18) mm long × $(1\frac{1}{2}$-$)2\frac{1}{2}$-4 (-7) mm broad, in 2 trimerous whorls; androecium (3-)4-seriate, comprising an outer whorl of 6, exceptionally more or less, stamens $(5\frac{1}{2}$-)6-10 (-13) mm long × $(1\frac{1}{3}$ -$)1\frac{1}{2}$-$2\frac{1}{4}$(-$2\frac{1}{2}$) mm broad, an inner whorl of (4-)6(-8) stamen-like staminodes $(2\frac{1}{2}$-$)3\frac{1}{2}$-7(-8) mm long × $(\frac{1}{2}$-$)\frac{2}{3}$ - $\frac{3}{4}$(-1) mm broad, and (1-)2 innermost whorls of (4-)8-12(-14) style-like staminodes 1-2(-$2\frac{1}{2}$) mm long × $\frac{1}{3}$ - $\frac{2}{3}$ mm thick; gynoecium of (6-)9-12(-15) carpels.

Ripe infructescences with peduncles $(\frac{1}{4}$-$)\frac{1}{2}$-1(-$1\frac{2}{3}$) cm long, 1-noded, the distal internode suppressed; fruiting hypanthium with 6-ribbed neck, the ribs extending on to or over hypanthium base, very prominent; bodies of ripe nutlets (3-)$3\frac{1}{2}$-5(-6) mm long × 2-3 mm thick, the hairs at the base of the styles (7-)8-12(-13) mm long.

Detailed Description

Slender trees (15-)20-50(-55) m high, but tall shrubs or young trees in open sites often flowering when 4-8 m high; bole (20-)50-120(-165) cm diameter breast height, not or slightly buttressed to a height of 1 m; crown usually short, ca $\frac{1}{8}$ - $\frac{1}{4}$ × length of bole or in southernlocalities up to $\frac{7}{8}$ × length of bole, widespreading and dense in open situations. Bark 5-15 mm thick when dry, outer surface rough, flaking, longitudinally cracked, or deeply furrowed, infrequently rather smooth, mid grey-brown to mid grey, rarely paler, inside usually salmon-cream to pale brownish cream, rarely darker, drying dirty cream-brown to reddish fawn. Wood rich or dark cream in sapwood to yellow-cream in heartwood, drying yellower to pale yellow*, often deeper yellow with dark streaks in the duramen, becoming dirty with age. Branchlet stems with ultimate 2-3(-5) internodes ($\frac{3}{4}$-)$1\frac{1}{2}$-$4\frac{1}{2}$(-8) cm long × 1-2(-$2\frac{1}{2}$) mm thick, compressed, often rounded, infrequently angular tetragonous, drying variously pale or mid grey to brownish, the ultimate internodes darkest occasionally blackish, glabrescent, the ultimate 1-3(-5) internodes usually very sparsely strigillose, rarely entirely glabrous; shaded and sapling branchlets with ultimate 2-4 internodes ($\frac{3}{4}$-)2-7(-9) cm long × (1-)$1\frac{1}{4}$-$2\frac{1}{2}$ mm thick, similarly compressed, ± smoother, almost entirely glabrous. Petioles (3-)4-8(-13) mm long × 1-$1\frac{1}{2}$(-2) mm thick, sparsely sordid white to brown strigillose, ultimately glabrescent. Leaf blades elliptic to lanceate or narrowly ovate, rarely broader or narrowly obovate, (1-)3-9(-13) cm long × ($\frac{3}{4}$-)$1\frac{1}{4}$-$3\frac{1}{2}$(-5) cm broad, broadly cuneate, rarely narrower or ± obtuse at the base, narrowly to acuminately mucronulate obtuse, rarely to retuse or acute at the apex; margins shallowly to deeply crenate-serrate, rarely finely crenate, slightly but distinctly recurved; texture quite coriaceous, less often thinly coriaceous; colour dull to ± glossy mid to rather dark green on upper face, duller and paler on lower, in shoot leaves glossy light green, often reddish tinted, in dry leaves pale mid brown to olive-brown or pale grey-green, rarely darker or tinted black on upper face, usually browner, greener, or similarly coloured on lower; nervation on lower face with (7-)8-12(-18) slenderly

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* Maiden (1903), Welch (1929), Francis (1929, 1951).

but conspicuously prominent main nerves, the vein reticulum conspicuous, hardly less prominent, rather closely interwoven, extending between the nerves to the midrib; generally glabrous; leaf blades on shaded and sapling branchlets more frequently narrowly obovate, $(2\frac{1}{2}-)5-12(-17)$ cm long × $(1-)2-4\frac{1}{2}(-6)$ cm broad, with more deeply crenate-serrate or dentate, ± planate margins, more thinly coriaceous almost chartaceous, nerves and vein reticulum more prominent on upper face.

Mature inflorescence buds and stipes $(\frac{3}{4}-)1-2$ cm long, the buds broadly compressed obcordiform, $(4-)5-9(-10)$ mm long × $(3\frac{1}{2}-)5-6(-8)$ mm broad. Mature inflorescences 3-flowered false dichasia*, not very congested on ultimate branchlets, with 1, less often 2 per leaf axil, ca $(1\frac{1}{4}-)1\frac{1}{2}-3$ cm long, generally pale grey-green or golden to grey-white hoary or silky strigillose. Peduncles ± 1-noded, the single (= base) internode peduncle-like, $(\frac{1}{4}-)\frac{1}{2}-1(-1\frac{1}{3})$cm long × $(1-)1\frac{1}{4}-2(-2\frac{1}{2})$ mm broad, very broadly compressed towards the apex, drying dark olive-brown to grey-brown, sometimes blackish, sparsely sordid stramineous to pale-greenish grey hispidulous-strigillose, sometimes rather densely haired, rarely quite glabrous; outer bracts ovate, deeply cymbiform, strongly bilaterally compressed, $(4-)5-8(-10)$ mm long × 3-5 mm broad, with mucronate acuminate, sometimes attenuate apices, and prominently carinate abaxial midribs, abaxial hairs usually densest along the margins and towards the apices, markedly enlarged to enclose the expanding inflores-

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* Very rarely 6-flowered with two 3-flowered "dichasia" on a common stipe in some inflorescences in Schodde 3519 and C.T.White 8520.

cence, caducous at or just before flowers opening; distal internode ± suppressed; inner bracts inserted at the base of the pedicel of the terminal flower or on the adjacent peduncle apex, rarely to half-way up "pedicel", oblanceate-obovate to oblong-elliptic, ± planate, (4-)6-8(-10) mm long × (2-)2½-3 mm broad, with an impressed or obscure prominently haired abaxial midrib, ± tepaloid, densely grey-white to pale grey-green sericeous-strigose, usually more sparsely haired adaxially, caducous with outer bracts; pedicels (1-)2-5(-7) mm long × (⅔ -)¾-1 mm thick, those of lateral flowers initially shorter, ultimately as long as or longer than those* of terminal flowers, ± terete, sometimes obscurely tegragonous under central flowers or slightly compressed under lateral flowers, densely sordid grey-white, pale grey, or grey-green silky strigillose. Mature flower buds all attenuately ovoid acute, sometimes rather fusiform, (5-)6-8(-9) mm long × (2-)2½-3(-3½) mm thick, densely sordid grey-white to pale grey-green silky strigillose, the hairs often denser on the hypanthium.

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* Pedicels of the terminal flower are only longer than those of mature lateral flowers when they bear the inner pair of peduncular bracts. Their greater length is then due to the obscure internode between the inner bract node and the first peduncle node which in turn is homologous with the distal internode of the inflorescence peduncle in *Doryphora aromatica*.

Open flowers. Hypanthium often obscurely rounded trigonous, (1-)1½-2 (-3) mm long × (1-)1½-2(-3) mm thick, sordid grey-white to pale grey-green, sometimes brownish, finely strigillose; rim (⅓ -)½ - ⅔(-¾) mm broad. Perianth sometimes tinted cream or pink, comprising 6, exceptionally 5, 7, or 8, tepals in 2 trimerous subequal whorls; tepals ± lanceate or narrowly elliptic, rarely almost ovate, (6-)7-13(-18) mm long × (1½-) 2½-4(-7) mm broad, with attenuately acute, almost caudate, rarely narrowly obtuse apices, finely strigillose abaxially, with midnerve hairs forming a prominent rib, particularly in tepals of outer whorl, rarely almost glabrous adaxially, with hairs occasionally denser or confined along midnerve, inner tepals shorter, more markedly caudate-acute, not often narrower than the outer. Androecium (3-)4-seriate, stamens 6, exceptionally 4, 7, or 8 in an outer whorl, (5½-)6-10(-13) mm long × (1⅓ -)1½-2¼ (-2½) mm broad × ± ½ mm thick at the pollen sacs; filaments (¾-)1-1¾(-2) mm long × (½-)¾-1(-1½) mm broad, rarely with an obscurely prominent abaxial midnerve; staminal glands lanceate- to ovate-deltate, rarely almost circular or rather thick and ellipsoid-cylindrical, acute to obtuse, (⅔ -)¾-1¾(-2) mm long × ½ - 1½ mm broad; anthers with flexuosely aristate apices (3½-)4½-7(-10) mm long, acute, rarely slightly expanded or compressed towards the tip, and pollen sacs (⅔ -)¾-1¼(-1½) mm long; stamen-like staminodes (4-)6(-8) in an inner whorl, flexuosely aristate, often variable in length, (2½-)3½-7(-8) mm long, (½-)⅔ - ¾(-1) mm broad at the base, glabrous, the glands oblong-cylindrical obtuse, rarely planate-deltate, (⅓ -)½-1(-1½) mm long, hardly or slightly stipitate, the longer staminodes infrequently partly fertile with 1 or 2 pollen sacs ca $\frac{1}{2}$ mm long, the shorter staminodes often strigillose adaxially, with glands sometimes reduced or partly aborted; style-like staminodes (4-)8-12(-14) in (1-)2 innermost whorls, 1-2(-$2\frac{1}{2}$) mm long × $\frac{1}{3}$ - $\frac{2}{3}$ mm thick, the longer staminodes infrequently rather sparsely haired and bearing vestigial gland(s) up to $\frac{2}{3}$ mm long. Gynoecium of (6-)9-12(-15) carpels; styles lateral, exserted ($\frac{1}{2}$-)1-$1\frac{3}{4}$(-2) mm beyond hypanthium rim in a slenderly to broadly cylindrical or conical column $\frac{1}{2}$-$\frac{3}{4}$ mm thick; stigmatic column connate at the base, usually stellately branched at the apex, ($\frac{1}{4}$-)$\frac{1}{2}$-$1\frac{1}{4}$(-2) mm long.

Ripe infructescences rarely appearing congested on branchlets, (2-)$2\frac{1}{2}$-4(-$4\frac{1}{2}$) cm long, 1-2(-3) hypanthia maturing per infructescence. Peduncles of the same dimensions, form, and colour as in inflorescence, usually more sparsely and paler brownish hispidulous-strigillose to glabrescent; pedicels (3-)5-9(-10) mm long. Fruiting hypanthium ± urceolate, rarely rather cylindrical, (12-)13-22(-25) mm long × (4-)5-8 mm thick at the base, 4-5 mm thick at the neck, with 6 prominent ribs usually extending broadly on to or over hypanthium base from the neck, slightly glossy pale green, drying pale to dark grey-brown, rarely blackish, sparsely grey-white to sordid stramineous strigillose, the hairs usually denser in the furrows between ribs and on young hypanthia; rim ($\frac{1}{2}$-)$\frac{2}{3}$ - $\frac{3}{4}$(-1) mm broad, all tepal scars ± contiguous. Nutlets elongating in maturing hypanthium to maintain or slightly increase the exsertion of the style apices (1-)$1\frac{1}{2}$-2(-3) mm beyond the hypanthium rim;

bodies of ripe nutlets ovoid to ellipsoid, (3-)$3\frac{1}{2}$-5(-6) mm long × 2-3 mm thick, entirely glabrous; sub-basal styles of ripe nutlets (10-)12-18 (-20) mm long, the basal hairs (7-)8-12(-13) mm long, fawn-to dark brown.

3-6-noded seedlings 5-10 cm high and 8-10-noded seedlings 20-25 cm high, the ultimate 3-6 internodes ± tetragonous with the angles usually flanged, 15-30 mm long × $\frac{3}{4}$-$1\frac{1}{4}$(-$1\frac{1}{2}$) mm thick, sparingly off-white strigose; cotyledons caducous; subsequent leaf pairs with petioles 1-2 mm long × $\frac{3}{4}$ mm thick in early leaves, 4-6 mm long × 1 mm thick in later, sparsely strigillose, and leaf blades elliptic to broadly elliptic, 15-35 mm long × 7-20 mm broad in early leaves, 35-80 mm long × 20-40 mm broad in later, with cuneate bases, broadly acute to acuminate or rounded obtuse apices,dentate-serrate planate margins, generally chartaceous texture, impressed midrib on upper face, conspicuously prominulous 5-9 main nerves and relatively spare vein reticulum on both faces, glabrous in early leaves, sparsely strigillose along the lower face midrib in later; later leaves of ultimate nodes approach the form and pubescence of leaves of adult trees.

The epithet *sassafras* refers to the aromatic safrol-like odour, reminiscent of that of the laurel genus *Sassafras*, which is emitted from all parts of the plant (cf. F.M.Bailey 1901, Maiden 1903, Francis 1929, 1951).

Aboriginal names: Boobin (northern districts of New South Wales - Maiden 1889, 1903), Caalang (Illawarra - Maiden 1889, 1903), Tdjeun-degong (Brisbane water - Maiden 1889, 1903).

Vernacular names: Australian sassafras (Metcalfe and Chalk 1950), Black sassafras (Maiden 1903, 1917, Welch 1929, Garratt 1934, Metcalfe and Chalk 1950, Hutchinson 1964 - possibly in error for <u>Atherosperma moschatum</u>), Canary sassafras (Swain 1928 [n.v.], Francis 1929, 1951, Garratt 1934, Turrill 1948, Webb 1948), Golden deal (Francis 1929, 1951, Turrill 1948), Grey sassafras (Welch 1929, Garratt 1934, Metcalfe and Chalk 1950, Hutchinson 1964), Native sassafras (Moore and Betche 1893), New South Wales sassafras or N.S.W. sassafras-tree (Maiden 1903, 1917, Guilfoyle 1911, Turrill 1948, Anderson 1956), Sassafras (Endlicher 1841, Lindley 1853, Woolls 1867, Maiden 1889, 1903, Pax 1889, Dixon 1906, Penfold 1921, Francis 1929, 1951, Welch 1929, Hurst 1942, Turrill 1948, Webb 1948, Anderson 1956, Baur 1962, Evans in Beadle, Evans, and Carolin 1963, McSkunming 2), Sassafrax (used by ignorant people according to Maiden 1903, 1917), Yellow sassafras (Francis 1929, 1951, Turrill 1948), Yellow wood (Ikin 9). The name "Sassafras" is by far the most widely used.

Series of specimens examined: 155 collections, comprising 36 with inflorescence buds, 40 with mature flower buds, 52 with open flowers, 13 with young (unelongated) fruiting hypanthia, 24 with near or quite mature (fully elongated) fruiting hypanthia, 3 of young plants ca 1 m high, and 2 of seedlings.

Geographic Distribution (map 9).

<u>Doryphora sassafras</u> occurs on the eastern scarp and summit ridges of the Great Dividing range and adjacent coastal areas of New South Wales,

and is almost confined to that State from the Macpherson range in Queensland on the New South Wales border, 28°10´S, south to about Mt.Dromedary, 36°30´S, or the Towamba river, 37°S, at Myrtle creek, Wyndham (Maiden 1903). Maiden (l.c.) suggests that the species extends into Victoria, but this seems unlikely in view of the recent enumerations of the flora of the subtropical rainforests at Mt.Drummer and of rainforest plants in east Gippsland which do not record it (Wakefield 1953, 1955).

Ecology (figures 49, 50, 55-58)

Doryphora sassafras is a frequent, often dominant or co-dominant canopy tree of primary, less often disturbed, cool subtropical or submontane* rainforest. In the northern parts of its range, it occurs in montane forests between the altitude of 600-1500 m in both sheltered gullies and on ridges sheltered by the main spine of the Great Dividing range from dessicating westerly winds (cf. Brough et al. 1924, Fraser and Vickery 1937, Turrill 1948, Baur 1957); it rarely descends to ca 50 m, as at Minyon Falls in Whian Whian State Forest (Johnson and Hayes 66) or Woolgoolga (de Beuzeville: L, NSW 18748), owing to local conditions. At its northern limit in the Macpherson range, it is confined to altitudes above about 900 m. In southern parts, it extends to lower altitudes in similarly cool and sheltered forest, being found at sea-level from Bulli and the Illawarra district southwards while still occurring on adjacent mountain ranges up to about 900-100 m s.m. at Mt.Wilson (Brough et al. l.c., C.T.White 8520, personal observations), and Mt. Budawang (Bäuerlen: NSW 67987, personal observations).

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* The pertinent aspect of subtropical rainforest here has been termed submontane rainforest by Webb (1959) and Baur (1962).

It shows a marked preference for red basaltic soil throughout its range (Woolls 1867, Brough et al. l.c., Anderson 1956, Baur 1957, C.T. White 6066, Constable: NSW 3665, Johnson and Hayes 66, C.W.E. Moore 3409, Schodde 3476, 5182); its occurrence in the Sydney and Blue Mountains sandstone area is confined locally to basalt sheets or caps or to alluvium in gullies derived from the erosion of basalt (Brough et al. l.c., Johnson: NSW 67961, NSW 67970). Elsewhere under suitable climatic conditions, it occurs on alluvium along creeks and rivers, such as on the Manning river (Florence 1963, Rudder: NSW 67955) and Currowan creek (Schodde 3459, 4194), and on soils of lower nutrient status derived from shales, for example at Mt.Coramba (Schodde 3527, 3527a), and the Narrabeen chocolate shales of the Illawarra district, and the Wianamatta shales of adjacent uplands (Baur 1957). Baur (l.c.) gives the soil nutrient level for Ceratopetalum-Doryphora rainforest associations, in which the species is a dominant, as 3180 p.p.m. total phosphate.

In its preferred habitat over much of its range, it is a co-dominant tree with Ceratopetalum apetalum, forming an association with that species on the Comboyne and Carrai plateaux, and at Mt. Wilson, the gorges in the Blue Mountains, and the Illawarra-Nowra district, but not on the intervening Barrington Tops or Mt.Coricudgy massif where C. apetalum is absent (Woolls l.c., Brough et al. l.c., Turrill l.c., Francis 1951, Baur 1957, Johnson: NSW 67970, NSW 67975, personal observations). Other trees with which it is commonly associated in these areas are Acmena *smithii*, *Laportea gigas*, *Quintinia sieberi*, and *Toona australis*. At its upper altitudinal limits in the Macpherson range, Dorrigo plateau, Point Lookout area, and Carrai plateau, it also frequently extends into ± temperate rainforest with *Nothofagus moorei*, and usually *Ceratopetalum apetalum*. At these limits on the Barrington Tops, it is associated with *Nothofagus moorei*, *Ackama paniculata*, *Cryptocarya glaucescens*, and *Schizomeria ovata* (Fraser and Vickery 1938, Baur 1957, 1962, Davis: NSW 67948, personal observations).

In the more northern parts of its range, it is a rather inconspicuous element of the floristically rich rainforest. There, as elsewhere, it is associated commonly with the forest canopy trees *Ackama paniculata*, *Acmena* sp., *Backhousia myrtifolia*, *Baloghia lucida*, *Callicoma serratifolia*, *Cinnamomum oliveri*, *Citronella moorei*, *Cryptocarya erythroxylon*, *C. foveolata*, *C. glaucescens*, *Daphnandra* sp., *Diospyros* sp., *Dysoxylum fraseranum*, *Elaeocarpus reticulatus*, *Endiandra discolor*, *Ficus* spp., *Geissois benthamii*, *Guioa semiglauca*, *Litsea reticulata*, *Longetia swainii*, *Mischocarpus* sp., *Orites excelsa*, *Pittosporum undulatum*, *Planchonella australis* *Polyosma cunninghamii*, *Quintinia sieberi*, *Scolopia* sp., *Schizomeria ovata*, *Sloanea australis*, *S. woollsii*, *Stenocarpus salignus*, *Tarrietia actinophylla*, and *T. trifoliata* of subtropical rainforest affinity (Fraser and Vickery 1938, Burges and Johnston 1953, Anderson l.c., Baur 1962, Florence l.c., Johnson: NSW 67961, personal observations).

In more southern parts of its range, it is often the single dominant rainforest tree as at Mt.Coricudgy (Johnson: NSW 67961), Currowan State

Forest (Schodde 3251), and Mt. Dromedary (note by Johnson on Dunn 74), or it may be associated with other single less frequent tree species such as *Eucryphia moorei* in the Mt. Budawang-Clyde mountain area (personal observations), and *Acacia melanoxylon* on the Robertson-Nerriga plateaux (Baur 1957, Gray 3533). The *Doryphora sassafras-Acacia melanoxylon* community has been regarded as a degenerate one considerably altered by man's activities (Baur 1957). Other associated species, mostly of temperate rainforest affinity, are *Atherosperma moschatum*, *Dicksonia antarctica*, *Elaeocarpus holopetalus*, and *Hedycarya angustifolia* (Brough et al. l.c., Fraser and Vicker 1938, Woolls: MEL 3250, personal observations).

Under optimal conditions in the central parts of its range on the Carrai and Dorrigo plateaux, it frequently grows to a height of 50-55 m as an emergent above the forest canopy. Under limiting conditions, such as extremes of altitude as on the Barrington Tops (Fraser and Vickery 1938), or man-altered environments, as on the Robertson plateau (Schodde 5182), it becomes stunted, compactly branched, and rather shrub-like in habit. Though normally an element of primary forest, it persists and regenerates easily in disturbed habitat by coppicing. In southern areas, it also extends along creeks into open eucalypt vegetation, forming a gallery forest (Brough et al. l.c., Schodde 4194) in much the same way as *Atherosperma moschatum* does in Victoria.

Phenology and Nutlet Dissemination

Flowering and fruiting is seasonally regular. Inflorescence buds as a rule first become noticeable between January and April in the late austral summer and autumn before dehiscence of the fruiting hypanthia of the previous season. They enlarge slowly until (mid May-) late June to late August in late winter when they and the flower buds burst in quick succession or almost concurrently. The flowers mature and the perianth falls between late August and late October. The fruiting hypanthia elongate in early summer months, ultimately maturing and dehiscing in late summer or early autumn (January-April, rarely May). The times of flowering and fruiting quoted by Francis (1929, 1951) and Turrill (1948) are a little early.

A single tree kept under observation in the Currowan State Forest between the years 1963-1965 was found to flower and fruit at the same time each year, irrespective of seasonal fluctuations of climate. It did not flower at all in 1966, a drought year. The following data were recorded: inflorescence buds first distinct as such, 5-9 mm long - mid February (Schodde 3459); inflorescence buds 8-15 mm long - late March (Schodde 3497, 3500); inflorescence buds mature - early to mid July (Schodde 3251); inflorescence and flower buds bursting, almost concurrently - late July (Schodde 3252); all flowers of inflorescence fully open or lateral flowers sometimes still in bud - late August (Schodde 4194); flowers mature and perianth falling - early to mid September (Schodde 3386, 3390); fruiting hypanthia remaining unenlarged as in flower and perianth fallen -

late October (Schodde 3401); fruiting hypanthia elongating and slender - early December (Pullen 3960); fruiting hypanthia fully elongated and becoming thickened and lignified - early January (Schodde 3428); fruiting hypanthia fully lignified - mid February (Schodde 3459); fruiting hypanthia dehiscing - late March (Schodde 3500).

There is an apparent interval of about two to three months between flowering (perianth fall) and commencement of elongation of the fruiting hypanthium. In the only other species in which the flowering cycle was observed over a year, Atherosperma moschatum, growth of the fruiting hypanthium followed flowering (perianth fall) without any apparent break in continuity of development. The causes of these apparent differences have not been investigated, though it is tempting to suggest that they may be correlated with time lags between pollination and fertilisation and differences in the relative position of the styles which are terminal in Atherosperma and lateral in Doryphora. In the other species of Doryphora, D. aromatica, there appears to be a similar but much shorter interval of perhaps only one month between perianth fall and the commencement of fruiting hypanthium elongation, judging from the frequency of such stages in herbarium collections.

All variation recorded in times of flowering appears to be more-or-less at random, rather than correlated with geographic position. Collections from the Macpherson range were in flower in July (England: BRI 052039), mid August (Blake 15886), and late August (Schodde 3373), from the Dorrigo area in mid May (Schodde 3519) and early September

(Floyd: COFFS), and from the Illawarra-Currowan State Forest area in late July - late August (Schodde 3252, 4194, 4195), early September (Schodde 3378), and early October (Fletcher: NSW 67981). Locally, however, trees at higher altitudes usually flower a little later than those below, as may be expected.

Dissemination of nutlets was observed in the study tree in Currowan State Forest in late March 1964 (Schodde 3500). The fruiting hypanthia split longitudinally while attached to the branchlets and recurve to allow the nutlets to fall out. The nutlets, small, light, thin-walled, and glabrous, bear a long plumosely-haired style, adapted to dispersal by wind (chapter IV.17). Wind, however, had little observable effect on the nutlets falling from the study tree, apparently because of the rapid speed of fall; virtually all nutlets landed within a radius of 8 m of the tree after falling from heights of between 10 and 25 m. It seems from this that, in view of the fragile wall of the nutlet body, the plumose style may play just as important a role in slowing the fall of the nutlet to the ground to prevent damage to its wall as in promoting dispersal by wind.

Infraspecific Variation

Two varieties are distinguishable and separated partly by their geographic and partly by their altitudinal distribution. The northern form, confined to higher altitudes than the southern form, is smoother barked and smaller in leaf size, inflorescence, floral parts, infructescence, and fruiting parts.

a. var. *sassafras*

Doryphora sassafras Endl., 1837, l.c.

Bark of bole deeply and rather coarsely furrowed and cracked; ultimate 2-3 crown branchlet internodes (1-)2-4½(-8) cm long × (1-)1¼-2 (-2½) mm thick, slightly more rounded compressed than in var. *microphylla*; petioles of crown leaves (3-)5-8(-10) mm long × 1-1½(-1¾) mm thick; blades of crown leaves (3-)6-9(-13) cm long × (1-)2-3½(-5) cm broad, with rather narrowly acuminate obtuse apices, and more distantly or obtusely crenate-serrate, less recurved margins than in var. *microphylla*, more thinly coriaceous than in var. *microphylla*, with lateral nerves noticeably prominulous on upper face, drying mid greenish-grey-brown, occasionally tinted black; leaf blades of shaded and sapling branchlets (4-)7-12(-17) cm long × (1½-)2½-4½(-6) cm broad, with usually deeply serrate-dentate margins; mature inflorescence buds including stipes (1-)1½-2 cm long, the buds (5-)6-9(-10) mm long × (3½-)5-6(-8) mm broad, the stipes (3-)5-9(-11) mm long, less broadly compressed than in var. *microphylla*, often rounded; mature inflorescences (1½-)2-3 cm long; inflorescence peduncles (¼-)⅔ - 1 (-1⅓) cm long × (1-)1½-2(-2½) mm broad; outer peduncular bracts (5-)6-8(-10) mm long × (3-)4-5 mm broad; tepals (7-)8-13(-18) mm long × (1½-)2½-4(-7)mm broad; stamens (6-)7-10(-13) mm long, with filaments (¾-)1¼-1¾(-2) mm long, staminal glands (⅔ -)1-1¾(-2) mm long, aristate apices (4-)5-7(-10) mm long; stamen-like staminodes (3-)5-7(-8) mm long; style-like staminodes (1-)1¼-2(-2½) mm long, the longer ones often bearing aborted staminal glands; spreading stigmatic filaments $(\frac{1}{4}-)\frac{1}{2}-1\frac{1}{4}(-2)$ mm long; mature infructescences $(2\frac{1}{2}-)3-4(-4\frac{1}{2})$ cm long; infructescence peduncles $(\frac{1}{2}-)\frac{3}{4}-1(-1\frac{1}{3})$ cm long × $(1-)1\frac{1}{4}-1\frac{3}{4}(-2)$ mm broad; infructescence pedicels (3-)5-9(-10) mm long; fruiting hypanthia (13-)16-22(-25) mm long × (4-)6-8 mm thick at the base; wall of fruiting hypanthium $(\frac{1}{2}-)\frac{2}{3}-\frac{3}{4}(-1)$ mm thick, the rim $(\frac{2}{3}-)\frac{3}{4}(-1)$ mm broad; styles of ripe nutlets (10-)13-18(-20) mm long, with basal hairs (7-)9-12(-13) mm long.

Series of specimens examined: 95 collections, comprising 21 with inflorescence buds, 27 with mature flower buds, 36 with open flowers, 8 with young (unelongated) fruiting hypanthia, 16 with near or quite mature (fully elongated) fruiting hypanthia, one of a young plant ca 1 m high, and 2 of seedlings.

Geographic Distribution (map 9)

Coastal areas and adjacent ranges of New South Wales from the Woolgoolga district, 30°10′S, south to the Mt.Dromedary-Towamba river district, 36°30′-37°S, between 0-900 m s.m.:

Woolgoolga; Pinacle creek; Patrick's Creek road, and Inlet creek area, Mt.Boss State Forest; Port Macquarie; Barrington; Gloucester river; Upper Gloucester; Nabiac; Parish of Fosterton; Upper Chichester; Williams river, near Barrington House; Allyn river; Massey creek, upper Paterson river; Martinsville; Mt.Coricudgy; Kurrajong Heights; Kurrajong; Grose river; North Shore, Sydney; Wahroonga; Port Jackson;

Mt.Wilson; Parramatta; Blue Mountains; Wentworth Falls; National Park; Bola creek, National Park; Lilyvale; Jenolan Caves; Camden; Burragorang valley; Picton; Austinmer; Bulli Gorge; Illawarra; Mt. Kembla; Mittagong range, near Berrima; Robertson; Macquarie Pass; Minnamurra Falls; Five Islands; Kiama; Fitzroy Falls, east of Moss Vale; Berry Mountain; Berry; Kangaroo Valley to Berry, Cambewarra range; Nowra side of Cambewarra range; Wingello; Ocean View-Sassafras Mt. or Sassafras range area (Nerriga-Nowra); Conjola; Shoalhaven; Clyde Mountain (Budawang range); Currowan creek, Currowan State Forest (foothills of Budawang range); Bateman's Bay; Mt. Dromedary; 20 miles south from Mt.Dromedary.

b. var. *microphylla* Schodde, var.nov.

Cortex trunci relative rasilis, laminae foliorum coronarum arborum (1-)3-6(-9) cm longae × ($\frac{3}{4}$-)1$\frac{1}{4}$-2$\frac{1}{2}$(-3) cm latae, inflorescentiae maturae (1$\frac{1}{4}$-)1$\frac{1}{2}$-2(-2$\frac{1}{2}$) cm longae, tepala (6-)7-10(-13) mm longa × 2$\frac{1}{2}$-3(-3$\frac{1}{2}$) mm lata, infructescentiae maturae 2-3 cm longae, hypanthia fructificantia (12-)13-16(-19) mm longa × (4-)5-8 mm crassa, et styli nucularum maturarum (10-)12-14(-15) mm longi. A var. *sassafras* foliorum, inflorescentiarum infructescentiarumque, et partium florium hypanthiorum fructificantiumque magnitudine minore et cortice trunci rasiliore recedit.

TYPUS: Schodde (and Hayes) 3519, vicinity of Forestry Hut, Oaks (= Oakes) State Forest: holotypus in CANB (135444), isotypi in A, AD, B, CANB, CHR, COFFS, G, K, L, NSW, PNH, W, WELT.

Bark of bole shallowly flaking or cracked, hardly deeply furrowed; ultimate 2-3 crown branchlet internodes (¾-)1½-3½(-6) cm long × 1-1½(-2) mm thick, slightly more angular compressed than in var. *sassafras*; petioles of crown leaves 3-6(-9) mm long × 1 - 1⅓(-1½) mm thick; blades of crown leaves (1-)3-6(-9) cm long × (¾-)1¼-2½(-3) cm broad, with rather broadly obtuse, sometimes slightly retuse apices, and more closely and shallowly crenate-serrate recurved margins than in var *sassafras*, ± thickly coriaceous, with lateral nerves frequently obscured on upper face, drying pale greenish brown, often tinted yellowish; leaf blades of shaded and sapling leaves (2½-)5-10(-17) cm long × (1-)2-4(-6) cm broad, with usually shallowly and bluntly serrate-crenate margins; mature inflorescence buds including stipes (¾-)1-1½ cm long, the buds (4-)5-7 mm long × (4-) 5 -5½(-6) mm broad, the stipes (2-)4-6(-8) mm long, broadly compressed; mature inflorescences (1¼-)1½-2(2½) cm long; inflorescence peduncles (⅓-)½-¾(-1¼) cm long × (1-)1¼-1¾ mm broad; outer peduncular bracts (4-)5-7(-7½) mm long ×3-4 mm broad; tepals (6-)7-10(-13) mm long × 2½-3(-3½) mm broad; stamens (5½-)6-9 mm long, with filaments 1-1½ mm long, staminal glands ¾-1¼(-1½) mm long, aristate apices (3½-)4½-6(-7) mm long; stamen-like staminodes (2½-)3½-4½(-5½) mm long; style-like staminodes 1-1½ mm long, the longer ones usually without vestiges of staminal glands; spreading stigmatic filaments ½-1 (-1½) mm long; mature infructescences 2-3 cm long; infructescence peduncles (⅓ -)½-¾(-1) cm long × 1-1½ mm broad; infructescence pedicels (3-)5-6(-8) mm long; fruiting hypanthia (12-)13-16(-19) mm long ×

(4-)5-8 mm thick at the base; wall of fruiting hypanthium $\frac{1}{2}$ - $\frac{2}{3}$ mm thick, the rim $\frac{1}{2}$ - $\frac{2}{3}$(-$\frac{3}{4}$) mm broad; styles of ripe nutlets (10-)12-14 (-15) mm long, with basal hairs 8-10(-11) mm long.

Series of specimens examined: 37 collections, comprising 8 with inflorescence buds, 5 with mature flower buds, 11 with open flowers, 3 with young (unelongated) fruiting hypanthia, 6 with near or quite mature (fully elongated) fruiting hypanthia, and 1 of a young plant ca 1 m high.

Geographic Distribution (map 9)

Mountain ranges between the Macpherson range, south-east Queensland, 28°10'S, and Barrington Tops, north-east New South Wales, 32°S, 600-1500 m s.m.:

Queensland. Tallebudgera scrubs; Beechmont; Springbrook; Roberts Plateau, Lamington National Park; O'Reilly's Lodge, Lamington Plateau; Lamington National Park; Mt.Lindsay; Killarney Forestry Camp.

New South Wales. Acacia Creek via Killarney; Acacia Plateau; Tweed; Nullum State Forest; Peach Mountain ridge, Whian Whian State Forest; Clarence river; summit of Mt.Coramba; Coffs Harbour (area); Wild Cattle Creek State Forest (Dorrigo); Brooklana; Dorrigo; eastern Dorrigo; State Forest 488, Dorrigo; Mt.Moonbill; Oakes State Forest; Oxley Highway, 62 miles west of Wauchope; Woolooma Mt., east of Scone; Stewart's Brook; Gloucester.

The differences between the two varieties are of degree not kind. The varieties are linked throughout their geographic and altitudinal range, moreover, by a number of collections with intermediate characters. These collections are from south-east Queensland (Wilsons Peak; Emu Vale via Warwick), from north-east New South Wales, 60-1350 m s.m. (Acacia Plateau; Whian Whian State Forest; Minyon Falls, Whian Whian State Forest; summit of Mt.Coramba; Bellinger river; Point Lookout; South Arm, west of Bowraville; Doyle's River; Oxley Highway; Manning river; Bowman and Barrington rivers; Wakivory creek, Gloucester; Craven State Forest, Gloucester; Lagoon Pinch to Scouts Alley, Barrington Tops; Barrington Tops above Williams river; Dingadee, Williams river), and from the central eastern tablelands of New South Wales, 900-1100 m s.m. (Mt. Wilson; Zigzag brush, Mt.Wilson; Sugarloaf Mountain, east of Braidwood (probably = Mt. Budawang)). They total 23, and comprise 7 with inflorescence buds, 8 with mature flower buds, 5 with open flowers, 2 with young (unelongated) fruiting hypanthia, 2 with mature (fully elongated) fruiting hypanthia, and 1 of a young plant ca 1 m high.

The characters distinguishihg the two varieties, when viewed together with those in the collections of intermediate form, vary clinally along either north-south geographic or altitudinal gradients or a combination of both. Altitude has a more marked effect on the size and form of the crown leaves, and to a lesser extent the lengths of the leaf internodes and fruiting pedicels, than does latitude. Crown leaf blades from the

Coffs Harbour area (Schodde 3519) and Mt. Budawang area (Bäuerlen: NSW 67987) between 600-1050 m s.m. are both 3-5½ cm long x 1¼-3 cm broad, whereas those from the same areas but at altitudes below 200 m s.m. (de Beuzeville: NSW 18748 and Schodde 3390, respectively) are ca 5½-10 cm long x 2-3½ cm broad.

Other characters such as those of the bark and size of flower and fruit parts vary according to geographic position. This is most strikingly illustrated by the lengths of the staminodes. The lengths of the stamen-like and innermost style-like staminodes are respectively 4-4½ mm and 1-1¼ mm in flowers from Beechmont (England: BRI 052039) and Springbrook (Blake 15886) in the Macpherson range, respectively 5-6 mm and 1½ mm in flowers from Nabiac (Gilbert: NSW 67949) and Bowman and Barrington rivers (Maiden: NSW 67950) on the lower north coast of New South Wales, and respectively 7 mm and 1¾-2 mm in flowers from Mt. Budawang (Bäuerlen: NSW 67987) and Currowan State Forest (Schodde 3390, 4194) on the south coast of New South Wales.

Of the characters which appear to vary according to a combination of geographic and altitudinal position, tepal length is the most well-marked. At altitudes between 600 and 1200 m, tepals vary from 6½-8(-9) mm long at Springbrook and Beechmont (Blake 15886, England: BRI 052039) in the Macpherson range, to 7-10 mm long at Oakes State Forest (Schodde 3519) in the Coffs Harbour area, and to 9-11 mm long at Mt. Wilson (Johnson: NSW 14558) in the Blue Mountains, and 8-10 mm long at Mt. Budawang (Bäuerlen: NSW 67987). At lower altitudes between sea level and about 300 m s.m. at the same latitudes, tepal lengths vary from 10-12 mm at Woolgoolga (de Beuzeville: NSW 18748) in the Coffs Harbour area, to 11-12 mm at Kurrajong Heights (Cleland: AD 97614025,6) in the Blue Mountains, and (9-)11-13 mm in the Currowan State Forest (Schodde 3390, 4194), Mt.Budawang area.

Taxonomic Notes and Typification

Since its description, Doryphora sassafras has been treated as a distinct species by all revisers. Hitherto no infra-specific taxa have been recognised.

The chromosome number, n = ± 82, has been reported by Ehrendorfer et al. (1968).

The illustration of its flowering hypanthium by S.Ross-Craig in Turrill (1948), though correct in details for each organ, gives a distorted impression of the flower as a whole whereas most other illustrations, as in Schnizlein (1849), Baillon (1869) (reproduced in Pax (1889) and Perkins and Gilg (1901)), and Maiden (1903), while depicting floral symmetry correctly, are less accurate in the details of floral parts.

The inner pair of bracts in the inflorescence of Doryphora sassafras, though clearly illustrated in Endlicher's Iconographia (1837) and Maiden's Forest Flora of New South Wales (1903), have not been recognised or described before. Sampson (1967) has drawn attention to them.

Endlicher described Doryphora sassafras from collections of Allan Cunningham's labelled "Atherosperma sassafras" by Cunningham (Endlicher 1837) and laid in herb. W (cf. Tulasne 1855). Notes by Endlicher (l.c.)

and Tulasne (l.c.) indicate that the year of collection was 1818. The locality, given vaguely by Endlicher, is stated as coastal and mountain forests by Tulasne when quoting Cunningham's annotations in herb.W. From the date, such a provenance can only mean the Illawarra district which Cunningham visited during the latter months of 1818 and also during July and August 1824 (Heward 1841). Endlicher's description of the genus Doryphora (1837) and plate of the species D. sassafras, which both set forth characters of flowers and young fruit, indicate that Doryphora sassafras was based on mixed collections.

The collections in herb. W having been lost in World War II, the only sheets traced in other herbaria with specimens consistent in form and annotations with the protologue are two in herb. K (one without any data other than the annotation Atherosperma sassafras C), one in herb. BM, one in herb. SING, and possibly one in herb. A labelled with the unlikely localities Moreton Bay and Blue Mountains. They comprise two different collections, one in flower bud and opening flower, the other in young fruit. When the dates and other data on the various sheets are collated, it becomes apparent that the collection in young flower, numbered 6, was gathered by Cunningham in the Illawarra district in August 1824, whereas the collection in young fruit, numbered 179, was gathered by him in the vicinity of Five Islands (Illawarra district) in November 1818 (see specimen in herb. BM). These dates are consistent with the flowering and fruiting stages of the specimens.

Notwithstanding that the date of the collection in fruit is mentioned specifically by Endlicher (Gen.Pl.1837), the collection in flower is selected as the type because Endlicher's original description of Doryphora and illustration of D. sassafras are based primarily upon it. The specimen of this collection in herb. K, which is mixed with Cunningham's collection in young fruit (n.179) on one sheet bearing a single label carrying full details for both collections, is selected as the lectotype.

The date of 1818 on the specimens in young flower in herb. SING would appear to be incorrect.

Chemistry

The essential oils in the bark, leaves, and fruit have been examined by Petrie (1912), and those in the leaves by Penfold (1921). Petrie isolated oil possessing the characteristic sassafras odour of the tree in proportions of 1.35% from the bark, 4.3% from the leaves, and 4% from the fruit. He suggested that a small fraction of the oil which gave the characteristic odour was safrol. Other estimated constituents of the bark were fixed oil 0.63%, aromatic resins 1.3%, tannins 1.3%, sugars 1.7%, and calcium oxalate 1.37%.

Penfold (l.c.), in a more thorough analysis, found the constituents safrol, camphor, d-pinene, eugenol, eugenol methyl ether, sesquiterpenes, and alcoholic bodies in leaf oil of the species. The oil, obtained by steam distillation, is deep yellow to dark brown in colour. Penfold's work indicated that the quantity of oil present in the leaves varies through the year: leaves harvested from Monga (Mt. Budawang area) yielded 1.05% oil in October, 0.85% in November, and only 0.1% in May. Moreover, it appears that the composition of the oil, constant in the leaves of individual trees or local populations, varies with the locality. The oil from Monga, altitude ca 600-750 m, comprised 60-65% safrol, 10-15% camphor, 10% d-pinene, 10% sesquiterpenes, and 1% eugenol. Oil from Currowan, in the same district but at an altitude of about 150 m, comprised 30% safrol, 30% camphor, 10% d-pinene, 3½% eugenol, and eugenol methyl ether, sesquiterpenes, and alcoholic bodies ca 26%.

An alkaloid doryphorine, given the provisional formula ($C_{18}H_{21}O_4N$), was isolated from the bark (estimated to contain 0.63% total alkaloids), leaves (0.3% total alkaloids), and fruit (0.1% total alkaloids)by Petrie (1912). Bick (pers.comm.) points out that no pure alkaloids were isolated and that this early work is unreliable.

Recently, the alkaloids of Doryphora sassafras have been re-examined by Gharbo et al. (1965). From the leaves they isolated the aporphine alkaloids liriodenine, the properties of which are described under Atherosperma moschatum, and the ubiquitous choline, $C_5H_{15}NO_2$. Other bisbenzylisoquinoline alkaloids found in smaller quantity were: A (m.p. 247°C); B, $C_{28}H_{15}O_4N$ (m.p.175°C); BHI (m.p.192°C); C (m.p.251°); doryafranine, having the formula $C_{19}H_{21}O_3N$ and a melting point of 92°-94°C; and doryanine, having the formula $C_{11}H_9O_3N$ and a melting point of 162°C.

Uses

Infusions from the bark and sometimes leaves have been used by aborigines and bushmen as medicinal tonics or an aromatic tea or carminative (Baillon 1886, Woolls 1887, Maiden 1889, Perkins and Gilg 1901,

Hutchinson 1964,

Maiden 1903, 1917, Petrie 1912, Perkins 1925, Garratt 1934, Webb 1948, Metcalfe and Chalk 1950, Anderson 1956. The alkaloids have potential use as drugs: Petrie's (l.c.) work indicates that their physiological action resembles that of the alkaloids in other members of the family. Oil from leaves, containing safrol, camphor, d-pinene, sesquiterpenes, and eugenol, has been marketed commercially (Penfold 1921).

The timber, dirty pale yellowish, without distinctive figure, and fragrant when freshly cut, is light and soft with an average lateral hardness of 443 kg (Welch 1929). It is easily worked and non-fissile, holds screws and nails well, is easily painted but difficult to glue, takes a long time to season, and is said to be resistant to white ants and borers. Being open grained, not particularly durable, and easily warped on exposure, it is useful only for general indoor purposes such as lining and flooring, cheap furniture, casing, tallow cask staves, and turned articles such as tool and broom handles, brush stocks, toys, and clothes pegs (Woolls l.c., Maiden 1889, 1903, Petrie l.c., Baker 1919, Swain 1928 [n.v.], Welch l.c., Garratt l.c., Turrill 1948, Metcalfe and Chalk l.c., Francis 1951, and Anderson l.c.). It was being milled in quantity at the Veneer and Plywood timber yard, Wauchope, New South Wales, during 1966 for architraves and mouldings in indoor construction and cabinet work, and for brush stocks.

The tree has also been cultivated as an ornamental (Turrill l.c., Anderson l.c.).

XIV. DAPHNANDRA Benth.

Daphnandra Benth., Fl.Austral. 5(1870)285; Baill., Adansonia 10 (1873)351,352; Benth.in B.& H., Gen.Pl. 3(1880)138,139,146; F.Muell., Syst.Cens.Austral.Pl. 1(1882)3; F.M.Bail., Synops. Queensl.Fl. (1883)422; Moore, Cens.Fl.N.S.Wales (1884)58; F.M.Bail., Queensl.Woods (1886)64 p.p., (1888)95 p.p.; Hobein, Bot.Jb.10(1888)53,55,72,73; F.Muell., Sec.Syst.Cens.Austral.Pl. 1(1889)5 p.p.; Pax, Pflzfm. 3,2(1889)95,96,97,102,103 p.p.?; F.M.Bail., Cat.Pl.Queensl. (1890)39 p.p.; Bancroft, Proc.Linn. Soc.N.S.Wales 4(1890)1061; Moore & Betche, Handb.Fl.N.S.Wales (1893)14,15; Solereder, Syst.Anat.Dicot. (1899) [transl.Boodle, Fritsch, & Scott, 2(1908)699 et seq.]; F.M.Bail., Queensl.Fl. 4(1901)1288,1295 p.p.; Perk.& Gilg, Pflzr. 4(1901)3,4,6,9,10,14, 75; Deane, Rec.Geol.Surv.Vict. 1(1902)17,27; Perk., Pflzr. 49(1911)44 p.p.; Petrie, Proc.Linn.Soc.N.S.Wales 37(1912)151,153; F.M.Bail., Compr.Cat.Queensl.Pl. (1913)430 p.p.; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80; Maiden, For.Fl.N.S.Wales 7(1921)368 et seq. p.p.; Domin, Bibl.Bot. 89,2(1925)674 p.p.; Perk., Gattung.Monim. (1925)6,8,11,15,47 p.p.; Francis, Austral.Rain-For.Trees (1929)94; Welch, J.Proc.Roy.Soc.N.S.Wales 62(1929)362 et seq. p.p.; Lemée, Dict.gen.phan. 2(1930)501 p.p.?; Willis, Dict.Fl.Pl.Ferns ed.6,(1931)206 p.p.?; Garratt, Trop.Woods 39(1934)21 et seq.; Berry, Bot.Gaz. 96(1935) f.1, n.17 p.p.; Berry, Geol.Soc.Amer.spec.pap. 12(1938) f.2, n.17 p.p.; A.C.Smith, J.Arn.Arbor. 22(1941)250; Bick & Todd, J.Chem.Soc.n.438(1948)2170; Pichon, Bull.Mus.Nat.Hist.Nat.Par.II,20(1948)383; Henry, Pl. Alkaloids ed.4,(1949)319,326; Metcalfe & Chalk, Anat.Dicot. 2(1950)1139 et seq.; Money, Bailey, & Swamy, J.Arn.Arbor. 31(1950) 374 et seq.; Francis, Austral.Rain-For.Trees ed.2,(1951)109,383; Croizat, Man.Phytogeogr. (1952)281, f.5, n.17 p.p.?; Bick, Doebel, Taylor & Todd, J.Chem.Soc. n.139(1953)692; Stern, Amer.J.Bot. 42(1955)874,881; Anderson, Trees N.S.Wales ed.3,(1956)369; Bick, Clezy, & Crow, Austral.J.Chem. 9(1956)111; L.S.Smith, Proc.Roy. Soc.Queensl. 69(1958)49; Bick, Clezy, & Vernengo, J.Chem.Soc. n.950(1960)4928 p.p.; Müller-Stoll & Mädel, Trans.Geol.Soc.S. Africa 65(1962) f.6; Burbidge, Dict.Austral.Pl.Gen. (1963)91; Evans in Beadle, Evans, & Carolin, Handb.Vasc.Pl.Sydney & Blue Mts. (1963)130; Buchheim in Melchior, Syllab.Pflzfm. ed.12,2(1964) 122; Good, Geogr.Fl.Pl. ed.3,(1964)101 p.p.; Hutchinson, Gen.Fl. Pl.1(1964)120 p.p.; Airy Shaw, Willis Dict.Fl.Pl.Ferns ed.7,(1966) 330 p.p.; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342.

TYPE SPECIES: *Daphnandra micrantha* (Tul.)Benth., only species.

Atherosperma auctt. [non Labill.]; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)294,418 p.p.; C.Muell.in Walp., Ann.Bot. 4(1857)83,117 p.p.; F.Muell., Pl.Colon.Vict. 1(1860)24 p.p.; A.DC., Prod. 16,2(1868) 675 p.p.; Baill., Hist.Pl. 1(1869)319,343 p.p.; Perk.& Gilg, Pflzr. 4(1901)77 p.p.

Figures 1H, 21, 22, 33-35, 36A, 37B, 46B, C, D.

Tall shrubs to medium-sized bisexual trees with ± short, spreading, ± corymbiform crowns; bark, wood, stems, and leaves ± odourless; secondary xylem vessels often solitary or up to 20 per cent in radial multiples of 2-5, ca (60-)70-90(-100) per sq.mm, (0.9-)1.1-1.4(-1.6) mm long × (30-)55-70(-110) μ inner tangential diameter, the perforation plates and vessel-ray pitting exclusively scalariform; fibres relatively thin-walled, (1.4-)2.0-2.2(-2.4) mm long × (15-)25-35(-50) μ outer tangential diameter, frequently libriform wood fibres with relatively frequent septae and predominantly simple pits, occasionally fibre tracheids with rather abundant bordered pits with reduced borders; multiseriate rays (0.2-)0.55-1.1(-1.8) mm high or more by aggregation × (2-)3-5(-6) cells wide, acicular crystals sparingly present in procumbent cells, oil cells absent or rarely present* in the margins; primary cortex not sclerosed, without large intercellular spaces**; ultimate branchlet stems rounded compressed, rarely tetragonous, ± glabrous to densely hispidulous-strigillose, the nodes on leader stems very broadly compressed, appearing fasciated; petioles shallowly to deeply sulcate, rarely planate; leaf

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* Oil cells were not observed in the series of secondary xylem sections examined in the present study. Garratt (1934, pl.31), however, records them as sporadic in occurrence in multiseriate rays of <u>D. apatela</u> (cited as <u>D. micrantha</u>).

** Data from Hobein (1888), Solereder (1899), Metcalfe and Chalk (1950) for <u>D. apatela</u> (cited as <u>D. micrantha</u>).

blades ± notophyllous to small mesophyllous, with margins variably crenate-serrate to undulate or repand, midribs planate to prominulous-lineate or sulcate on upper face; hypodermis absent from upper face*, oil cells in epidermis and mesophyll**.

Inflorescence buds hardly compressed, stipitate before expansion; mature inflorescences elaborately thyrsiform, with (3-)7-42(- ± 50) flowers; accessory axillary flowers usually present; bracts small, ± isomorphic, $(\frac{1}{2}-)\frac{3}{4}-4(-6)$ mm long × $\frac{1}{4}-1$ mm broad, usually caducous in young bud or before anthesis; bracteoles present, ± herbaceous, ± contiguous with tepals on hypanthium as the outer perianth whorls, persistent with tepals.

Flowers bisexual; perianth rotatiform, differentiated into 2(-3) outer whorls of (4-)5(-6) sepaloid bracteoles and 1-2 inner whorls of (4-)6-8(-10) ± ovate-elliptic, obtuse, palminerved petaloid tepals, $(2-)2\frac{1}{2}-4\frac{1}{4}(-5)$ mm long × $(\frac{1}{2}-)1-2(-2\frac{1}{2})$ mm broad, in hemicyclic to ± spiral arrangement; androecium 2-4-seriate, the outer whorl comprising (3-)4-7(-9) stamens, $(\frac{2}{3}-)1-1\frac{1}{3}(-1\frac{2}{3})$ mm long × $(\frac{1}{3}-)\frac{2}{3}-1(-1\frac{1}{4})$ mm broad × $\frac{1}{4}-\frac{1}{2}$ mm thick, with depressed elliptic peltate glands appressed to abaxial face of filament, and broadly truncate extrorsely-dehiscing anthers, the inner whorls (spirals) of ± isomorphic oblong-cylindrical to ± spathulate-batilliform staminodes, $\frac{1}{2}-1(-1\frac{1}{4})$ mm long × $\frac{1}{4}-\frac{1}{2}(-\frac{3}{4})$ mm broad; pollen grains slightly ellipsoidal to near spheroidal, suboblate, Lg (18-)21-28(-31) μ × long. Lt (24-)26-32(-34) μ , the colpi transversales of irregular length, 10-24(-25) μ long, often only one well developed, the interstitial

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*Hobein (1888), Solereder (1899), Money et al. (1950).

**Hobein (1888).

equatorial depressions rather extensive but often wholly or partly obscure, the grain walls ($1\frac{1}{2}$)2-$2\frac{1}{2}$ μ thick, the surface sculpture with lumina irregular to rather circular in outline, $\frac{1}{2}$-$2\frac{1}{2}$ μ long; gynoecium of (3-)4-12(-18) carpels, the styles terminal, hispid, the stigmatic column hemispherical, shortly conical, or apparently absent*; ovule ellipsoid, variably rostrate at chalazal end, anatropous-hemitropous on sub-basal placenta.

Fruiting hypanthium slenderly cylindrical-urceolate to quite urceolate, or ampulliform-broadly obpyriform, or globose, (4-)5-24(-30) mm long × (1-)2-7(-10) mm thick, levigate with outer perianth bracteoles often attached on neck, glabrous or glabrescent, dehiscing by a single fissure; perianth and androecium persistent until after hypanthium dehiscence; nutlets attached superficially (in shallow pits) to hypanthium wall, uniformly silky hirsute, the bodies ± ellipsoid, the styles terminal, subulate.

Additional Characters Common to Infrageneric Taxa

Average tree height range 4-25 m; bole hardly or not all buttressed; crown branches horizontal or obliquely horizontal, attached to trunk in swollen "socket-like" joints; wood with growth rings obscure, and parenchyma very sparse and diffuse, occasionally grouped close to vessel members, but not vasicentric in disposition; branchlet stems with ultimate 1-3 internodes ± tetragonous on leader, less often lateral stems, smooth and variably finely striate, the pubescence, where present, sordid white to stramineous or brownish and most persistent about nodes, with simple or

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*In <u>Daphnandra johnsonii</u> and <u>D. melasmena</u>.

often tufted hairs, the nodes of branchlet stems broadened, sometimes swollen, often finely pusticulate at area of divergence of lateral stems, very broadly compressed to $(\frac{2}{3}-)\frac{3}{4}-3(-4)$ cm broad on leader stems; vegetative buds narrowly obcordiform-conical, the enveloping pair of bract-like leaves densely off-white, greyish green, or stramineous strigose, with conspicuous divergent glabrous mucronate apices, expanding when buds ca 5 mm long; buds on ultimate leader stem nodes arranged in a series of (5-)7 or 11 along the node apex of terminal nodes,and in series of 3 or 5, rarely 4, in the leaf axils at subterminal nodes, conical to depressed conical, quite sessile, only the central buds on the terminal and subterminal nodes developing; petiole hairs, where present, sordid white to stramineous or brownish; leaf blades with margins slightly but conspicuously recurved to sometimes almost planate, midribs conspicuously prominent on lower face, and nerves anastomosing towards blade margins in a fine, ± open, rarely close vein reticulum extending uniformly from blade margin to midrib on lower face, generally glabrous on upper face.

Inflorescence buds narrowly obcordiform, initially sessile and complanate with stem when 1-2 mm long, the enveloping pair of bracts linear-lanceate navicular, white to sordid grey-green or stramineous strigillose, eventually $(1\frac{1}{2}-)2-3$ mm long, with diverging apices; buds subsequently elongating through the development of a compressed stipe (= base internode of primary peduncle of mature inflorescence) up to 5-10 mm long below the bracts which later diverge gradually and recurve at the apices to allow expansion of the ultimate inflorescence axes and flower buds; mature inflorescences variably pendulous, occasionally two (or three) per leaf axil, the adaxial ones much shorter and fewer flowered than the outer; primary peduncles broadly compressed at base internode, more slender, often tetragonous at distal internodes, smoothly striate, drying dark brown to blackish, rarely paler, the subterminal 1-2 nodes usually bearing solitary opposite flowers and the basal nodes 1-3(-4)-noded secondary peduncles with solitary opposite flowers or opposite simple dichasia; solitary flowers at subterminal nodes on primary peduncles usually opening before any in dichasial groups, central flowers in dichasial groups usually opening before flanking flowers, and accessory axillary flowers opening last; secondary peduncles similar in form to primary peduncle; peduncular bracts herbaceous, linear- to lanceate-deltate, navicular, sometimes ovate-deltate navicular, mucronate acute, longer and more slender at basal than at distal nodes, usually cadücous before inflorescence anthesis, occasionally indiscriminately persistent through flowering; pedicels slender, usually longest in solitary flowers at distal primary peduncle nodes or terminally central flowers, occasionally bracte(ol)ate in terminally central flowers, the bract(eole)s early caducous; bracteoles similar in form to secondary peduncle bracts, rarely subtending hypanthium in single pairs, very early caducous; mature flower buds obovoid-turbinate or almost napiform-globose to depressed turbinate, the outermost pair of perianth bracteoles short, the superjacent bracteoles valvate to imbricate, enclosing tepals.

Open flowers small; hypanthium broadly to deeply obconical-cyathiform; perianth of unequal whorls; perianth bracteoles bract-like to sepaloid, in ± decussate arrangement, the outer bracteoles entirely herbaceous with narrowly obtuse, rarely acute mucronulate apices, ± entire margins, abaxially prominent midnerves, without conspicuous nerving, glabrous adaxially, the inner bracteoles successively more petaloid than outer, with broadly obtuse or rounded, rarely apiculate apices, ± broadly petaloid margins, herbaceous median areas with 1, 3, or 5 obscure to conspicuous nerves, glabrous adaxially; tepals uniformly petaloid, narrowly obtuse at the apex, generally glabrous, infrequently sparsely strigillose towards the base, imbricate, in obscurely tetramerous or ± spiral arrangement, the inner tepals usually longer and narrower than the outer; androecium with inner (staminode) whorls sometimes appearing disposed in a close spiral; stamens squat, erect or slightly incurving towards the apex, laterally contiguous, sometimes partly aborted, the filaments dorsiventrally compressed, glabrous abaxially and variously strigillose adaxially, the staminal glands finely pitted, subsessile, paired on the abaxial face of the filament immediately beneath the anther, the anthers glabrous, with short elliptic valves which recurve up over the anther apex after dehiscing; staminodes erect, ± dorsiventrally compressed, with flat scarious rounded to ± acute deltate glabrous apices drying dark brown or blackish, the inner staminodes slightly shorter and narrower than the outer.

Ripe infructescences with several to most hypanthia maturing per infructescence, the peduncles and pedicels drying dark grey-brown to blackish, very rarely with one or two bracts persisting in indiscriminate position; fruiting hypanthium relatively levigate, with outer perianth bracteoles attached along neck with variable frequency, drying blackish, infrequently brownish, in dehiscence with 1 to several incipient fissures developing from the rim, of which only 1 extends towards the base so that the neck flattens out and recurves to allow dissemination of nutlets; nutlets attached to lower sides and base of hypanthium chamber, with straight*, sordid brownish, rarely paler hairs becoming gradually shorter and rather paler to hispidulous towards the style apices.

The name *Daphnandra* is derived from δάφνη for the sweet bay or laurel (*Laurus nobilis*) and ἀνδρος for a man, probably in allusion to the resemblance of the anthers to those of *Laurus* (F.M.Bailey 1901, Perkins and Gilg 1901, Maiden 1921, and Francis 1929, 1951).

Species, Geographic Distribution, and Ecology

The genus *Daphnandra* comprises six species in coastal eastern Australia, one in north-east Queensland between 15°30′ and 18°S, and five in south-east Queensland and eastern New South Wales between 26°20′ and 34°40′S (maps 2,10). The records of this genus from New Guinea (see chapter X) are all apparently attributable to *Dryadodaphne*.

The species occur on the margins of and within both secondary and primary subtropical rainforest between sea-level and altitudes of ca 1150 m. Unlike the species of all other genera in the family, they are often

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* Except in D. johnsonii.

important and characteristic elements of rainforest secondary growth and seres, and grow in more marginal habitats, such as semi-sclerophyllous vegetation along damp creeks and gullies.

Germination of seeds occurs in the leaf litter and soil of the forest floor (personal observations,and young plants and saplings of *D. apatela*: Schodde 3475, *D. melasmena*: Schodde 3524, *D. micrantha*: Schodde 5141, *D. repandula*: Schodde 3278, 3344, L.S.Smith: BRI 052024, and *D. tenuipes*: Schodde 3568, Webb & Tracey: BRI 033056, 037449). Regeneration by suckering has so far been recorded in *D. apatela* (Maiden 1921, quoting A.H.Lawrence), *D. johnsonii* (Schodde 5167, 5183), and *D. repandula* (cf. C.T.White 1918, Hurst 1942).

Flowering appears to be strictly seasonal but varies from species to species. *Daphnandra repandula* and *D. tenuipes* flower usually in austral autumn and winter months (March-August) and fruit in summer months (December-March),whereas *D. apatela*, *D. johnsonii*, *D. melasmena*, and *D. micrantha*, all of which are southern species, flower in spring months (August-November) and set fruit in late summer or autumn (January-May, rarely June),under prevailing seasonal conditions of rather uniform rainfall but warmer summer and colder winter temperatures. The two species flowering in autumn and winter months are the only ones occurring entirely within the zone of maximum rain in summer months on the east coast of Australia (cf. Burbidge 1960, f.1). It is uncertain whether their flowering period is influenced by this, or by slightly more uniform temperatures throughout the year, or slightly less variable day length.

Notes on Generic Characters

The genus Daphnandra is well-defined and summarily distinct from all other genera of the family in its usually small tree form, its secondary xylem with a greater frequency of vessels in radial multiples, relatively larger but less heterocellular multiseriate rays, and greater frequency of septate fibres, its extraordinarily flattened nodes on leader branchlets which bear multiples of shoot buds, its elaborate thyrsiform inflorescences with accessory axillary flowers, its rather dimorphic perianth comprising relatively irregular numbers of outer sepaloid bracteoles and inner petaloid tepals, its relatively irregular number of squat stamens with broadly truncate apices, extrorsely-dehiscing valves, and depressed elliptic peltate glands on the abaxial face of the filaments, its elongate fruiting hypanthia with persistent perianth and androecia, and which dehisce usually by a single fissure only, and its general ecological preference for disturbed and secondary growth rainforest. These critical characters have been assessed as being among the most specialised in the family (chapters IV, XVI, table IV). Some of them and others are discussed further below.

The rather distinctive features of the secondary xylem, summarised above and treated in more detail in chapter IV.2, have not been recognised previously. They are illustrated in figures 33-35, and 37B.

The flattened terminal nodes of leader stems, often so broadly compressed as to appear fasciated, are found in all species of the genus, and provide a useful diagnostic character for them in the field (see also

Maiden 1921). Shoot buds are arranged in a series of (5-)7 or 11 along the apex of the node. Under normal conditions, the central bud develops first into the leader branchlet shoot, and the central buds of the resulting (2-)3 or 5 axillary buds develop later into lateral branchlet shoots; the buds remaining do not expand further and are lost. Where the central bud or leader stem has been broken, the lateral buds apparently develop in its place, as for example in a specimen of D. tenuipes (Schodde 3568 : CANB) in which four shoots sprout from one node.

The form of the leader stem terminal node, with its number of shoot buds, is unique in the family. It may be that it evolved* concomitantly with the ecological preferences in the genus for disturbed habitat because such ecological preferences, likewise, are not found in other genera of the family. It can be expected that Daphnandra saplings would be subject to more frequent obstacles in the tangled vegetation and greater competition from adjacent plants during their growth than those of the other genera on the more open floor of primary forest. It does not seem unreasonable to suggest that, in response to such pressure, the broad leader stem nodes were formed to assist and strengthen the growth of the sapling through relatively dense vegetation,and that the multiple buds,

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* Because it is concluded in chapter XVI that Daphnandra is the most advanced genus in the family, those characters peculiar to it may be regarded, by implication, as derived.

able to expand and shoot quickly, were developed to make good in as short a time possible any damage or impairment to the growth of the rather brittle terminal shoot stems.

Though the inflorescence in its early ontogeny follows the pattern of development in *Dryadodaphne*, *Doryphora*, and *Nemuaron*, it ultimately expands in much more elaborate profusion. Its structure and the homologies of its parts are discussed in chapter IV.6 in detail.

The perianth is the most complex in the family. It comprises, on even superficial examination, two distinct groups of members. Those of the outer group are sepaloid, and on account of their small size, herbaceous texture, shape, pubescence, and essentially decussate arrangement (at least in the two outer pairs) are interpreted as bracteoles (chapter IV.6). They may represent the homologues of the pairs of perianth bracteoles in *Laurelia* and *Nemuaron*, and those subtending the floral hypanthium in *Dryadodaphne*. The members of the inner group are petaloid, and on account of their larger size, petaloid texture, brighter colours (reddish in one species), rather conspicuous venation, hemicyclic or seemingly spiral arrangement, and irregular number of usually 8 or less, are considered to be homologous with the tepals of other genera of the family. The difference between the bracteoles and tepals is rarely clear-cut because the inner bracteoles are somewhat transitional in form between the outer bracteoles and the tepals. Patterns of vascularisation that may clarify the origin of these parts remain to be studied. It can be suggested, nevertheless, that the development of a dimorphic perianth in *Daphnandra* parallels the evolution of calyx and corolla in higher angiosperms and perhaps attempts similar functions.

It appears that the size and possibly shape of the microsporoderm lumina may vary according to the species. In the few pollen samples studied from each species, the reticulum is coarsest, and the lumina largest ($1\frac{1}{2}$-$2\frac{1}{2}$ μ long) and most variable in size in *D. johnsonii* and *D. tenuipes*; the lumina are smallest ($\frac{1}{2}$-1(-$1\frac{1}{2}$) μ long) in *D. micrantha*, and most regular in size in *D. repandula* (see f.46 B-D). The similarity of microsporoderm sculpturing in the latter two species is consistent with their close relationship indicated by other morphological characters. Nevertheless, because of the small range of pollen studied in the genus, comprehensive descriptions of the form of the luminae for each species have not been prepared; conclusions as to whether the observed variations are consistent and characteristic for each species are premature.

One of the main characters that has been used to distinguish *Daphnandra* from other genera of the family is the supposedly pendulous orthotropous ovule (Bentham 1870, Baillon 1873, Bentham 1880, Moore and Betche 1893, Pax 1889, F.M.Bailey 1901, Perkins and Gilg 1901, Maiden 1921, Perkins 1925, Lemée 1930, A.C.Smith 1941, Hutchinson 1964, and Airy Shaw 1966). Bentham (l.c.) expressly mentions that, in many flowers of various specimens examined, the ovule was always pendulous. Pichon (1948) went further to suggest that, despite its uniquely orthotropous orientation, the position of the ovule was not anomalous in the family because the funicle had merely become adnate to the wall of the locule, not to the ovule itself as in other genera. Money, Bailey, and Swamy (1950) also mention concrescence of the funicle with the wall of the locule in *Daphnandra*, and L.S.Smith (1958) states that the ovule is "attached above the middle of the cell".

An examination of the ovules from an extensive range of all species collected during the present study revealed, on the contrary, that placentation is always sub-basal with little adnation of the funicle to the wall of the locule. Ovule orientation as a result is anatropous-hemitropous. The ovules are also characteristically rostrate at the chalazal end, and it is not unlikely that the beaks formed have misled the earlier investigators to interpret them as funicles and hence postulate a pendulous orthotropous position for the ovule.

Affinities

Since its description in 1870, the genus *Daphnandra* has been accepted by all revisers. Earlier Tulasne (1855a, 1855), C.Mueller (1857), A. de Candolle (1868), and Baillon (1869), having only meagre flowering material, had referred the only known species, *D. micrantha*, to *Atherosperma*. Certain floral characters of *Daphnandra*, particularly the truncate anthers with extrorse dehiscence, resemble those of *Atherosperma* rather than *Doryphora* or *Laurelia*, the only genera known in the family at that time. Even F.Mueller (1877) and

Perkins and Gilg (1901) were later misled by floral structure* to place a second species, *Daphnandra repandula*, under *Atherosperma*.

More recently, the New Guinea species of *Dryadodaphne* have been confused with *Daphnandra* (Perkins 1915, 1925, Gilg and Diels 1925, Lemée 1951, van Royen 1959, Good 1964, and Airy Shaw 1966), as a result of Perkins (l.c.) and Gilg and Diels (l.c.) referring fruiting collections of *Dryadodaphne* to it. *Daphnandra*, as it happens, resembles *Dryadodaphne* as much in fruit as it does *Atherosperma* in flower.

Daphnandra is distinct from *Atherosperma* in the characters of its secondary xylem and form of its perianth, as well as through all the features of the tribe Laurelieae except anther structure. The dissimilarity in the form and disposition of the staminal glands between the two genera suggests, furthermore, that the similarity in anther structure is the result of parallel evolution. *Daphnandra* also differs from *Dryadodaphne* in the structure of its perianth, stamens, and rather thinly lignified fruiting hypanthium with persistent perianth and androecium.

Daphnandra is not closely related to any genus of the Laurelieae

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* Although the collections Mueller cited with the original description of *Atherosperma repandulum* included fruiting specimens (Bailey: Trinity Bay), it is evident from the description and notes on herbarium sheets that his conception of the species was at the time based on flowering material only, that collected by Dallachy at Rockingham Bay.

except, in some respects, *Dryadodaphne*. Affinity between them is indicated by those characters enumerated in chapter X, and their thyrsiform inflorescences with similar ontogeny and small early caducous bracts. These characters are in general distinct from those linking *Dryadodaphne* with *Nemuaron* and *Laurelia*, and imply, therefore, that *Daphnandra* is related to the latter only through *Dryadodaphne*.

Chemistry

The species of *Daphnandra* have become well known for their bitter alkaloids. In the four so far examined (*D. apatela*, *D. melasmena*, *D. repandula*, and *D. tenuipes*), all alkaloids isolated have been of the bisbenzylisoquinoline type (Pyman 1914, Bick and Whalley 1946, 1947, Bick and Todd 1950, Bick, Taylor, and Todd 1953, Bick, Harley-Mason, and Vernengo 1963) whereas none of the aporphine alkaloids which occur in *Atherosperma*, *Doryphora* (*D. sassafras*), *Laurelia* (*L. novae-zelandiae*), and *Nemuaron* have been found. All, moreover, have two diphenyl ether linkages except micranthine in *Daphnandra apatela* which has three. The alkaloids isolated number about twelve (Bick, pers.comm.), and only two of them have been found in other genera of the family. These are aromoline and daphnoline which occur also in *Doryphora aromatica* (Bick and Whalley 1948), but in such proportions as to negate close taxonomic relationship between this species and the two species of *Daphnandra* in which they occur. The formulae, properties, and occurrence of the alkaloids are described under the species from which they have been recorded.

The pioneering work of Bick and others originally indicated that the alkaloids and their proportions of occurrence may be different for each of the species in the genus. To test this, small samples of leaf and bark material of all species were sent to Bick for analysis (chapter II). The samples were numbered in code without indication of their taxonomic status and included material of three collections of uncertain identity (see following section); several species were represented by two or three samples. Though the samples examined were too meagre in quantity to permit a thorough investigation of the alkaloids of each species, the resulting analysis confirmed in general that the alkaloids were different between but similar or identical within the species recognised here (Bick, pers.comm.). Moreover, the alkaloids in the three collections of uncertain identity provided no further indication of taxonomic position or affinity.

Interspecific Relationships

Daphnandra, with six species, is the largest genus in the family. Its relative diversification may be related to its unique exploitation of disturbed and marginal rainforest habitat. Its centre of diversity is in north-east New South Wales where four of the six species are found, several of them narrow endemics. All of its species are very closely related, differing from each other in the combination of a number of slightly differing morphological characters rather than by any absolute individual differences such as distinguish the species of *Doryphora* or *Laurelia*. This suggests that speciation has been both relatively recent and rapid.

The slightly differing characters, in summary, are (1) the size of the mature tree, (2) the texture and thickness of the outer bark and intensity of yellow colour in the fresh inner bark, (3) the density or near absence of pubescence on ultimate branchlets, (4) the shape, size, texture, marginal indentations, colour when dry, and venation of the leaves, including whether the midrib is impressed or planate-prominulous on the upper face of the blade, (5) the degree of elaboration and density of branching of the inflorescence, (6) the mean number, size, and life colour of the perianth and androecium parts, (7) the mean number of carpels, (8) the degree of exsertion of the stigmatic column, (9) the size, shape, and degree of lignification of the fruiting hypanthium, and the density of pubescence on its inner walls, and (10) the dimensions and hair forms of the ripe nutlets. The form of seedlings and micro-sporoderm sculpturing, which appear to vary from species to species, are still insufficiently documented.

It may be argued that it is unrealistic to separate species on such slender morphological differences as has been done here. Nevertheless, the geographic integrity of the taxa distinguished, their rather specific ecological preferences, their differing flowering seasons, their generally distinct alkaloids, and their sympatry (except in the case of *D. johnsonii* and *D. repandula*), compel their recognition as species.

Because of the slight reticulated differences between the species, an appraisal of their interrelationships and relative morphological specialisation is difficult to make. It can be suggested, however, that *D. repandula* is the least specialised member of the genus on the following grounds. First, its perianth and androecium parts are altogether more variable in number with a higher mean ((11-)13-14(-15) perianth parts, (4-)6-7(-9) stamens, and (5-)6-9(-12) staminodes). Second, its androecium with frequent partly aborted anthers, and occasional staminodes with vestigial staminal glands generally intermediate in form between stamens and staminodes, is not completely differentiated into fertile and sterile parts as in other species. It is the only species of the genus occurring in north-east Queensland, within the tropics.

Daphnandra micrantha from lower north-east New South Wales appears to be more closely allied to *D. repandula* than any other species; the two replace each other geographically. Features common to them are bright yellow **inner** bark, large leaves with midribs impressed on the upper face of the blade, very long lax inflorescences of relatively large green-pigmented flowers, and slender fruiting hypanthia with thin or somewhat papyraceous walls. *D. micrantha* has also outer staminodes with similar vestiges of staminal glands. Its incompletely known alkaloids, however, neither confirm nor contradict this relationship.

None of the remaining species bear a similarly close relationship to each other. The link between *D. apatela* and *D. melasmena* on the one hand and between *D. melasmena* and *D. tenuipes* on the other through apparent intermediates is of a different nature, possibly resulting from occasional introgression between D. melasmena and the two other species, as discussed below.

If D. repandula is the least specialised member of Daphnandra, D. apatela may be regarded as the most advanced. Not only does it have the fewest and most constant number of perianth and androecium parts and carpels in the genus ((8-)10-11(-13) perianth parts, (3-)4-5 (-6) stamens, (3-)5-7(-9), usually 6 staminodes, and (3-)4-6(-9) carpels), but both stamens with aborted anthers intermediate in form between stamens and staminodes, and staminodes with vestigial glands, are apparently lacking. Differentiation of the androecium into fertile and sterile parts is here virtually complete. D. apatela is, moreover, the most widespread and successful species of the genus in south-east Queensland and north-east New South Wales; it tolerates a wider and often more marginal range of rainforest habitats than any other species, and has a relatively shorter flowering and fruiting season perhaps developed through adaptation to such conditions. Its major alkaloids, micranthine, daphnoline, and daphnandrine, have not been found in any other species of the genus. Over its geographic range, it is sympatric with D. melasmena, D. micrantha, and D. tenuipes in one area or another.

Superficially, D. johnsonii appears to be closely allied to D. apatela, replacing it in the Illawarra district of New South Wales, as has been implied by Anderson (1956). Both have the distinctive planate-prominulous midrib on the upper face of the leaf blade not found in the other species*, rather short inflorescences of small green-pigmented

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* occasional specimens of D. melasmena excepted.

flowers with relatively few parts, and the same flowering and fruiting season (austral spring and summer). The flowering hypanthia of D. johnsonii are strigillose, like those of D. apatela, though generally more sparsely so. It has, however, sulphureous yellow inner bark, similar to that in D. melasmena, D. micrantha, and D. repandula, and its non-phenolic alkaloids, though poorly known, comprise at least tenuipine-nortenuipine, and indicate a relationship with these species and D. tenuipes rather than with D. apatela. From these data it is concluded that D. johnsonii is hardly more closely related to one species than it is to any other.

Daphnandra tenuipes, an endemic confined to extreme north-east New South Wales, is morphologically the most distinct of all species of Daphnandra. Its reddish pigmented flowers and fruiting hypanthia are unique* in the genus. Other characteristic features are its small size as a mature tree, rather divaricately branched inflorescences and infructescences with flowers and fruiting hypanthia on long pedicels, and large ampulliform, obpyriform, less often rather urceolate-cylindrical fruiting hypanthia. Its perianth and androecium parts are relatively large and variable in number, comprising 12-14(-15) perianth parts, (4-)5 stamens,

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* One indeterminable specimen of Daphnandra, Blake 15898, is also stated to have reddish flowers. Its taxonomic position is discussed at the end of this section.

and (4-)5-10(-13) staminodes, and it has (8-)10-12(-18) carpels; it resembles *D. repandula* in some of these respects. Of its non-phenolic alkaloids, repanduline and tenuipine occur also in *D. repandula*, and tenuipine and nortenuipine in *D. melasmena*. It flowers during early months of the austral winter (April to July) at a time when all other species of the genus occurring in the region (*D. apatela* and *D. melasmena*) have usually finished or are just finishing fruiting.

Under *Daphnandra melasmena* are brought together forms with deeply yellow-coloured inner bark, small leaves with rather impressed midribs on the upper face and which dry olive-black or blackish, small inflorescences and relatively small pale greenish-white flowers like those of *D. apatela* but which are almost completely glabrous, and infructescences and fruiting hypanthia similar in form to those of *D. apatela* but usually borne conspicuously below the leaves on ultimate branchlets. They have the same range of perianth segment and carpel numbers as *D. micrantha*, and a smaller number of staminodes (5-7(-8)), as in *D. apatela*. Though they are perhaps more like *D. apatela* than any other species in overall features, their alkaloids are consistently different, comprising, among others, laevo-rotary tenuipine and nortenuipine.

D. melasmena is the most difficult species in the genus to define, partly because none of its characters are particularly distinctive and partly because of differences between the forms referred to it. The latter are discussed under *D. melasmena*.

Clouding the picture of interspecific relationships further are specimens of *D. apatela* and *D. tenuipes* which have characters approaching *D. melasmena*. The characteristics and provenance of these specimens are stated under *D. apatela* and *D. tenuipes* respectively. They may be the result of introgression between *D. melasmena* and either of these species; all have been collected in areas where *D. melasmena* overlaps geographically with one or the other. The two specimens linking *D. apatela* with *D. melasmena* (Hayes s.n., from Bundagen, and Crawford s.n., from Moona river, Walcha) bear flowers, while of those linking *D. tenuipes* with *D. melasmena*, two (Betche s.n., from Tweed river district (type of *D. tenuipes*), and Jones 467, from Red Scrub, Whian Whian) are in flower, and one (Hayes (1.xii.1952), from Whian Whian) is in well-developed fruit. While it may be thought that the flowering season of *D. tenuipes* would prevent any introgression with either *D. melasmena* or *D. apatela* which flower usually between August and October, it must be pointed out that individual trees of the latter two species occasionally flower out of season, facilitating cross pollination. As an example, the tree of *D. melasmena* from which the type collection came, (Schodde 3523), was commencing to flower in June. A number of flowering collections of *D. apatela*, perhaps significantly from the region of the New South Wales-Queensland border where *D. melasmena* and *D. tenuipes* occur, have also been gathered in the unseasonal months between February and May.

It has been mentioned that the centre of diversity in *Daphnandra* is in north-east New South Wales where, in the region of the Nightcap range and Tweed river alone, there are three species, *D. apatela*, *D. melasmena*, and *D. tenuipes*, which occur with occasional trees of apparently intermediate character. From the adjacent Macpherson range come four collections that cannot be referred with certainty to any of the species distinguished here.

The first of these, taken from a small tree flowering in mid-August on the margin of rainforest at Springbrook at 900 m s.m. (Blake 15898), resembles *D. micrantha*, from which it is separated geographically by over 200 miles, in the prominent nerving of the lower surface and impressed midrib on the upper face of its leaf blades, in its relatively long, lax inflorescences with shortly pedicellate flowers, and its general glabrousness. It differs from that species, on the other hand, in its generally smaller lanceate to ovate leaves (4-7 cm long × 1¾-2¾(-3) cm broad) with prominently crenate margins, and its small red-pigmented flowers (cf. *D. tenuipes*) in which the inner tepals are only 3-3½ mm long.

The second collection, comprising sterile shade shoots from a large tree in rainforest on the upper Coomera river also at 900 m s.m. (Johnson: NSW 67896), may belong to the same taxon. It has similarly nerved, more broadly ovate leaves with an impressed midrib on the upper face, and densely pustuled branchlet stems. Its larger leaves, 9-12 cm long × 4-5 cm broad, with more deeply serrate-crenate margins, are of the form to be expected from a shaded habitat.

The third collection from 800 m s.m. in tall rainforest on the Sarabah range (Schodde 3366) is of 20-40 cm high seedlings. It may also be referable to this taxon. The seedlings, without cotyledons, have chartaceous ovate leaves 4-9½ cm long × 1½-4 cm broad,with slightly impressed midribs, crenulate-serrulate margins, and olive-black colour when dry.

The fourth collection from Mt.Lindsay (Forsyth: NSW 67893) comprises leafy branchlets bearing fruit in September. In hairiness, and overall shape, margins, and venation of the leaves, in which the midrib is impressed on the upper face of the blade, it resembles *D. melasmena* or the hairy forms of *D. tenuipes.* The mature fruiting hypanthia, being urceolate with a well marked neck, small (10-12(-14) mm long × 4-5(-6) mm thick), and quite lignified with walls ½-1 mm thick, are more like those of *D. melasmena.* The time of fruiting, moreover, though more consistent with that of *D. tenuipes,* lies between the main fruiting periods of both these species. This collection may represent one of the supposed hybrids between *D. melasmena* and *D. tenuipes.*

Alkaloid tests on several leaves of all these collections except Schodde 3366 (seedlings) indicated that Blake 15898, and Johnson: NSW 67896 had identical non-phenolic alkaloids whereas those in Forsyth: NSW 67893 were partly different. Tenuipine was the major alkaloid found in all.

The diversity in *Daphnandra* in far north-east New South Wales remains incompletely understood,and further critical study of local populations in the region of the Macpherson range, Tweed river, and Nightcap range is needed.

Key to the Species of Daphnandra

1a. Midribs slightly prominulous or planate on upper face of leaf blades, rarely shallowly impressed near petiole; stigmatic column usually exserted to near tips of stamens; flowers small, with petaloid tepals (2-)$2\frac{1}{2}$-$3\frac{1}{2}$(-4) mm long 2

2a. Fruiting hypanthia ± globose, (4-)5-7(-8) mm long, on pedicels (4-)5-8(-10) mm long; leaf blades with margins deeply and rather distantly coarse crenate-serrate for $\frac{1}{2}$ - $\frac{2}{3}$ of length of blade from its apex, nerves conspicuously prominulous on upper face; margins of petaloid tepals entire; [floral hypanthia sparsely strigillose]........................... 5. D. johnsonii Schodde

2b. Fruiting hypanthia (cylindrical-) urceolate, (5-)8-20 mm long, on pedicels (2-)3-6(-9) mm long; leaf blades with margins shallowly fine crenate-serrate to crenulate-serrulate for $\frac{3}{4}$ - $\frac{7}{8}$ of length of blade from its apex, nerves obscure on upper face; margins of petaloid tepals fimbriolate, rarely almost entire ... 3

3a. Floral hypanthia strigillose-puberulous; inner bark yellowish cream; leaf blades drying ± pale grey-green on upper face, sometimes blackish-, rarely olive-tinted; margins of leaf blades crenate-serrate .... 6. D. apatela Schodde

3b. Floral hypanthia glabrous; inner bark deep sulphureous yellow; leaf blades drying olive-black to dark olive-brown on upper face; margins of leaf blades ± crenulate .... 4. D. melasmena Schodde

1b. Midribs impressed on upper face of leaf blades; stigmatic column usually exserted no farther than tips of staminodes*; flowers larger, with petaloid tepals ($2\frac{3}{4}$-)3-$4\frac{1}{4}$(-5) mm long* 4

4a. Fruiting hypanthia slenderly urceolate-fusiform,(10-)15-24 (-30) × ($1\frac{1}{2}$-)3-4(-5) mm, with ± papyraceous walls $< \frac{1}{2}$ mm thick; leaf blades ($3\frac{1}{2}$-)7-17(-22) cm long, with nerves ± thickly prominent on lower face; inflorescences ($2\frac{1}{2}$-)5-12 (-$18\frac{1}{2}$) cm long, [slenderly elongate]; tepals green-white or pale yellow 5

5a. Leaf blades lanceate to elliptic, ± chartaceous; margins of petaloid tepals coarsely fimbriate; stems usually pubescent; stamens (4-)6-7(-9); petioles (4-)7-12(-15) mm long, straight and diverging from stem; [floral hypanthia usually strigose]. .... 1.*D. repandula* (F.Muell.)F.Muell.

5b. Leaf blades obovate to elliptic, ± coriaceous; margins of petaloid tepals finely or obscurely fimbriolate; stems ± glabrous; stamens (4-)5(-7); petioles (4-)5-8(-10) mm long, often incurved towards stem; [floral hypanthia glabrous].................... 2.*D. micrantha* (Tul.)Benth.

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* Stigmatic column exserted to near tips of stamens, and flowers and petaloid tepals smaller in *D. melasmena*.

4b. Fruiting hypanthia (cylindrical-)urceolate to obpyriform or ampulliform, (5-)7-20 × (1-)3-7(-10) mm, with ligneous walls $(\frac{1}{4}-)\frac{1}{2}-\frac{3}{4}(-1)$ mm thick; leaf blades $(3-)4-9(-12\frac{1}{2})$ cm long, with nerves slenderly prominulous on lower face; inflorescences $(1\frac{1}{2}-)2-6(-9)$ cm long, [slender or divaricate]; tepals green-white or reddish; [floral hypanthia glabrous]. 6

6a. Tepals green-white; pedicels 1-3 mm long in flower; leaf blades closely crenulate to near base; fruiting hypanthia (cylindrical-)urceolate, on pedicels (2-)3-6(-9) mm long; inner bark deep sulphureous yellow..4. *D. melasmena* Schodde

6b. Tepals reddish; pedicels (2-)4-10(-14) mm long in flower; leaf blades finely crenate on upper $\frac{2}{3}$; fruiting hypanthia obpyriform to ampulliform, rarely urceolate, on pedicels (5-)8-12(-16) mm long; inner bark brownish cream to pale yellowish brown .... 3. *D. tenuipes* Perk.

1. *Daphnandra repandula* (F.Muell.)F.Muell.

Daphnandra repandula (F.Muell.)F.Muell., Syst.Cens.Austral.Pl. 1(1882)3; F.M.Bail., Synops.Queensl.Fl. (1883)422; F.M.Bail., Queensl.Woods (1886)65; Bancroft, Australas.J.Pharm. 2(1887)103; Bancroft, J.Proc.Roy.Soc.N.S.Wales 20(1887)69; Bancroft, Proc. Roy.Soc.Queensl. 4(1887)13; Bailey, Queensl.Woods (1888)95; Bancroft, Res.pharm.Queensl.pl. (1888) [n.v.]; Maiden, Useful Nat.Pl.Austral. (1889)167,414; F.Muell., Sec.Syst.Cens.Austral. Pl. 1(1889)5; F.M.Bail., Cat.Pl.Queensl. (1890)39; J.F.Bail., Queensl.Ag.J. 5(1899)401; F.M.Bail., Queensl.Fl. 4(1901)1295, 1296; [Perk.& Gilg, Pflzr. 4(1901)79 pro syn. *Atherospermatis repanduli*]; Perk., Pflzr. 49(1911)44 p.p., f.14; Petrie, Proc. Linn.Soc.N.S.Wales 37(1912)152; F.M.Bail., Compr.Cat.Queensl.Pl. (1913)430; White, Queensl.Ag.J. 9(1918)147; Maiden, For.Fl. N.S.Wales 7(1921)369,370; Domin, Bibl.Bot. 89,2(1925)674; Perk., Gattung.Monim. (1925)50; Welch, J.Proc.Roy.Soc.N S.Wales 62(1929)356,364, f.4; Garratt, Trop.Woods 39(1934)19; Lahey & Jones, Proc.Roy.Soc.Queensl. 50(1939)142 "Daphnandra rapandula"; Hurst, Poison Pl.N.S.Wales (1942)122,123; Bick & Whalley, Univ. Queensl.Pap. I, 28(1946)1, I, 30(1947)2, I, 33(1948)1,2; Bick & Todd, J.Chem.Soc. (1948)2170,2172; Webb, C.S.I.R. Bull. n.232 (1948)109; Henry, Pl. Alkaloids ed.4,(1949)326; Francis, Austral.Rain-For.Trees ed.2,(1951)401; Bick,Doebel, Taylor, & Todd, J.Chem.Soc. (1953)692,694; Bick, Taylor, & Todd, ibid.

(1953)696,697,698; Kulka in Manske, Alkaloids 7(1960)443,451, 460; Ehrendorfer, Krendl, Habeler, & Sauer, Taxon 17(1968)342.

Atherosperma repandulum F.Muell., Fragm. 10(1877)105; Perk. & Gilg, Pflzr. 4(1901)79; [Perk., Pflzr. 49(1911)44 p.p. pro syn. *Daphnandrae repandulae*]; Kulka in Manske, Alkaloids 4(1954)217; Hutchinson, Gen.Fl.Pl. 1(1964)122.

TYPE: Dallachy, Dalrymple Gap, Rockingham Bay —— lectotype in MEL (3181), isolectotypes in BRI, NSW; F.M.Bailey, Trinity Bay —— syntype in MEL.

Daphnandra dielsii Perk.,Pflzr. 49(1911)46; Maiden, For.Fl.N.S. Wales 7(1921)369; Domin, Bibl.Bot. 89,2(1925)674; Bick & Whalley, Univ.Queens.Pap. I, 30(1947)2, I, 33(1948)2; Bick & Todd, J.Chem.Soc. (1948)2170; Webb, C.S.I.R.Bull. n.232(1948)109; Bick, Doebel, Taylor, & Todd, J.Chem.Soc. (1953)692; Bick, Taylor, & Todd, ibid. (1953)696,697,698; Kulka in Manske, Alkaloids 7(1960)443,460,461.

TYPE: L.Diels 8401, Ober-Barron, 500 m s.m. —— B (lost); Schodde 3258, Wongabel Forest Reserve, c. 7 miles south of Atherton —— neotype in CANB (127665), isoneotypes in A, AD, ATHERTON, B, BRI, CANB, G, L, P, SING, WELT.

Figures 21, 33, 46C1.

Diagnosis:

Average tree height 10-20 m; inner bark bright yellow, less often pale; ultimate branchlet stems densely, less often sparsely hispid-strigose, rarely entirely glabrous; petioles straight, (4-)7-12(-15) mm long; crown leaf blades narrowly to broadly lanceate or narrowly elliptic, (3½-)8-17(-22) cm long × (1-)2-5½(-8) cm broad, ± chartaceous, drying dull mid olive-green to blackish, with margins finely denticulate to undulate-denticulate, midrib shallowly to deeply impressed on upper face, ascending nerves ± obscure, on upper face, sparsely, rarely densely hispid-strigose on lower face.

Inflorescences borne among and below persisting leaves, laxly thyrsiform, (2½-)5-12(-18½) cm long, generally hispid-strigose, sometimes glabrescent, bearing (15-)18-42(-50) flowers; pedicels (1-)2-5(-8) mm long.

Open flowers with hypanthium usually ± densely, less often sparsely hispidulous-strigillose, rarely entirely glabrous; perianth pale green to greenish white, (11-)13-14(-15)-partite, the inner tepals (2¾-)3½-4¼ (-5) mm long × (1-)1¼-2(-2¼) mm broad, with ± deeply fimbriate-crenate margins; androecium of (4-)6-7(-9) stamens 1-1⅓(-1½) mm long, and (5-)6-9(-12) staminodes, the outer staminodes occasionally bearing vestiges of staminal glands; gynoecium of (5-)8-12(-16) carpels, the stigmatic column shortly and thickly hemispherical, rarely conical, exserted to apices of staminodes, rarely beyond.

Ripe infructescences usually borne below persisting leaves, (2½-)

6-12(-14) cm long; pedicels (3-)4-7(-12) mm long, often conspicuously expanded under fruiting hypanthium; fruiting hypanthium narrowly cylindrical-urceolate, approaching fusiform, (10-)15-24(-30) mm long × ($1\frac{1}{2}$-)3-4(-5) mm thick, thinly lignified or papryaceous with walls $< \frac{1}{2}$ mm thick; hairs on ripe nutlet bodies (8-)9-10 mm long; styles of ripe nutlets 11-16 mm long.

Detailed Description

Small to medium-sized trees (3-)10-20(-25) m high; bole ca 8-40 cm diameter breast height, rarely coppicing, sometimes suckering; crown umbrageous-corymbiform to slightly cylindrical, shorter than bole, the leaves often ± pendulous. Bark 4-7 mm thick when dry, outer surface finely cracked and pustuled, greyish to fawn-grey or mid grey-brown, inside bright, less often pale yellow, drying dull, rarely yellowish, biscuit-brown. Wood bright to pale creamy yellow, drying cream grey with a strong yellowish wash. Branchlet stems ± loosely branched, with leaves confined to ultimate 3-5(-6) nodes, the ultimate 4-6 internodes (1-)2-6(-10) cm long × (1-)$1\frac{1}{2}$-$2\frac{1}{2}$(-4) mm thick, thicker on leader stems, slenderest on laterals, sometimes faintly furrowed and pustuled below, drying mid grey-brown to blackish, often tinted olive, rarely fawn, densely, less often sparsely hispid-strigose, rarely entirely glabrous; shaded and sapling branchlet stems with ultimate 4-6 internodes (1-)4-8(-12) cm long, more broadly flattened at the nodes, more sparingly pubescent to frequently glabrous, except buds. Petioles straight, divergent, (4-)7-12(-15) mm long × ($\frac{3}{4}$-)1-2(-$2\frac{1}{4}$) mm thick, drying mid brown to dark olive or blackish, sparsely to densely hispid-strigose, sometimes glabrescent, rarely entirely glabrous except on shaded and sapling branchlets. Leaf blades narrowly to broadly lanceate or narrowly elliptic, exceptionally oblanceate, broadly elliptic, or ovate, ($3\frac{1}{2}$-)8-17(-22) cm long × (1-)2-$5\frac{1}{2}$(-8) cm broad, broadly obtuse, infrequently ± cuneate or almost cordate at the base, frequently attenuately acuminate mucronate obtuse to acute at the apex; margins finely denticulate to undulate-denticulate, less often repand, shallowly crenate, or entire; texture chartaceous, rarely thinly coriaceous, the upper face usually finely wrinkled with a finely prominulous vein reticulum; colour rather glossy mid to dark green on upper face, paler and duller, sometimes greyish with pubescence on lower, in dry leaves duller mid olive-green to blackish olive on upper face, paler on lower; nervation with midrib shallowly to deeply impressed on upper face, on lower with (4-)6-8(-9) slenderly to ± thickly prominent main nerves ascending from the midrib, the vein reticulum usually more finely prominulous than the nerves; generally sparsely, rarely densely pale tawny to sordid grey-white rather curling hispid-strigose on lower face, sometimes glabrescent, very rarely quite glabrous, the hairs invariably denser on nerves and midrib; leaf blades on shaded and sapling branchlets larger, with more conspicuously denticulate margins, more prominulous vein reticulum on upper face, and sparser pubescence, often glabrous. Bark, stems, and leaves not or very weakly aromatic, sometimes with an obscure stale odour when crushed.

Inflorescences borne rather sparingly at ultimate (1-)2-7(-12) leaf nodes among and below persisting leaves, markedly pendulous, laxly thyrsiform, ($2\frac{1}{2}$-)5-12(-$18\frac{1}{2}$) cm long, sordid grey-white to stramineous hispid-strigose, sometimes glabrescent, rarely almost entirely glabrous, bearing (15-)18-42(-50) flowers. Primary peduncles ($1\frac{3}{4}$-)4-10(-$18\frac{1}{2}$) cm long, the base internode (1-)$1\frac{1}{2}$-2(-$2\frac{1}{2}$) mm thick, the distal internodes hardly tetragonous, usually sparsely to densely off-white to brownish hispid-strigose, with base internode sometimes glabrescent, rarely quite glabrous, (2-)4-7(-10)-noded, with subterminal 1(-2) nodes usually single flowered; accessory axillary flowers frequent, solitary or in simple dichasia; bracts of primary peduncle (1-)$1\frac{1}{2}$-4(-6) mm long × ± 1 mm broad, sparsely to densely sordid white to brownish strigose abaxially, more sparsely pubescent to glabrous adaxially, occasionally foliose and up to 1-$2\frac{1}{2}$ cm long × $\frac{1}{2}$-$\frac{3}{4}$ cm broad, with sparsely strigose midribs; secondary peduncles ($\frac{1}{2}$-)$\frac{3}{4}$-3(-6) cm long, more slender than primary peduncle, sometimes more densely pubescent, 1-3-noded; bracts of secondary peduncle usually more ovate than those on primary peduncle, ($\frac{1}{2}$-)1-$1\frac{1}{2}$ mm long × $\frac{1}{4}$-1 mm broad; pedicels (1)2-5(-8) mm long × ± $\frac{1}{4}$ mm thick, terete, sometimes tetragonous under flowers in terminally central position in inflorescence, hardly expanded under hypanthium, densely, infrequently sparsely hispid-strigose, rarely completely glabrous. Mature flower buds ($1\frac{1}{2}$-)2-$2\frac{3}{4}$(-3) mm long × (1-)$1\frac{3}{4}$-$2\frac{1}{4}$(-3) mm thick, frequently densely pale stramineous to tawny strigillose on hypanthium and outer perianth bracteoles with inner tepals sparsely hairy or glabrous, infrequently uniformly sparsely strigillose, rarely quite glabrous.

Open flowers. Hypanthium 1-1½(-2) mm long × (¾-)1-1½ mm thick, usually rather densely sordid white to fawn hispidulous-strigillose, less often sparsely hairy, rarely glabrous, occasionally bearing outer 1-2 perianth bracteoles below rim towards base; rim flat to slightly rising, ± ⅓ mm broad. Perianth pale green to greenish white, (11-) 13-14(-16)-partite in 3-5 whorls, the outer (2-)3 whorls of ± opposite bracteoles, the inner 1-2 whorls comprising 7-8(-10) tepals; outer perianth bracteoles broadly ovate-deltate, (½-)1-1½(-2) mm long × (½-) ¾-1(-1½) mm broad, pubescent as hypanthium abaxially, infrequently sparsely strigillose adaxially; inner (1-)2 pairs of perianth bracteoles depressed circular to broadly-based broad elliptic, ovate, or obovate, (1-)1½-2¾(-3) mm long × (1-)1½-2(-2½) mm broad, with entire to fimbriolate margins, uniformly sparsely, rarely densely strigose abaxially, or the hairs confined to the median region, very rarely entirely glabrous; tepals variously lanceate, sometimes narrowly elliptic or narrowly ovate, (2¾-)3½-4¼(-5) mm long × (1-)1¼-2(-2¼) mm broad, with deeply, rarely finely fimbriate-crenate margins towards the apex, conspicuously (3-)5-nerved, with obscure vein reticulum. Androecium entirely pale green, (2-)3-4-seriate; (4-)6-7(-9) stamens 1-1⅓(-1½) mm long × (⅓ -)⅔ mm broad × ⅓ - ½ mm thick, sometimes narrower, ⅔ mm broad through occasional abortion of one pollen sac and the associated staminal gland; filaments broad and short, ¼-¾ mm long below staminal glands × (⅓ -)⅔ -1 mm broad × ¼ - ⅓ mm thick, entirely glabrous, rarely strigillose adaxially;

staminal glands depressed elliptic, peltate, $\frac{1}{4}$ - $\frac{1}{3}$(-$\frac{1}{2}$) mm long × $\frac{1}{3}$ - 2 mm broad; anthers compressed, slightly depressed cubical, $\frac{1}{2}$ - $\frac{2}{3}$ mm long × ($\frac{2}{3}$ -)$\frac{3}{4}$(-1) mm broad × $\frac{1}{3}$ - $\frac{1}{2}$ mm thick; (5-)6-9(-12) staminodes oblong to usually somewhat clavate, rarely rather batilliform, ($\frac{2}{3}$ -)$\frac{3}{4}$-1 mm long × $\frac{1}{4}$-$\frac{1}{2}$ mm thick, the base thicker than the apex, with a prominent abaxial midnerve, rarely strigillose abaxially, variously strigillose towards the base adaxially, the outer staminodes with vestiges of staminal glands occasionally present as hyaline areas or aborted flaps of tissue. Gynoecium of (5-)8-12(-16) carpels; styles exserted $\frac{3}{4}$-1(-$1\frac{1}{4}$) mm beyond hypanthium rim in a broad cylindrical to subglobular, rarely narrowly conical column ca $\frac{1}{2}$ - $\frac{2}{3}$ mm thick; stigmatic column short and thickly hemispherical to infrequently narrowly conical, $\frac{1}{4}$ - $\frac{1}{3}$ mm long, exserted to apices of staminodes, rarely beyond.

Ripe infructescences borne at ultimate (1-)3-10(-14) leaf nodes, usually below leaves on branchlets, ($2\frac{1}{2}$-)6-12(-14) cm long, the axes sparsely, rarely densely strigose. Primary peduncles ($\frac{1}{2}$-)5-8(-12) cm long, the base internode $1\frac{3}{4}$-$2\frac{1}{2}$(-3) mm thick, of the same form and pubescence as in inflorescence, sometimes rather glabrescent; secondary peduncles ($\frac{1}{2}$-)$\frac{3}{4}$-$1\frac{3}{4}$(-$2\frac{1}{2}$) cm long, of the same form as in inflorescence, usually more densely pubescent than primary peduncle; pedicels (3-)4-7(-12) mm long, of the same form as in inflorescence, often conspicuously expanded under fruiting hypanthia, persistently if more sparsely pubescent. Fruiting hypanthium narrowly cylindrical-urceolate or urceolate, approaching fusiform, (10-)15-24(-30) mm long × ($1\frac{1}{2}$-)3-4(-5) mm thick, narrowed into a long neck ca ½ × length of hypanthium, tapered towards the base, levigate to faintly striate, dull to rather glossy light green, sparsely sordid whitish strigillose or glabrescent, thinly lignified or papyraceous, with walls < ½ mm thick; hypanthium chamber long and narrow, generally glabrous on the neck, long dirty brown silky hirsute towards the base among nutlets. Nutlets enlongating in maturing hypanthium to maintain the exsertion of the style apices beyond the hypanthium rim as in flower; bodies of ripe nutlets narrowly ellipsoid, almost fusiform, 5-7 mm long × 1-2 mm thick, the hairs (8-)9-10 mm long; styles of ripe nutlets 11-16 mm long, hardly expanded at base and conspicuously demarcated from body of nutlet, the apical 1-1½ mm shortly hispid.

10-20-noded young plants 30-100 cm high, the ultimate 4-6 internodes compressed, rather tetragonous, 1½-9 cm long × 1-2 mm thick, smooth, drying blackish, glabrous, rarely sparsely strigillose, the nodes broadly compressed; cotyledons caducous; subsequent leaf pairs with petioles 5-10 mm long × 1-2 mm thick, sparsely strigillose to glabrous and leaf blades elliptic to lanceate, 9-21 cm long × 2¾-6½ cm broad, with obtuse bases, acuminate obtuse mucronate apices, shallowly repand/or undulate flat, rarely shallowly crenate margins, thinly chartaceous texture, slightly glossy dark green colour on upper face, drying dark brownish olive, deeply impressed midrib on upper face, finely and closely reticulating nerves and veins on both faces, glabrous on upper face, generally glabrous on lower, but later leaves often sparsely sordid stramineous strigillose towards base of midrib and blade.

The epithet *repandula* alludes to the usually slightly repand leaf blade margins that are rather characteristic of this species (F.Mueller 1877, F.M.Bailey 1883).

Vernacular names: Cheese-wood (Tardent:BRI), Sassafras or Grey Sassafras* (Welch 1929), Northern Yellow Sassafras (Francis 1951), Yellow Sassafras (Francis 1951), Yellow-wood (Bick and Whalley 1947).

Series of specimens examined: 36 collections, comprising 16 with flower buds, 21 with open flowers, 8 with near or fully mature fruiting hypanthia, and 2 of young plants.

Geographic Distribution (map 10)

Daphnandra repandula is widespread on the coastal ranges of north-east Queensland, from the Mt.Finnigan area south to the Mt.Spurgeon-Mt.Lewis range, Atherton and Evelyn Tablelands, and adjacent coastal areas between Trinity Bay and Rockingham Bay, 15°30′-18°S:

Upper Parrot creek, Annan river; Mt.Lewis, ca 10 miles north of Mt. Molloy; Trinity Bay; Cairns; Davies Creek; Barron; Danbulla; Forest Reserve 185, Danbulla; Moomin Forest Reserve; Atherton; Gadgarra; Forest Reserve 310, Gadgarra; Lake Eacham; Wongabel; Wongabel Forest Reserve; Malanda; Malanda District; Jaggan; Ravenshoe; Johnstone river, near Geraldton; Mourilyan Harbour; Kamerunga; Laceys Creek,

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* Evidently in error for *Doryphora aromatica* (F.M.Bail.)L.S.Smith.

Mission Beach area; Dalrymple Gap, Rockingham Bay.

Ecology (figure 52)

D. repandula occurs frequently to sparingly as a subcanopy tree, rarely as a canopy tree in stunted forest at high altitudes, in both primary and secondary rainforest and rainforest margins, between the altitudes of 30 and 1200 m. It is most common between the altitudes of 500 and 750 m on the Atherton and Evelyn tablelands,and shows a preference for rocky sites and sloping ground on the sides of damp gullies.

Phenology

Inflorescence expansion, flowering, and fruiting appear to occur exclusively in austral autumn, winter, and spring months, during which period any or all stages may occur together on the one tree. Inflorescence buds usually expand between February and May (-August), flower opening takes place between April and August (-October), and fruit development and maturation between(May-) June and October. All October-January collections from adult trees seen have been sterile. This flowering and fruiting season is similar to that for sympatric Doryphora aromatica.

Infraspecific Variation

Daphnandra repandula is a polymorphic species, as might be expected from its tolerance of a rather wide range of altitudinal and other environmental conditions. Variation is most marked in the occurrence of indumentum on the ultimate branchlet stems, leaves, and inflorescence, in the size and shape of the leaves, in the length of the inflorescences and infructescences, and in the length of the mature fruiting hypanthia. The variability of each of these characters is discussed below.

1. Presence or absence of pubescence, which has been used as the criterion for distinguishing two species (Perkins 1911), appears to be subject merely to individual variation and tree age. Mature trees and adjacent seedling saplings collected at Moomin Forest Reserve near Atherton and at Mt.Lewis show that the saplings (Schodde 3278, 3344) are invariably glabrous, and the adult trees (Schodde 3277, 3343) pubescent on the ultimate stems and lower faces of the leaves to a greater or lesser degree. It is also significant that, of all the more-or-less glabrous forms examined in herbarium collections, all except one were taken from small shrubs or trees which may well have been juvenile and precociously in flower. The single exception, Brass 20250, was taken from a tree 20 m high. All pubescent collections seen are from small trees (Jones 1110) to trees 19 m high (Schodde 3258).

There does not seem to be any geographic pattern to indumentum variation. Densely hispid-strigose forms are known from near the northern and southern limits of the range of the species, and glabrous forms have the same or greater range.

2. There is a trend to smaller leaves in far northern forms, despite a general overlap in leaf sizes at the centre of the geographic range of the species. The uniformly smallest leaves are from Annan river (Brass 20250) at 250 m s.m., Mt.Lewis (Schodde 3343) at 1200 m s.m., and Gadgarra

(anonym.: ATHERTON 1655, and Tardent: BRI 052028) at 600-700ms.m.; the uniformly largest are from Mourilyan Harbour (F.M.Bailey: NSW 67920) at ± sea-level, Moomin Forest Reserve (Schodde 3278) at 1100 m s.m., and Wongabel (Jones 1110) at ca 700 m s.m.

3. In leaf shape, there is a cline from narrowly attenuate leaf apices in northern forms (Brass 20250, Schodde 3343) to broader obtuse leaf apices in southern populations (Dallachy: MEL 3181, Smith and Webb 4890).

4. Variation in the length of inflorescence and infructescence appears to be at random rather than subject to geographic position. The shortest inflorescences and infructescences recorded are respectively from Rockingham Bay (Dallachy: MEL 3181) and Mt.Lewis (Schodde 3343), at the southern and towards the northern limits of the geographic range of the species. The longest inflorescences (up to 18½ cm long) are from Wongabel (Schodde 3258) near the centre of the geographic range.

5. Differences in the lengths of the fruiting hypanthia also appear to be at random, judging from the geographic overlap in hypanthium dimensions. The shortest recorded are from Mt.Lewis (Schodde 3343) and Jaggan on the Atherton tableland (Smith and Webb 3336), and the longest from Trinity Bay (F.M.Bailey: MEL 3182) and Jaggan (Webb 1061).

The adult trees collected at Annan river and Mt.Lewis (Brass 20250 and Schodde 3343 respectively), which differ from all other collections of the species in their small attentuate leaves and short inflorescences, merit further attention because they are from the northern geographic limit of the species. The collection localities, moreover, are separated by ca 150 and 50 miles respectively from those further south. It has been pointed out above that the form of the leaf apices represent part of a clinal trend. In the case of the Mt.Lewis specimens, it might also be argued that the remaining characters, ± dense pubescence on the ultimate branchlets and leaves, small leaf size, and short infructescences and fruiting hypanthia, have been induced by the environment in which the tree grew, at 1200 m s.m. in stunted well-mossed montane forest at the highest altitude recorded for the species. In the only other collection from a comparable altitude, Schodde 3277 at 1100 m s.m. from Moomin Forest Reserve some 70 miles further south, the leaves are more glabrous and of average to large dimensions. The forest at Moomin is tall, poorly mossed, and of the kind found at altitudes as low as 600 m s.m. The leaves of the Annan river specimens, from 250 m altitude, are as small as and even narrower than those from Mt.Lewis, and the inflorescences are as short. Thus the comparison is inconclusive for determining whether the form of these characters in the Mt.Lewis collection have been brought about by environmental conditions or genetic differences. In view of the physiognomy of the forest on the summit of Mt.Lewis, it nevertheless seems likely that the leaf characters of the specimens from there have been at least partly affected by the environment.

There is also marked individual variation in many characters in <u>D. repandula</u>, as in the large number of fertile stamens (9) and staminodes (12) per flower in Schodde 3258, from Wongabel, compared with the exceptionally small number of stamens (5) and staminodes (5-6) per flower in Haines 188, from Atherton plateau, and herb. F.M.Bailey: AD 96714020, from Kamerunga; in the occasional abortion of some (1-3) stamens in Schodde 3254, from Gadgarra, and L.S.Smith 4190, from Lake Eacham; in the few (5) carpels per flower in herb. F.M.Bailey: AD 96717020, from Kamerunga, compared with the very many (16) carpels in Tardent: BRI 052028, from Gadgarra; and in the occasional occurrence of the outer perianth bracteoles down the sides to the base of the floral and fruiting hypanthium, as in Dallachy: MEL 3181, from Rockingham Bay, and McAdam: BRI 051806, from Atherton Tableland.

Taxonomic Notes and Typification

Daphnandra repandula was initially referred to the genus Atherosperma by F.Mueller (1877) when describing the species, and by Perkins and Gilg (1901) when treating it in their first revision of the Monimiaceae. Mueller appears to have done this on the grounds that it was very closely related to D. micrantha which he had previously (1860) retained in Atherosperma with some diffidence. Though the binomial "Daphnandra repandula F.M. coll."* was mentioned in the original description as a manuscript name, it was not until 1882 that Mueller, in the Systematic Census of Australian Plants, accepted it. Lacking examples of the species, Perkins and Gilg (l.c.) nevertheless maintained it in Atherosperma. By 1911, Perkins had several collections available (e.g. Diels

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* The name written by Mueller on the lectotype sheet in MEL is "Daphnandra repanda".

8299 and 8513),and was able to conclude that the species belonged in Daphnandra.

Mueller cited two collections - Dallachy: Rockingham Bay, and Bailey: Trinity Bay - when describing the species, without indicating either as the type. Dallachy's collection from Rockingham Bay has been chosen as the lectotype, because sheet 3181 bearing this collection in MEL carries annotations on floral characterx by Mueller, whereas Bailey's collection from Trinity Bay comprises discordant flowering and fruiting elements that are obviously from different trees.

Perkins (1911) also described a further species, Daphnandra dielsii, from north-east Queensland, said to differ from the above in its pilose lower leaf face, hardly denticulate leaf margins, and more densely pubescent inflorescences and juvenile branchlets. The occurrence of pubescence in D. repandula has already been discussed and shown to be largely dependant on the age of the individual tree. Moreover, those forms of Daphnandra from north-east Queensland which agree in all essential details with Perkin's description of D. dielsii fall well within the range of variation of D. repandula.

Bick and Whalley (1947) nevertheless suggested that there were alkaloid differences between collections purported to be D. repandula and D. dielsii sent to them for analysis. D. repandula was found to contain the alkaloids repanduline and repandine, while in D. dielsii only repanduline was isolated. Their data were based on single collections of both "species". Bick, Taylor, and Todd (1953) subsequently re-examined the two forms, using more refined analytical techniques, and found two minor alkaloids, O-methylrepandine and repandinine in both. In the material of "D. dielsii", a further minor alkaloid, tenuipine, was isolated, but repandine was again absent. Bick (pers.comm.) has since informed me that he does not believe these differences between the two forms to have much taxonomic significance.

The type of Daphnandra dielsii (Diels 8401) was lost in herb. B in the second World War, and no duplicate has been traced, Because D. dielsii has been at times recognised as a species by foresters and ecologists, it seemed desirable to select a neotype. Accordingly, Schodde 3258 has been chosen, on account of its rather dense hispid pubescence on the lower face of the leaves, the inflorescence, and ultimate branchlets, and its flowering condition which is consistent with Perkins original description. Its collection locality, Wongabel, is in the same region as "Ober-Barron", the locality of Diels 8401.

The chromosome number, 2n=44, has been reported by Ehrendorfer et al (1968) for D. repandula.

Chemistry

The alkaloids of this species were first studied by Bancroft (1887 a, b, c) who found them to be remarkably rich in the bark, totalling about 6%, a figure since confirmed approximately by Bick and Whalley (1946, 1947).

The chemical and physical properties of the bark alkaloids were first examined by Bick and Whalley (1946, 1947), Bick and Todd (1948), and Bick, Doebel, Taylor, and Todd (1953), and summarised by Kulka in Manske (1954, 1960). Two major alkaloids are recorded. One, repanduline, has the formula $C_{37}H_{34}O_{7}N_{2}$ (Bick et al. 1953), contains one methoxy-group, two methylimino-groups, and at least one methylenedioxy-group, forms bright yellow crystals when pure which decompose rather rapidly at temperatures above 183°C, and possesses very high positive specific rotation. It is unique among the known alkaloids of Daphnandra in being yellow; the others are colourless. The other major alkaloid, repandine, has the formula $C_{37}H_{40}O_{6}N_{2}$ (Bick and Todd 1948), contains three methoxy-groups, two methylimino-groups, and no methylenedioxy-group, forms fine colourless or whitish needles which melt at 255°C, and possesses a negative specific rotation. It is an optical isomer of oxyacanthine. The presence of repanduline and repandine together and of repanduline only in respective samples of "D. repandula" and "D. dielsii" investigated has been discussed above.

Three colourless minor alkaloids isolated subsequently (Bick, Taylor, and Todd, 1953) were identified as O-methylrepandine, $C_{38}H_{42}O_{6}N_{2}$, m.p. 211°-212°C; repandinine, $C_{38}H_{40}O_{7}N_{2}$, which contains three methoxy-, two methylimino-groups, and at least one methylenedioxy-group, has a melting point of 243°C, is non-phenolic, and has zero optical rotation; and tenuipine in laevo-rotary form, an alkaloid found also in D. tenuipes and described under that species. Bick, Harley-Mason, and Vernengo (1963) have since shown that repandinine is a racemic form corresponding to (+) and (-) tenuipine.

The essential oils of D. repandula have been examined by Lahey and Jones (1939). The yield of oil was too small to permit a thorough investigation other than to establish that the principal constituents were sesquiterpenes, with pinene and esters as minor constituents.

Uses

From the point of view of potential drug use, Bancroft (1877b,c) found that alkaloid extracts from the bark were very poisonous in action, paralysing cats, guinea pigs, frogs, grasshoppers, fish, molluscs, and infusoria, by affecting the heart, respiration, and motor nervous system. They resemble the digitalis group of poisons in their action on the heart. They were also antagonistic to strychnia, deodorised and retarded the decay of putrid meat by inhibiting bacterial action, checked the growth of grass, and would kill some water plants, for example Lemna. [White (1918) conjectured that the bark poisons might extend to the leaves which could be dangerous to stock as the species sometimes suckers in paddocks.] The physiological effects of the alkaloids reported by Bancroft have been summarized by Maiden (1889, 1921), Hurst (1942), and Webb (1948).

The wood, which is light glossy yellow-brown in colour, close-grained and firm, is nicely figured and resembles Holly (Ilex aquifolium) (F.M.Bailey 1886, 1888, 1901, 1913). It is useful for cabinet work, carving, and engraving, according to F.M.Bailey (ll.cc.), Maiden (1889), and J.F.Bailey (1899). Welch (1929) records the timber as yellowish to brownish-yellow, close-textured, with an average lateral hardness equal to 489 kg, and that it may be used for the same purposes as that of <u>D. micrantha</u> (= <u>D. apatela</u>), namely for turned articles, small tool handles, door knobs, brush stocks, broom handles, flooring, lining, interior fittings, and case material.

2. Daphnandra micrantha (Tul.)Benth.

Daphnandra micrantha (Tul.)Benth., Fl.Austral. 5(1870)285 p.p.; F.Muell., Syst.Cens.Austral.Pl. 1(1882)3 p.p.; C.Moore, Cens. Pl. N.S.Wales (1884)58 p.p.; Hobein, Bot.Jb. 10(1888)72 p.p.?; F.Muell., Sec.Syst.Cens.Austral.Pl. 1(1889)5 p.p.; Pax, Pflzfm. 3,2(1889)103 p.p.?, f.67E; Perk. & Gilg, Pflzr. 4(1901)75 p.p.; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80 p.p.?; Maiden, For.Fl.N.S.Wales 7(1921)368,371 p.p.

Atherosperma micranthum Tul., Ann.Sci.Nat. IV,3(1855)46; Tul., Arch.Mus.Hist.Nat.Par. 8(1855)421,423, f.34,II; C.Muell.in Walp., Ann.Bot. 4(1857)118; F.Muell., Pl.Colon.Vict. 1(1860)24 p.p.; A.DC., Prod. 16,2(1868)676 "A. micrantha"; Baill., Hist.Pl. 1(1869)319; [Benth., Fl.Austral. 5(1870)285 p.p.pro syn. Daphnandrae micranthae]; Baill., Adansonia 10(1873)351; F.Muell., Fragm. 10(1877)106 p.p.?

TYPE: C.Fraser, Banks of the Hastings (river) —— holotype in W (lost), isotypes in OXF, P.

Daphnandra tenuipes auctt. [non Perk.]: Maiden, For.Fl.N.S.Wales 7(1921) f.259 N; Chisholm, Proc.Linn.Soc.N.S.Wales 50(1925)288, 296.

Figures 10, 11, 46B.

Diagnosis

Average tree height 4-12 m; inner bark cream-yellow to pale yellow; ultimate branchlet stems generally glabrous, the penultimate internodes or nodes very sparsely hispidulous-strigillose; petioles often incurved towards stem, (4-)5-8(-10) mm long; crown leaf blades obovate to elliptic, very rarely ± ovate, ($3\frac{1}{2}$-)7-12(-16) cm long × ($1\frac{1}{2}$-)$2\frac{1}{2}$-$4\frac{1}{2}$(-6) cm broad, ± coriaceous, drying dull mid olive-grey to blackish olive, with margins distantly and shallowly ± serrate, midribs shallowly to ± deeply impressed on upper face, ascending nerves finely lined on upper face, generally glabrous, or occasional hairs towards base of blade on lower face.

Inflorescences borne among, rarely below persisting leaves, laxly thyrsiform, (3-)5-11(-17) cm long, generally glabrous, bearing (9-)18-39 (- ± 50) flowers; pedicels (2-)3-6(-7) mm long.

Open flowers with hypanthium glabrous; perianth pale green to cream or pale yellow, (10-)12(-14)-partite, the inner tepals ($2\frac{3}{4}$-)3-4(-$4\frac{1}{2}$) mm long × 1-$1\frac{3}{4}$(-$2\frac{1}{2}$) mm broad, with finely or obscurely fimbriolate margins; androecium of (4-)5(-7) stamens 1-$1\frac{1}{4}$(-$1\frac{1}{2}$) mm long,and (5-)6-8(-11) staminodes, the outer staminodes often bearing vestiges of staminal glands; gynoecium of (5-)6-8(-12) carpels, the stigmatic column shortly hemispherical to conical, exserted to beyond apices of staminodes.

Ripe infructescences usually borne among, sometimes below persisting leaves, (3-)5-13(-16) cm long; pedicels 5-8(-10) mm long, gradually expanded under fruiting hypanthia; fruiting hypanthium narrowly cylindrical-urceolate, approaching fusiform, (12-)17-22(-27) mm long × ($2\frac{1}{2}$-) 3-$3\frac{1}{2}$(-$3\frac{3}{4}$) mm thick, thinly lignified or papyraceous, with walls $\frac{1}{4}$-$\frac{1}{2}$ mm thick; hairs on ripe nutlet bodies 7-8 mm long; styles of ripe nutlets (12-)14-18 mm long.

Detailed Description

Small trees ($2\frac{1}{2}$-)4-12(-15) m high; bole (5-)10-20(-25) cm diameter breast height, coppicing and suckering unrecorded; crown umbrageous, loosely to compactly corymbiform, much shorter than bole, the leaves horizontal to slightly pendulous. Bark (3-)4-5(-6) mm thick when dry, outer surface coarsely striate to furrowed with a cork-like appearance, greyish fawn, rarely darker, inside cream-yellow to pale yellow, drying browner. Wood cream-yellow, drying duller. Branchlet stems closely to ± loosely branched, the ultimate 4-6 internodes (1-)3-5(-$7\frac{1}{2}$) cm long × (2-)3-4 mm thick on leader stems, (1-)2-3 mm thick on lateral stems, usually finely to coarsely grey-fawn whitish pustuled below, drying dark olive or grey-brown to blackish, generally glabrous, the penultimate internodes or nodes very sparsely hispidulous-strigillose; shaded and sapling branchlet stems with ultimate 4-6 internodes (3-)$3\frac{1}{2}$-7(-10) cm long, slenderer, $1\frac{1}{2}$-2(-$2\frac{1}{2}$) mm thick on lateral branchlets, often more conspicuously tetragonous, similarly hispidulous-strigillose. Petioles often incurved towards stem rather than straight and divergent, (4-)5-8 (-10) mm long × ($\frac{3}{4}$-)1-$1\frac{1}{2}$(-2) mm thick, drying usually blackish, sometimes dark grey-brown, usually sparsely hispidulous-strigillose or glabrescent, similarly pubescent on shaded and sapling branchlets. Leaf blades obovate to elliptic, very rarely somewhat ovate, $(3\frac{1}{2}-)7-12(-16)$ cm long × $(1\frac{1}{2}-)2\frac{1}{2}-4\frac{1}{2}(-6)$ cm broad, narrowly obtuse to cuneate, rarely rather oblique at the base, shortly, rarely attenuately or acuminately mucronate obtuse to acute at the apex which is occasionally curved away from the axis of the stem; margins distantly and shallowly ± serrate, rarely crenate-serrate; texture thinly to quite coriaceous, the upper face finely lined with prominulous nerves, less often vein reticulum; colour glossy mid to dark green on upper face, paler and duller on lower, in dry leaves duller mid olive-grey to blackish olive on upper face, paler and browner on lower; nervation with midrib shallowly to ± deeply impressed on upper face, on lower with (3-)4-6(-9) ± thickly prominent main nerves ascending widely from the midrib, the vein reticulum usually conspicuously prominent yet more slender than the nerves; generally glabrous, often very sparsely sordid stramineous to pale brown hispidulous-strigillose towards base of blade and midrib on lower face of younger leaves; leaf blades on shaded and sapling branchlets more frequently ovate and larger, with more deeply serrate margins, more thinly coriaceous almost chartaceous, nerves and vein reticulum more prominent. Bark, stems, and leaves hardly or very weakly aromatic when crushed, the odour evanescing in these parts when dried.

Inflorescences borne at ultimate (1-)2-5(-7) leaf nodes among, rarely below persisting leaves, markedly pendulous, laxly thyrsiform, (3-)5-11(-17) cm long, generally glabrous, bearing (9-)18-39(- ± 50) flowers. Primary peduncles $(2\frac{1}{2}-)4-10(-17)$ cm long, the base internode

($\frac{3}{4}$-)1-1$\frac{1}{2}$(-2) mm thick, the distal internodes often tetragonous, generally glabrous, but basal 1-2 internodes often very sparsely sordid stramineous to whitish hispidulous-strigillose, (3-)4-7(-9)-noded, with subterminal 1-2(-3) nodes usually single flowered; accessory axillary flowers frequent, solitary, rarely in simple dichasia; bracts of primary peduncle ($\frac{3}{4}$-)1-2(-3) mm long × $\frac{2}{3}$ - $\frac{3}{4}$(-1) mm broad, rather uniformly densely whitish strigillose abaxially, glabrous adaxially, very infrequently foliose and ca 1 cm long, with serrate margins; secondary peduncles ($\frac{1}{2}$-)1-2$\frac{1}{2}$(-4) cm long, more slender than primary peduncle, glabrous, 1-3(-4)-noded; bracts of secondary peduncle ($\frac{1}{2}$-)1-1$\frac{1}{2}$(-2) mm long, more sparingly haired than those on primary peduncle; pedicels (2-)3-6(-7) mm long × $\frac{1}{4}$ - $\frac{1}{3}$ mm thick, terete or slightly compressed, hardly expanded under hypanthium, glabrous. Mature flower buds ($\frac{3}{4}$-) 1$\frac{1}{3}$ - 2(-2$\frac{1}{4}$) mm long × (1-) ± 1$\frac{1}{2}$(-2$\frac{1}{2}$) mm thick, glabrous except for sparsely whitish strigillose outermost perianth parts.

Open flowers. Hypanthium 1-1$\frac{1}{4}$(-1$\frac{1}{2}$) mm long × (1-)1$\frac{1}{4}$-1$\frac{1}{2}$(-2) mm thick, glabrous, often bearing outer 1-2 perianth bracteoles below rim towards base; rim rather convex to infrequently flat or concave, $\frac{1}{4}$(-$\frac{1}{2}$) mm broad. Perianth pale green to cream or pale yellow, the inner petaloid tepals brightest, (10-)12(-14)-partite in 3 whorls, the outer 2(-3) whorls of ± opposite bracteoles, the inner 1-2 whorls comprising (6-)7-8(-9) tepals; outer pair of perianth bracteoles ovate-deltate, rarely broadly elliptic or obovate, ($\frac{3}{4}$-)1-1$\frac{1}{2}$(-2) mm long × ($\frac{1}{2}$-)1-1$\frac{1}{4}$(-1$\frac{1}{2}$) mm broad, sparsely strigillose towards the apex abaxially or entirely glabrous;

inner 1(-2) pairs of perianth bracteoles circular-elliptic, less often depressed circular or obovate, $(1-)1\frac{1}{2}-2\frac{1}{2}(-2\frac{3}{4})$ mm long × $(1-)1\frac{1}{4}-2(-2\frac{1}{2})$ mm broad, with entire margins, generally glabrous, very rarely sparsely strigillose abaxially towards the apex; tepals narrowly lanceate to narrowly ovate, rarely oblong-lanceate, $(2\frac{3}{4}-)3-4(-4\frac{1}{2})$ mm long × $1-1\frac{3}{4}(-2\frac{1}{2})$ mm broad, with finely, sometimes obscurely fimbriolate margins towards the apex, conspicuously 3 or 5(-7)-nerved with obscure vein reticulum. Androecium entirely pale green or the staminodes with red-brown apices, 2-3(-4)-seriate; (4-)5(-7) stamens often surrounding the shorter staminodes and gynoecium like a pallisade, $1-1\frac{1}{4}(-1\frac{1}{2})$ mm long × $(\frac{2}{3}-)\frac{3}{4}-1(-1\frac{1}{4})$ mm broad × $\frac{1}{4}-\frac{1}{3}$ mm thick, sometimes narrower × $\frac{1}{2}-\frac{2}{3}(-\frac{3}{4})$ mm through abortion of one pollen sac and its associated staminal gland, occasionally one or two stamens partly aborted when $>$ 5 stamens present; filaments broad and short, $\frac{1}{3}-\frac{1}{2}$ mm long below staminal glands × $(\frac{1}{2}-)\pm\frac{3}{4}$ (-1) mm broad, either entirely glabrous or sparsely strigillose adaxially; staminal glands broadly depressed elliptic-circular, peltate, $\frac{1}{4}-\frac{1}{3}$ mm long × $\frac{1}{3}-\frac{1}{2}$ broad; anthers compressed,depressed cubical, $(\frac{1}{3}-)\frac{1}{2}-\frac{2}{3}$ mm long × $(\frac{1}{2}-)\frac{2}{3}-\frac{3}{4}$ mm broad × $\pm\frac{1}{4}-\frac{1}{3}$ mm thick; (5-)6-8(-11) staminodes oblong-cylindrical to narrowly or broadly batilliform, $\frac{1}{2}-1$ mm long × $(\frac{1}{4}-)\frac{1}{2}(-\frac{3}{4})$ mm thick, the base hardly thicker than apex, often with a prominent abaxial midnerve, glabrous to sparsely strigillose abaxially towards the base, densely strigillose adaxially, the outer staminodes with vestiges of staminal glands often present as rather circular hyaline flaps of tissue. Gynoecium of (5-)6-8(-12) carpels; styles exserted $\frac{3}{4}-1$ mm beyond hypanthium rim in a cylindrical to rather conical column; stigmatic column shortly hemispherical to conical and curling, ca $\frac{1}{4}$-$\frac{1}{2}$ mm long, exserted to beyond apices of staminodes.

Ripe infructescences borne at ultimate (1-)3-6 leaf nodes usually among but sometimes below leaves on branchlets, (3-)5-13(-16) cm long, glabrous. Primary peduncles of similar dimensions and form as in inflorescence, often more thickly lignified, glabrescent; secondary peduncles ($\frac{1}{2}$-)$1\frac{1}{2}$-$3\frac{1}{2}$ cm long, of the same form as in inflorescence; pedicels 5-8(-10) mm long, of the same form as in inflorescence, but gradually and conspicuously expanded under fruiting hypanthia. Fruiting hypanthium narrowly cylindrical-urceolate, approaching fusiform, (12-)17-22(-27) mm long x ($2\frac{1}{2}$-)3-$3\frac{1}{2}$(-$3\frac{3}{4}$) mm thick, levigate finely striate, glabrous, thinly lignified or papyraceous, with walls $\frac{1}{4}$-$\frac{1}{2}$ mm thick; hypanthium chamber long and narrow, densely short sordid hispid on the neck, longer dirty brown hirsute towards the base among nutlets. Nutlets elongating in maturing hypanthia to maintain or slightly increase the exsertion of the style apices to 1-$1\frac{3}{4}$ mm beyond the hypanthium rim; bodies of ripe nutlets ellipsoid, 4-5 mm long x ± 2 mm thick, the hairs 7-8 mm long; styles of ripe nutlets (12-)14-18 mm long, not expanded at base into body of nutlet, the apical $\frac{1}{4}$-$\frac{1}{2}$ mm usually glabrous.

20-noded young plants ca 100 cm high, the ultimate 4-6 internodes strongly compressed, hardly tetragonous, 4-10 cm long x 2-3 mm thick on leader stems, $1\frac{1}{2}$-2 mm thick on lateral stems, smooth, drying black, glabrous or sparsely sordid hispidulous-strigillose, the nodes on leader stems broadly compressed, up to $2\frac{1}{2}$ cm broad; cotyledons caducous; subsequent leaf pairs with petioles 6-10 mm long × $(\frac{3}{4}-)1-1\frac{1}{2}$ mm thick, sparsely hispidulous, early glabrescent, and leaf blades ovate to obovate, 12-16 cm long × 4-5 cm broad, with broadly cuneate to obtuse bases, narrowly acuminate obtuse apices, distantly rather deeply serrate, almost planate margins, chartaceous texture, glossy dark green colour on upper face, drying dull mid to dark olive-green, shallowly impressed midrib on upper face, nervation and vein reticulum on both faces similar to that on leaves of mature trees, glabrous on both faces, but later leaves often sparsely sordid hispidulous-strigillose towards base of midrib and blade as in younger leaves of mature trees.

The epithet _micrantha_ is derived from μικρος, meaning small, and ἀνθος, meaning flower (F.M.Bailey 1883*, Maiden 1921, Francis 1929, 1951*). Although the species is far from the smallest flowered in _Daphnandra_, Tulasne apparently chose the name to contrast it with the much larger flowered _Atherosperma moschatum_, with which it was originally associated in the genus _Atherosperma_ (Tulasne 1855a, 1855).

Vernacular names: Socket wood (Cousins: BELANGRY), Yellow wood (Hardeman: NSW 67932, Rudder: NSW 67929).

Series of specimens examined: 19 collections, comprising 2 with inflorescence buds, 11 with flower buds, 10 with open flowers, 4 with

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* In misapplication for _D. apatela_.

near or fully mature fruiting hypanthia, and 1 of a young plant.

Geographic Distribution (map 10)

Daphnandra micrantha is confined to the coastal watersheds of the Hastings and northern Manning river systems and adjacent coastal areas, lower north-east New South Wales, 31°10′-50′S:

Quarry Dump road, Belangry State Forest; Hastings Forestry Highway, 5 miles north of Belangry Forestry Office; Bottlebrush creek, Belangry State Forest; Hastings river; Port Macquarie; Comboyne; Kendall-Comboyne road, 6 miles east of Comboyne; Forster Kendall (= Kendall district); Camden Haven; south slopes of Comboyne plateau; South Brother, Johns river; Lansdowne river; Wingham; Taree district.

The fairly extensive collections in the genus Daphnandra from the lower north coast of New South Wales indicate that D. micrantha is entirely confined to the area defined above. Its distribution given in virtually all published treatments applies instead to D. apatela.

Ecology (figure 57)

Usually solitary, less often in loose colonies, Daphnandra micrantha is a small subcanopy tree of the rainforest mid- or sub-stage on forest margins and in secondary growth between sea-level and 450 m altitude. It appears to prefer steep, often rocky, well-drained but permanently moist sites at the heads of creeks or on gully sides adjacent to creeks, in either primary rainforest or more usually disturbed and regenerating forest, at 150-300 m s.m. (Schodde 5138, 5141, 5146, 5154, 5156, and anonym.: MEL 3193). According to Boorman (BRI 051798, NSW 67928), it is confined to deep damp shady places at South Brother, Johns river, never occurring in the open. It has been observed in association with *Bosistoa euodiiformis*, *Sloanea woollsii*, and *Pennantia cunninghamii* (Cousins: BELANGRY), and recorded with *Cuttsia* in gully gallery rainforest margined with *Eucalyptus* and overtopped by *Tristania conferta* at about 450 m s.m. (Schodde 5146).

Daphnandra apatela, the only other species of the genus sympatric with *D. micrantha*, occurs usually though not exclusively at higher altitudes (ca 700-850 m) in the areas where both species overlap.

Phenology

Flowering and fruiting is seasonally regular. Inflorescence development occurs during the austral ~~and~~ winter months and flower bud expansion from August to early October in spring, followed by flower opening in late October, flower maturation and initial fruiting hypanthium elongation in November, and ultimate maturation and dehiscence of the fruiting hypanthia during January and February in summer. Inflorescence buds of the ensuing season first appear during October-December, before maturation of the fruiting hypanthia of the current season. Flower buds or flowers were never recorded together with mature fruiting hypanthia on any collection cf. *Daphnandra repandula*.

Infraspecific Variation

The series of collections examined indicates that the species is morphologically rather uniform, as might be expected from its narrow geographic range. Variation is most marked in leaf size, shape, and texture, with Cleland: NSW 67931 from Wingham having the largest leaves, and Boorman: NSW 67928 from South Brother, and L. Fraser: NSW 67926 from Comboyne, having the smallest. These differences apparently result from the position on the trees (exposed or shaded) from which the leaves were collected rather than geographic locality or altitude.

There nevertheless seems to be an overall tendency for trees at low altitude coastal localities to have longer inflorescences and infructescences than those from higher altitudes further inland. For example, specimens from Wingham (Boorman: NSW 67930, Rudder: NSW 67929), and Camden Haven (anonym.: MEL 3191) near sea-level have inflorescences up to 12 and 17 cm long, whereas those from Belangry State Forest (Floyd and Hayes: COFFS),and the east and south slopes of the Comboyne plateau at 270 m s.m. and 400 m s.m. respectively (Schodde 5154, 5156),all have short inflorescences 3-7 cm long. Specimens from the highest known altitude, at 450 m s.m. in Belangry State Forest (Schodde 5146), however, have inflorescences 6-11 cm long.

Taxonomic Notes and Typification

Although *Daphnandra micrantha* was first referred to the genus *Atherosperma* (Tulasne 1855a, 1855), it has all the characteristics of *Daphnandra* as the species on which the latter genus is based (Bentham 1870).

Bentham (l.c.) included two species in his circumscription of *Daphnandra micrantha*, the second being *D. apatela*. The latter species, the most common and widespread of any in the genus, has been exclusively referred to as D. micrantha by all subsequent authors, leading to the paradoxical situation where the original D. micrantha has been confused with a third species, D. tenuipes, by Maiden (1921) and Chisholm (1925).

The only mention of any specimens by Tulasne (1855a) when describing Atherosperma micranthum is the phrase "Herb. mus. vindobon.". In a more elaborate description in his Monographia Monimiacearum published in the same year, he makes a more detailed reference: "Oritur in Nova-Hollandia orientali, circa sinum Jacksonis, testibus celeb. Frasero et Galdichaldo nostro. (Herb. Mus. par. et vindobon.)". The single relevant specimen in herb. P carries the data, written in Gaudichaud's hand, "C. Gaudichaud ..... Port Jackson Fraser commun.", thus indicating that the collections referred to in Tulasne's second description are in fact a single collection of Fraser's. That Charles Fraser and not Gaudichaud was the collector is clear because the specimen and Tulasne's second description and accompanying figure, which is outstanding for its accuracy and detail, are of a species confined to a small area on the lower north coast of New South Wales, which was visited twice by Fraser in 1818 and 1819 (Hist.Rec.Austral. 1922, p.200), but never by Gaudichaud.

The relevant specimen(s) in herb. W was lost in the second World War. It seems certain, nevertheless, that it was a duplicate of Fraser's collection in herb. P, for the following reasons. First, the original description is in every way consistent with Tulasne's second one and specifically states that the flowers are glabrous on the outer surface. The only other collections of Daphnandra available in European herbaria before about 1870 are of D. apatela, in which the outer surface of the flowers is invariably finely strigillose. Second, a herb. W collection is cited in association with Fraser's collection in Paris by Tulasne in the second description published in the same year as the original. Third, collections of Fraser's are known to have been sent to Vienna (Hist.Rec.Austral. 1917, pp.83-4).

There is a third Fraser specimen of this species in the Fielding herbarium at Oxford. The locality on the label, written in Fraser's hand, is "Banks of the Hastings", which fits the known distribution of the species. It is so consistent with Tulasne's descriptions and figure, and with the Fraser specimen in Paris as to form and stage of flower maturation, that it is undoubtedly a duplicate of the herb. P collection. Both the Paris and Oxford specimens are treated therefore as isotypes. The Oxford sheet, with its accurate field data, and specimen with a stem of 4 nodes bearing three pairs of leaves and seven inflorescences with many flowers both open and in expanding bud, provides the most adequate material for future study; the herb. P collection is very scanty, comprising a stem with two leaf nodes and three broken inflorescences with only a single remaining flower.

Chemistry

No information has been published. Small samples of leaves tested (Boorman: NSW 67930, F.M.Bailey: NSW 67927) possessed the alkaloids tenuipine and nortenuipine (Bick, pers. comm.). Rotation was not distinguished. The formulae and characteristics of these alkaloids are described under *Daphnandra tenuipes*.

Uses

No uses have been recorded. Because of its small size, *D. micrantha* is unlikely to be of value as a timber tree.

3. Daphnandra tenuipes Perk.

Daphnandra tenuipes Perk. in Perk. & Gilg, Pflzr. 4(1901)75, f.20 C-G; Maiden & Betche, Proc.Linn.Soc.N.S.Wales 28(1903)911; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80; Maiden, For.Fl. N.S.Wales 7(1921)368, f.259H-M, O; Perk., Gattung. Monim. (1925)4, f.36C-G; Bick, Doebel, Taylor, & Todd, J.Chem.Soc. (1953)692; Bick, Taylor, & Todd, ibid. (1953)696 et seq. p.p.; [Anderson, Trees N.S.Wales ed.3,(1956)223 pro syn. D. micranthae]; Kulka in Manske, Alkaloids 7(1960)443,460,461; Bick, Harley-Mason, & Vernengo, Anal.Asoc.Quim.Argentina 5(1963)135 p.p.; Florence, Proc.Linn.Soc.N.S.Wales 88(1963)170?

TYPE: E.Betche, Tweed River district —— holotype in B (lost), isotypes in MEL, NSW, US.

Daphnandra micrantha auct. [non (Tul.)Benth.]: Anderson, Trees N.S. Wales ed.3,(1956)223 p.p.

Figures 12, 34, 36A.

Diagnosis

Average tree height 5-12 m; inner bark pale brownish cream to pale yellowish brown; ultimate branchlet stems generally glabrous, the penultimate internodes often sparsely hispidulous; petioles usually incurved towards stem, (2-)3-5(-7) mm long; crown leaf blades lanceate to ovate, or ± elliptic, (3-)5-9(-12½) cm long x (1-)2-3½(-5) cm broad, ± coriaceous, drying dull mid to dark olive-green or brownish, rarely blackish, with margins finely, distantly crenulate, infrequently almost entire, midrib shallowly, rarely deeply impressed on upper face, ascending nerves finely or obscurely lined on upper face, generally glabrous, or occasional hairs confined to base of midrib on lower face.

Inflorescences borne among and below persisting leaves, ± divaricately thyrsiform, $(1\frac{1}{2}-)2\frac{1}{2}-6(-9)$ cm long, generally glabrous, bearing (5-)7-11(-21) flowers; pedicels (2-)4-10(-14) mm long.

Open flowers with hypanthium glabrous; perianth mauve-pink, reddish, or pale marone, 12-14(-15)-partite, the inner tepals 3-4 mm long × $(1-)1\frac{1}{2}-2$ mm broad, with conspicuously fimbriolate margins; androecium of (4-)5 stamens $1-1\frac{1}{3}(-1\frac{2}{3})$ mm long,and (4-)5-10(-13) staminodes, the outer staminodes without vestiges of staminal glands; gynoecium of (8-)10-12 (-18) carpels, the stigmatic column shortly and thickly hemispherical, exserted to apices of staminodes, rarely beyond.

Ripe infructescences borne usually among, sometimes below persisting leaves, $(2\frac{1}{4}-)3-4\frac{1}{2}(-6)$ cm long; pedicels (5-)8-12(-16) mm long, broadly expanded under fruiting hypanthia; fruiting hypanthium ampulliform to broadly obpyriform, sometimes cylindrical-urceolate, (5-)7-12(-17) mm long × (2-)5-7(-10) mm thick, lignified, with walls $(\frac{1}{4}-)\frac{1}{2}-\frac{3}{4}(-1)$ mm thick; hairs on ripe nutlet bodies (4-)5-6(-8) mm long; styles of ripe nutlets (5-)6-8(-10) mm long.

Detailed Description

Small trees 5-12(-15) m high; bole (6-)10-20(-25) cm diameter breast height, coppicing and suckering unrecorded; crown umbrageous, rather compactly corymbiform, much shorter than bole. Bark 2-3 mm thick when dry, outer surface smooth and finely striate, blotched pale to mid grey and brownish, inside pale brownish cream to pale yellowish brown, rarely markedly yellow, drying browner. Wood pale brownish cream, sometimes washed pinkish or greyish. Branchlet stems ± closely branched, the ultimate 4-6 internodes $(\frac{1}{2}-)2-4(-6)$ cm long × 2-4 mm thick on leader stems, $1-1\frac{3}{4}$ mm thick on lateral stems, usually pustulad or rarely coarsely cracked below, drying mid to brownish grey or blackish, sometimes entirely olive-brown, generally glabrous, the penultimate internodes often sparsely, rarely densely hispidulous, the vesture sometimes denser on nodes; shaded and sapling branchlet stems with ultimate 4-6 internodes up to 6-9 cm long, usually blacker, more extensively glabrous. Shoots often nitid marone-green or tinted marone. Petioles usually incurved towards stem rather than straight and divergent, $(2-)3-5(-7)$ mm long × $(\frac{1}{2}-)\frac{3}{4}-1(-1\frac{1}{2})$ mm thick, drying variously dark brown to blackish, rarely dark olive, glabrous to sparsely hispid in younger leaves and on shaded and sapling branchlets. Leaf blades lanceate to ovate, or ± elliptic, $(3-)5-9(-12\frac{1}{2})$ cm long × $(1-)2-3\frac{1}{2}(-5)$ cm broad, broadly to narrowly obtuse, infrequently cuneate at the base, variously attenuately or acuminately mucronate obtuse, less often acute at the apex which is often curved away from the axis of the stem; margins finely, often distantly crenate, infrequently rather undulate or almost entire; texture thinly to quite coriaceous, the upper face sometimes finely or obscurely lined with prominulous nerves and vein reticulum; colour dull light to dark green on upper face, paler and often glossier on lower, in dry leaves dull mid to dark olive-green or brownish, rarely blackish on upper face, paler on lower; nervation with midrib shallowly, rarely deeply impressed on upper face, on lower with (4-)5-7(-14) slender but conspicuously prominent main nerves ascending widely from the midrib, the vein reticulum usually more finely prominulous than nerves; generally glabrous, usually with a few stramineous to brownish hispid hairs towards base of midrib on lower face of younger leaves; leaf blades on shaded and sapling branchlets larger, with more deeply serrulate margins, chartaceous, nerves and vein reticulum more prominent on both faces, more densely and extensively pubescent on lower face. Bark, stems, and leaves hardly or very weakly sweetly aromatic when crushed, the odour evanescing in these parts when dried.

Inflorescences borne at ultimate (1-)2-5(-7) leaf nodes among and below persisting leaves, laxly, ± divaricately thyrsiform, $(1\frac{1}{2}-)2\frac{1}{2}-6(-9)$ cm long, generally glabrous, bearing (5-)7-11(-21) flowers. Primary peduncles $(\frac{3}{4}-)2-4(-8)$ cm long, the base internode $\frac{3}{4}-1$ mm thick, the distal internodes rounded compressed, hardly tetragonous, usually glabrous but base internode sometimes sparsely, rarely densely sordid stramineous to brownish hispid, (1-)3-4(-5)-noded, with subterminal 1-2 nodes usually single flowered; accessory axillary flowers usually absent; bracts of primary peduncle $(\frac{3}{4}-)1-2(-3)$ mm long × $\frac{1}{2}-\frac{3}{4}$ mm broad, sparsely sordid white strigillose along the abaxial midrib, glabrous adaxially; secondary peduncles $(\frac{1}{3}-)\frac{1}{4}-1\frac{3}{4}(-2\frac{1}{2})$ cm long, more slender than primary peduncle, ± entirely glabrous, 1(-2)-noded; bracts of secondary peduncle $\frac{3}{4}$-1 mm long, ± broader than those on primary peduncle; pedicels (2-)4-10(-14) mm long × $\frac{1}{4}$ mm thick, not expanded under hypanthium, glabrous. Mature flower buds 2-2$\frac{1}{2}$ mm long × 1$\frac{1}{2}$-2(-2$\frac{1}{2}$) mm thick, glabrous except for sparsely whitish strigillose outermost perianth parts.

Open flowers. Hypanthium 1-1$\frac{1}{2}$ mm long × 1-1$\frac{1}{2}$ mm thick, glabrous, rarely bearing outer 1-2 perianth bracteoles below rim to near base; rim poorly defined, flat, almost concave, $\frac{1}{3}$ - $\frac{1}{2}$ mm broad. Perianth with perianth bracteoles dull pale green and tepals mauve-pink, reddish, or pale marone, 12-14(-15)-partite in 3-4(-5) whorls, the outer 2(-3) whorls of opposite bracteoles, the inner 1-2 whorls comprising 7-8(-10) tepals; outer pair of perianth bracteoles ovate-deltate, ($\frac{3}{4}$-)1-1$\frac{1}{4}$(-1$\frac{1}{2}$) mm long × $\frac{3}{4}$-1(-1$\frac{1}{2}$) mm broad, sparsely strigillose abaxially towards the apex, rarely entirely glabrous; inner 1(-2) pairs of perianth bracteoles circular to elliptic, (1$\frac{1}{2}$-)1$\frac{3}{4}$-2$\frac{1}{2}$(-3) mm long × (1$\frac{1}{4}$-)1$\frac{3}{4}$-2(-2$\frac{1}{2}$) mm broad, with entire, rarely obscurely fimbriate margins, generally glabrous, rarely sparsely strigillose abaxially towards the apex; tepals lanceate to ovate, 3-4 mm long × (1-)1$\frac{1}{2}$-2 mm broad, with conspicuously fimbriolate margins, conspicuously 3- or 5-nerved with obscure vein reticulum. Androecium marone-pink to red, 2-3-seriate; (4-)5 stamens often surrounding the shorter staminodes and gynoecium like a pallisade, 1-1$\frac{1}{3}$(-1$\frac{2}{3}$) mm long × ($\frac{3}{4}$-)1 mm broad × ± $\frac{1}{4}$ mm thick, very rarely with one partly aborted; filaments broad and short, $\frac{1}{2}$-$\frac{3}{4}$ mm long below staminal glands × $\frac{2}{3}$(-$\frac{3}{4}$) mm broad × ± $\frac{1}{4}$ mm thick, usually sparsely strigillose adaxially, the vesture sometimes extending to the connective; staminal glands depressed elliptic,peltate, ($\frac{1}{4}$-)$\frac{1}{3}$(-$\frac{1}{2}$) mm long × $\frac{1}{3}$ - $\frac{1}{2}$ mm broad; anthers compressed,slightly depressed cubical, $\frac{1}{2}$ - $\frac{2}{3}$ mm long × ($\frac{2}{3}$ -)$\frac{3}{4}$ (-1) mm broad × ± $\frac{1}{4}$ mm thick; (4-)5-10(-13) staminodes oblong-cylindrical to rarely somewhat clavate or narrowly batilliform, ($\frac{1}{2}$-)$\frac{2}{3}$ - 1 (-1$\frac{1}{4}$) mm long × $\frac{1}{3}$ - $\frac{1}{2}$ mm thick, the base thick, with a prominent abaxial midnerve, sparsely strigillose to glabrous abaxially, densely strigillose adaxially, without vestiges of staminal glands. Gynoecium of (8-)10-12(-18) carpels; styles exserted $\frac{3}{4}$-1 mm beyond hypanthium rim in a broad cylindrical column ca $\frac{2}{3}$ mm thick; stigmatic column short, thick, hemispherical, ca $\frac{1}{4}$ - $\frac{1}{3}$ mm long, exserted to apices of staminodes, rarely beyond.

Ripe infructescences borne at ultimate (1-)2-8(-10) leaf nodes usually among, sometimes below leaves on branchlets, (2$\frac{1}{4}$-)3-4$\frac{1}{2}$(-6) cm long, glabrous. Primary peduncles ($\frac{3}{4}$-)1-3(-4) cm long, the base internode ($\frac{3}{4}$-)1-1$\frac{1}{2}$ mm thick, of the same form as in inflorescence, but more lignified, completely glabrous; secondary peduncles of the same dimensions and form as in inflorescence, more lignified; pedicels (5-)8-12(-16) cm long × ($\frac{1}{4}$-)$\frac{1}{3}$ - $\frac{1}{2}$ mm thick at the base, somewhat lignified, rather conspicuously expanded under fruiting hypanthia to (1-)1$\frac{1}{2}$(-2) mm thick, the thickening often extending down ca half the length of pedicel. Fruiting hypanthium ampulliform to broadly obpyriform, sometimes cylindrical-urceolate, (5-)7-12(-17) mm long × (2-)5-7 (-10) mm thick*, narrowed into a short neck ca $\frac{1}{4}$ - $\frac{1}{3}$ × length of hypanthium,

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* The shape and dimensions are often affected by insect infestation.

smooth or often irregularly marked towards the base with the outline of nutlet bodies, greenish orange to pink-or orange-red, glabrous, lignified, with walls ($\frac{1}{4}$-)$\frac{1}{2}$-$\frac{3}{4}$(-1) mm thick; hypanthium chamber rounded at the base, densely sordid hispid below the rim, sparsely pubescent to glabrous on the neck, rather densely long dirty brown hirsute towards the base among nutlets. Nutlets elongating in maturing fruiting hypanthium to slightly increase the exsertion of the style apices beyond the stamens and (2-)3-4(-6) mm beyond the hypanthium rim; bodies of ripe nutlets ellipsoid to broadly ellipsoid, (3-)4-5(-6) mm long x (1-)1$\frac{1}{2}$-2 mm thick, the hairs (4-)5-6(-8) mm long; styles of ripe nutlets (5-)6-8(-10) mm long, hardly expanded at base into body of nutlet, the apical ($\frac{1}{2}$-)1-1$\frac{1}{2}$ mm glabrous.

7-noded seedlings ca 14-15 cm high, the ultimate 2-3-internodes rather compressed, 7-10 mm long x ± 1 mm thick, smooth, drying dark olive-brown, glabrous, the shoots densely sordid strigillose; cotyledons caducous; subsequent leaf pairs with petioles 5-7 mm long x $\frac{1}{2}$ mm thick, glabrous, and leaf blades narrowly lanceate-elliptic, 50-70 mm long x 15-20 mm broad, with narrowly cuneate bases, narrowly obtuse apices, finely serrulate planate margins, chartaceous-papyraceous texture, dull mid olive-green colour when dry, shallowly impressed midrib on upper face, finely prominulous nerves but little vein reticulum on both faces, quite glabrous.

The epithet tenuipes, though not explained by Perkins when describing the species, evidently refers to the long slender pedicels that are a feature of this species.

Vernacular names: none recorded.

Series of specimens examined: 20 collections, comprising 5 with flower buds, 8 with open flowers, 7 with near or fully mature fruiting hypanthia, and 1 of seedlings.

Geographic Distribution (map 10)

Daphnandra tenuipes is confined to the Nightcap range - Tweed river district, north-east New South Wales, 28°30′-40°S, and is presently known only from Peach Mountain ridge, and the southern scarp of the Nightcap range between Minyon Falls and the "Red Scrub", Whian Whian State Forest:

Tweed river district; Peach Mountain ridge, Whian Whian State Forest; Nightcap range, 1½ miles north-west of Peach Mountain; below Minyon Falls, Whian Whian State Forest; Red Scrub, Whian Whian State Forest.

In suitable habitat, Daphnandra tenuipes may also occur on the northern scarp of the Nightcap range along the watersheds of the Tweed river as far as the Macpherson range or its southern foothills near Murwillumbah where Betche is reputed to have collected the type (Maiden 1921). Nevertheless, it seems unlikely that it extends into south-east Queensland (cf. Maiden 1921). It does not occur at Doyles river (near Wauchope) or in Oakes State Forest (near Macksville) in lower north-east New South Wales as stated by Bick, Taylor, and Todd (1953) and Bick et al. (1963).

These records apply respectively to *Daphnandra micrantha* (probably) and *D. melasmena*.

Ecology (figure 56)

Daphnandra tenuipes is a frequent small tree of the rainforest mid- or sub-stage on forest margins on the Nightcap range between altitudes of (60-)250-600 m. The rainforest growing on the summit ridges where it occurs is not at all luxuriant like the rainforests on basalt soils at lower altitudes, and is much intersected by sclerophyllous eucalypt forest. *Doryphora sassafras* and *Ackama paniculata* are frequent trees of the forest canopy.

Daphnandra tenuipes has been recorded growing on soils developed from shales (Schodde 3563, 3567, 3568, 3570, and 3572) and acid volcanic rock (Johnson and Constable: NSW 42344), in contrast to the other species of *Daphnandra* in the area and elsewhere which occur usually on soils developed from basalt. If *D. tenuipes* is confined to such soils, in this case Triassic and Jurassic sedimentary rocks and acid volcanics (Atlas of Australian Resources, Geology, 1966), its occurrence in the region would be limited to the Nightcap range and Tweed river headwaters where these rocks outcrop. One collection (Jones 467), however, is from the "Red Scrub", Whian Whian State Forest, on soils developed from basalt. This specimen has rather pubescent stems and blackish dry leaves, and in these characters approaches the related species *D. melasmena* which is common in the "Red Scrub". It may represent a hybrid between the two species (see interspecific relationships under *Daphnandra*, and below).

Phenology

Flowering and fruiting appears to be seasonally regular. Flower bud expansion and flower opening occurs between March and June in the austral autumn and early winter, flower maturation and initial enlargement of the fruiting hypanthia during winter and early spring between June and August, and fruiting hypanthium maturation and dehiscence between December and March in summer. Flower buds and mature flowers were never found together with near mature fruiting hypanthia on any collection of. *Daphnandra repandula*.

Infraspecific Variation

There appears to be little morphological variation within *Daphnandra tenuipes*, as might be expected from its confined geographic range. Some variation was observed ~~occurs~~ in the shape, size, texture, and colour of the dry leaves, and the density of pubescence on the ultimate stems, petioles, and young leaf blades. This appears to be subject largely to the age of the tree (whether a sapling or ± mature) and the position on the tree (whether exposed or shaded) from which the collected branchlets came. But some of the differences in the presence and density of pubescence, such as between the glabrous stems of Schodde 3567 and Tracey 2450, and the somewhat hispid ultimate stems of Betche: NSW 67922 and Hayes 1.xii.1952: COFFS, and in the colour of dry leaves, such as between the olive-green leaves of Schodde 3570 and the blackish leaves of Jones 467 on the more exposed branchlets of ± mature trees, indicate not only a degree of genetic diversity but also the possibility that there is some introgression between this species and D. melasmena.

The mature fruiting hypanthia vary rather markedly from frequently ampulliform or obpyriform (Hayes 1.xii.1952: COFFS) to less frequently oblong-urceolate (Tracey 2450). They are nevertheless so often distorted by insect infestation, as shown by Constable: NSW 22195, that the significance of these differences are difficult to assess. The infestation appears to be of the kind found in D. johnsonii.

It is noteworthy that the ultimate branchlet stems and leaves of saplings and shaded branchlets are usually more pubescent than their counterparts on exposed parts of mature trees. This contrasts with the development and pattern of stem and leaf pubescence in some other species of the genus, for example, D. apatela and D. repandula, and all other genera of the family.

Taxonomic Notes

Despite the opinion expressed by Anderson (1956) that Daphnandra tenuipes is not distinct from D. micrantha*, it differs from the latter and all other species in the genus in a number of small but well-marked characters. These have been pointed out by Maiden and Betche (1903) and Maiden (1921), and reiterated above.

The alkaloids of D. tenuipes appear to differ partly in kind and largely in proportion from those found in other species of Daphnandra. They comprise repanduline and laevoratary tenuipine as major alkaloids,

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* = D. apatela, not D. micrantha.

and aromoline and laevorotary nortenuipine (de-N-methyl-tenuipine) as minor alkaloids.

Chemistry

The alkaloids of Daphnandra tenuipes have been examined in detail by Bick, Taylor, and Todd (1953), and Bick et al. (1963), and reviewed by Kulka in Manske (1960). As the alkaloids ascribed to this species from material collected from the Oakes State Forest (Bick et al. 1963) belong to D. melasmena, only the alkaloids extracted from verified material of D. tenuipes from Whian Whian State Forest are discussed here. Bick, Taylor, and Todd (l.c.) found that the two major alkaloids present in the bark were repanduline, which is described under D. repandula, and tenuipine in a laevorotary form. Tenuipine is a colourless alkaloid with the formula $C_{38}H_{40}O_7N_2$, and contains three methoxy- and two methylimino-groups. Very small amounts of aromoline were also isolated. This alkaloid occurs in larger quantities in Doryphora aromatica and its characteristics are treated under that species.

A further minor alkaloid, laevorotary nortenuipine, was found in the leaves (Bick, Taylor, and Todd l.c., Bick et al. 1963). It is a colourless base, has the formula $C_{37}H_{38}O_7N_2$, and apparently contains two methoxy-groups and one methylimino-group. It was called de-N-methyl-tenuipine by Bick, Taylor, and Todd (l.c.) and Kulka (l.c.).

Uses

No uses have been recorded.

4. Daphnandra melasmena Schodde, sp.nov.

Daphnandra tenuipes auct. [non Perk.]: Bick, Harley-Mason, & Vernengo, Anal.Asoc.Quim.Argentina 5(1963)135 p.p.

Arbor altitudinis mediae 10-20 m alta, cortex interior lignumque in vivo sulphureus, folia matura relative parva, (3-)4-8(-10) cm longa × ($1\frac{1}{4}$-)$1\frac{3}{4}$-3(-4) cm lata, in sicco plerumque olivaceo-vel fusco-nigrescentium, cum costis supra vadose impressis, raro usque ad planas, nervis gracilibus, et marginibus crenulatis, flores relative parvi, cum hypanthiis glabris, et tepalis interioribus ($2\frac{1}{2}$-)$2\frac{3}{4}$-3(-$3\frac{1}{2}$) mm longis, viridi-albis, ad margines subtiliter fimbriatis, et hypanthia fructificantia (cylindrico-)urceolata, (5-)9-20 mm longa × (1-)3-6(-$6\frac{1}{2}$) mm crassa, ad basim cum parietibus ligneis, ($\frac{1}{4}$-)$\frac{1}{2}$-$\frac{3}{4}$(-1) mm crassis. Ab omnibus speciebus Daphnandrae combinatione horum characterum differt.

TYPUS: R. Schodde (and H.C.Hayes) 3523, Vicnity of Forestry Hut, Oaks (= Oakes) State Forest —— holotypus in CANB (135436), isotypi in A, AD, B, CANB, CHR, COFFS, G, K, L, NSW, WELT.

Figure 13.

Diagnosis

Average tree height 10-20 m; inner bark deep sulphureous or greenish yellow; ultimate branchlet stems sparsely to densely ± hispidulous; petioles straight, 2-4(-5) mm long; crown leaf blades lanceate, less often narrowly elliptic or ovate, (3-)4-8(-10) cm long × ($1\frac{1}{4}$-)$1\frac{3}{4}$-3 (-4) cm broad, ± thinly coriaceous, drying blackish or olive-black, sometimes dark olive-brown, with margins ± crenulate, midrib shallowly impressed to almost planate on upper face, ascending nerves finely lined on upper face, ± sparsely strigillose on lower face.

Inflorescences borne among and below persisting leaves, ± congestedly thyrsiform, (1½-)2-3½(-4) cm long, sparsely strigillose to almost glabrous, bearing (11-)15-27(-41) flowers; pedicels 1-3 mm long.

Open flowers with hypanthium glabrous; perianth pale greenish white, (10-)11-12(-13)-partite, the inner tepals (2½-)2¾-3(-3½) mm long × (1-)1¼-1¾(-2) mm broad,with conspicuously fimbriolate margins; androecium of 5(-6) stamens (1-)1-1⅓(-1½) mm long,and 5-7(-8) staminodes, the outer staminodes without vestiges of staminal glands; gynoecium of (4-)6-8(-10) carpels, the stigmatic column of apparently free, obtuse filaments, exserted to apices of stamens.

Ripe infructescences borne usually well below persisting leaves, (2-)2½-5(-5½) cm long; pedicels (2-)3-6(-9) mm long, hardly expanded under fruiting hypanthia; fruiting hypanthium (cylindrical-)urceolate, rarely broadly urceolate, (5-)9-20 mm long × (1-)3-6(-6½) mm thick, lignified, with walls (¼-)½-¾(-1) mm thick; hairs on ripe nutlet bodies (6-)8-10 mm long; styles of ripe nutlets (5-)6-10(-13) mm long.

Detailed Description

Medium-sized trees 10-20 m high, young trees in open sites often flowering when 3-5 m high; bole ca 15-30 cm diameter breast height, rarely coppicing, sometimes suckering spontaneously; crown umbrageous-corymbiform to ± cylindrical, shorter than or sometimes as long as or longer than bole, the leaves ± horizontal. Bark 3-4 mm thick when dry, outer surface finely pustuled to striate or finely cracked, pale to mid grey-brown, inside deep sulphureous or greenish yellow, drying dirty brown-black or blackish. Wood pale yellow or cream-yellow in sapwood, brighter, rather intensely yellow in heartwood, similarly coloured when dry. Branchlet stems ± closely branched, the ultimate 4-6 internodes (1-)$1\frac{1}{2}$-5(-7) cm long × 2-4(-5) mm thick on leader stems, 1-$2\frac{1}{2}$(-3) mm thick on lateral stems, often pale grey pustuled below, drying invariably black, sometimes tinted olive, sparsely to densely hispidulous or hispidulous-strigillose, the vesture denser and paler on penultimate internodes, longer strigose on leader stems; shaded and sapling branchlet stems with ultimate 4-6 internodes (1-)2-6(-8) cm long, not slenderer, usually more extensively and densely hispid. Petioles straight, divergent, 2-4(-5) mm long × ($\frac{1}{2}$-)$\frac{3}{4}$-1(-$1\frac{1}{2}$) mm thick, drying black, rather densely or uniformly hispid, rarely glabrescent, often more densely pubescent on shaded and sapling branchlets. Leaf blades lanceate, less often narrowly elliptic or ovate, (3-)4-8(-10) cm long × ($1\frac{1}{4}$-)$1\frac{3}{4}$-3(-4) cm broad, obtuse, infrequently widely cuneate at the base, shortly mucronate obtuse, rarely acuminate or acute at the apex; margins crenulate, infrequently serrulate or crenate; texture thinly coriaceous to almost chartaceous, the upper face sometimes finely lined with obscurely prominulous nerves and vein reticulum; colour glossy dark green on upper face, dull or duller and paler on lower, paler bright green in shoot leaves, in dry leaves dull to sometimes nitid blackish or olive-black, infrequently dark olive-brown on upper face, dull and rather paler on lower; nervation with midrib shallowly impressed to almost planate on upper face, on lower with (4-)5-6(-8) slenderly prominulous main nerves ascending from the midrib, the vein reticulum usually a little less prominulous than the nerves; usually very sparsely off-white to sordid stramineous strigillose on lower face, rarely quite glabrous, the hairs usually denser, more hispid on midrib and nerves towards base of blade; leaf blades on shaded and sapling branchlets hardly larger, with crenulate-denticulate margins, prominulous nervation, and pubescence as in crown leaves. Bark, stems, and leaves very faintly aromatic, with an obscure astringent or stale odour when crushed.

Inflorescences borne at ultimate 1-6 leaf nodes among and below persisting leaves, ± congestedly thyrsiform, ($1\frac{1}{2}$-)2-$3\frac{1}{2}$(-4) cm long, sparsely sordid white strigillose to almost entirely glabrous, bearing (11-)15-27(-41) flowers. Primary peduncles (1-)$1\frac{1}{2}$-3 cm long, the base internode $\frac{2}{3}$ - $\frac{3}{4}$(-1) mm thick, the distal internodes hardly tetragonous, glabrous or sparsely sordid white strigillose, with hairs ± densest on base internode, 3-5(-6)-noded, with ± all subterminal nodes bearing secondary peduncles; accessory axillary flowers occasional, solitary; bracts of primary peduncle 1-$1\frac{3}{4}$ mm long × ± $\frac{1}{2}$ mm broad, longest and narrowest at base nodes, sparsely, sometimes densely sordid white strigillose abaxially, the hairs often confined to the midrib, glabrous adaxially; secondary peduncles ($\frac{1}{2}$-)$\frac{3}{4}$-1 cm long, more slender and sparsely strigillose than primary peduncle, 1-3-noded; bracts of secondary peduncle $\frac{3}{4}$-1 mm long, broader than those on primary peduncle, more sparsely haired to almost glabrous; pedicels 1-3 mm long × $\frac{1}{4}$ mm thick, slightly expanded under hypanthium, glabrous, rarely sparsely strigillose, Mature flower buds 1-$1\frac{1}{2}$ mm long × 1-$1\frac{1}{2}$ mm thick, glabrous except for sparsely sordid white bearded outer perianth bracteoles.

Open flowers. Hypanthium 1-$1\frac{1}{2}$ mm long × $\frac{3}{4}$-1 mm thick, glabrous, occasionally bearing outer pair of perianth bracteoles below rim, rarely to near base; rim ± flat, ± $\frac{1}{3}$ mm broad. Perianth apparently pale greenish white, (10-)11-12(-13)-partite in 3-4 whorls, the outer 2(-3) whorls of ± opposite bracteoles, the inner 1(-2) whorls comprising (4-)6-7(-8) tepals; outer pair of perianth bracteoles ovate-deltate, 1-$1\frac{1}{2}$ mm long × ($\frac{3}{4}$-)1(-$1\frac{1}{4}$) mm broad, bearded abaxially towards the apex with fine sordid whitish strigillose hairs; inner 1(-2) pairs of perianth bracteoles circular to elliptic, ($1\frac{1}{4}$-)$1\frac{1}{2}$-2(-$2\frac{1}{2}$) mm long × (1-)$1\frac{1}{4}$-2 mm broad, with entire to obscurely fimbriolate margins, generally glabrous, infrequently sparsely strigillose abaxially towards the apex; tepals lanceate to ovate, rarely broadly ovate, ($2\frac{1}{2}$-)$2\frac{3}{4}$-3(-$3\frac{1}{2}$) mm long × (1-)$1\frac{1}{4}$-$1\frac{3}{4}$(-2) mm broad, with conspicuously fimbriolate margins, conspicuously 5-nerved with obscure vein reticulum. Androecium pale whitish green, 2(-3)-seriate; 5(-6) stamens (1-)$1\frac{1}{4}$-$1\frac{1}{3}$(-$1\frac{1}{2}$) mm long × $\frac{3}{4}$-1 mm broad × $\frac{1}{3}$ - $\frac{1}{2}$ mm thick, very rarely one partly aborted; filaments broad and short, ($\frac{1}{2}$-)$\frac{2}{3}$(-$\frac{3}{4}$) mm long below staminal glands × $\frac{3}{4}$-1 mm broad × ± $\frac{1}{4}$ mm thick, usually sparsely strigillose adaxially; staminal glands depressed elliptic,peltate, ($\frac{1}{4}$-)$\frac{1}{3}$ mm long × $\frac{1}{3}$ - $\frac{1}{2}$ mm broad; anthers compressed, depressed cubical, $\frac{1}{2}$ - $\frac{2}{3}$ mm long × ± $\frac{3}{4}$ mm broad × $\frac{1}{3}$ mm thick; 5-7(-8) staminodes broadly to narrowly oblong-cylindrical, sometimes narrowly spathulate-batilliform, ($\frac{2}{3}$ -)$\frac{3}{4}$(-1) mm long × $\frac{1}{3}$ - $\frac{1}{2}$ mm thick, the base thick, almost swollen, sparsely haired to glabrous abaxially, densely strigillose adaxially, without vestiges of staminal glands. Gynoecium of (4-)6-8(-10) carpels; styles exserted $1\frac{1}{4}$-$1\frac{1}{2}$ mm beyond hypanthium rim in a cylindrical column ca $\frac{1}{2}$ - $\frac{2}{3}$ mm thick to apices of stamens; stigmatic column of apparently free, obtuse filaments, [illegible] exserted to apices of stamens.

Ripe infructescences borne at ultimate (4-)5-12 leaf nodes usually well below leaves on branchlets, (2-)$2\frac{1}{2}$-5(-$5\frac{1}{2}$) cm long, sparsely strigillose to entirely glabrescent. Primary peduncles 1-$1\frac{1}{2}$ mm thick at base internode, of the same length and form as in inflorescence, with vesture persistent only on base internode; secondary peduncles ($\frac{1}{2}$-)$\frac{2}{3}$ - 1 (-$1\frac{1}{2}$) cm long, of the same form as in inflorescence, quite glabrescent; pedicels (2-)3-6(-9) mm long, of the same form as in inflorescence, hardly expanded under fruiting hypanthia, glabrescent. Fruiting hypanthium (cylindrical-) urceolate, rarely broadly urceolate, (5-)9-20 mm long × (1-)3-6(-$6\frac{1}{2}$) mm thick, narrowed into a neck ca ($\frac{1}{4}$-)$\frac{1}{3}$ - $\frac{1}{2}$ × length of hypanthium, levigate often faintly striate, rather glossy light to dark green, glabrous, lignified, with walls ($\frac{1}{4}$-)$\frac{1}{2}$-$\frac{3}{4}$(-1) mm thick; hypanthium chamber narrowly rounded at the base, densely short sordid off-white to stramineous hispid immediately below the rim, sparsely hirsute on the neck, denser long sordid stramineous to pale brown hirsute towards the base among nutlets. Nutlets elongating in maturing hypanthium to maintain the essertion of the style apices up to $\frac{1}{2}$ mm beyond the hypanthium rim; bodies of ripe nutlets ellipsoid, (4-)5-6 mm long x ± 2 mm thick, the hairs (6-)8-10 mm long; styles of ripe nutlets (5-)6-10(-13) mm long, hardly expanded at base into body of nutlet, the apical $\frac{1}{2}$-1 mm glabrous.

15-25-noded young plants ca 100 cm high, the ultimate 4-6 internodes compressed somewhat tetragonous, 2-11 cm long x 1$\frac{1}{2}$-2 mm thick on leader stems, slenderer on lateral stems, smooth, drying black, rather densely sordid white hispid-strigose, more sparsely haired below, ultimately glabrescent, the nodes (on leader stems) broadly compressed, finely pusticulate about the base of lateral branchlets; cotyledons caducous; subsequent leaf pairs with petioles 2-3(-4) mm long x 1-1$\frac{1}{2}$ mm thick, rather densely hispid-strigose, and leaf blades lanceate to broadly ovate, 3-9 cm long x (1$\frac{1}{2}$-)2-5 cm broad, with obtuse to almost cordate bases, shortly narrowed to acuminately acute or mucronate obtuse apices, crenate to crenulate, almost planate margins, chartaceous texture, slightly glossy mid green colour on upper face, drying generally blackish, shallowly impressed midrib on upper face, finely prominulous nerves and vein reticulum on both faces, generally glabrous on upper face, with sparse sordid hispid hairs confined to base of midrib, on lower sparsely hispid-strigose, with denser, longer hairs.

The epithet *melasmena* is derived from μεμελασμενα , meaning the state of having been made black, and alludes to the marked blackening of the stems and leaves of this species when dried. Mature trees growing in their usual habitat within tall rainforest also appear relatively dark in the field.

Vernacular names: none recorded.

Series of specimens examined: 11 collections, comprising 4 with enlarged inflorescence and flower buds, 3 with open flowers, 4 with near or fully mature fruiting hypanthia, and 1 of a young plant.

Geographic Distribution (map 10)

Daphnandra melasmena is disjunct and confined to the Nightcap range - Lismore district, 28°30′-50′S, and Taylors Arm - Bellingen district, north-east New South Wales, 30°25′-35′S:

South-west of Mullimbimby; Red Scrub, Whian Whian State Forest; Tintenbar; Wollongbar; Bellinger river, Bellinger valley district; Oakes State Forest.

Ecology (figure 56)

Singly or in loose colonies, *Daphnandra melasmena* is not uncommon where it occurs as a medium-sized tree in the midstage of tall rainforest, between the altitudes of (10-)50-600 m. It is found more frequently within ± primary forest than on forest margins*. It appears to be con-

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* Only saplings have been recorded on forest margins and in regrowth on cleared land.

fined entirely to the deep red soils developed from basalt in the Lismore district, as for example in the "Red Scrub" at Whian Whian State Forest, between the altitudes of 50 and 200 m. In the Bellinger valley district, it has been recorded in regrowth on the rich alluvium of the river valley at 10 m altitude, and in tall rainforest on soils developed from mixed sedimentary rocks and volcanics (Atlas of Australian Resources, Geology, 1966) on a well-drained ridge in the Oakes State Forest at ca 600 m s.m.

Phenology

Flowering and fruiting is apparently seasonally regular. Inflorescences develop and enlarge during the austral autumn and winter, flower bud expansion and opening and flower maturation occur in spring between August and October, and maturation and dehiscence of the fruiting hypanthium takes place during the following autumn and early winter, up until June or July. A single collection (Schodde 3523) with expanding flower buds and flowers in May is in all likelihood anomalous,because the tree from which it came was the only one flowering in about ten mature trees examined at the collection site; the remainder were either in very young inflorescence bud or sterile.

Infraspecific Variation

Although Daphnandra melasmena appears to be a rather polymorphic species, all except one of its varying characters seem to reflect merely differences in the ages of the trees collected or the habitat in which they grew; none exhibit discernible geographic trends. The pubescence on the ultimate branchlets,for example,is usually denser in saplings than in mature trees, as in Daphnandra tenuipes.

The one character that would seem unlikely to be much affected by tree age or habitat is the form of the fruiting hypanthium. It varies from narrowly (cylindrical-)urceolate and 10-20 mm long × 5-6½ mm thick (Schodde 3574) to more broadly urceolate and 9-15 mm long × 4-6 mm thick (Schodde 3575). The collections exhibiting these differences are from adjacent localities in the Lismore district. The former was taken from a small tree in an open field, and it may not be coincidental that all other collections of this species with relatively long slender fruiting hypanthia come from trees growing in similarly exposed positions.

Taxonomic Notes

It has been mentioned above under the genus Daphnandra and D. tenuipes that introgression may occur between this species and D. tenuipes on the one hand, and D. apatela on the other.

The only reference to this species in the literature has been by the chemists Bick, Harley-Mason, and Vernengo in 1963 when describing its alkaloids from material collected in the Oakes State Forest. They recorded it as Daphnandra tenuipes. In the material, they could find no repanduline which is a major alkaloid of D. tenuipes, while tenuipine and nortenuipine were both present in unique dextro-rotary stereoisomeric forms.

Chemistry

So far, only the major alkaloids tenuipine and nortenuipine in dextro-rotary form have been recorded from the bark of D. melasmena (Bick et al.

1963). The formulae and characteristics of these alkaloids are described under D. tenuipes.

Uses

No uses have been recorded.

5. Daphnandra johnsonii Schodde, sp.nov.

Daphnandra micrantha auctt. [non Perk.]: Anderson, Trees N.S.Wales ed.3,(1956)223 p.p.; Evans in Beadle, Evans, & Carolin, Handb. Vasc.Pl.Sydney & Blue Mts. (1963)130.

Arbor parva usque ad altitudinem mediam, (2-)5-20 m alta, cortex interior in vivo sulphureus, folia matura relative parva, (4-)5-8(-12) cm longa × (1½-)2-4(-6) cm lata, rectinervia, in sicco plerumque subcinerascenti- vel subinfuscato-viridia, cum costis supra peranguste prominulis, raro ad planas, et marginibus profunde grosseque crenato-serratis, flores relative parvi, cum hypanthiis parce strigillosis, et tepalis interioribus 2½-3 mm longis, viridi-albis, ad margines integris, et hypanthia fructificantia globosa, (4-)5-7(-8) mm longa × (3-)4-5(-6) mm crassa, cum parietibus tenuiter ligneis, $\frac{1}{4}$ - $\frac{1}{3}$ mm crassis, et nuculis parvis, pilis brevibus, et stylis 2½-3 mm longis. Ab omnibus speciebus Daphnandrae combinatione horum characterum differt.

TYPUS: H.C.Hayes, L.A.S.Johnson, and E.F.Constable, Spring Creek, 1 mile west of Kiama, 7 Sept. 1960: holotypus in CANB (157257) (leg. Hayes; Johnson, and Constable), isotypi in COFFS (leg. Hayes), L (leg. Johnson and Constable), NSW (leg. Johnson and Constable).

Figures 14, 22, 46C2, 46D.

Diagnosis

Average tree height 5-20 m; inner bark deep sulphureous yellow; ultimate branchlet stems generally glabrous, the penultimate internodes sometimes sparsely hispid-strigose; petioles straight, (3-)4-6(-7) mm long; crown leaf blades ± elliptic to ovate, (4-)5-8(-12) cm long × ($1\frac{1}{2}$-)2-4(-6) cm broad, ± coriaceous, drying pale greyish green, with margins deeply and distantly coarsely crenate-serrate, midrib planate to slenderly prominulous on upper face, ± straight nerves prominently lined on upper face, generally glabrous,or occasional hairs confined to base of midrib on lower face.

Inflorescences borne among persisting leaves, ± congestedly thyrsiform, $2\frac{1}{2}$-4 cm long, generally glabrous, bearing (3-)7-13(-25) flowers; pedicels 3-5 mm long.

Open flowers with hypanthium sparsely strigillose; perianth pale greenish white, 11-12-partite, the inner tepals $2\frac{1}{2}$-3 mm long ×($\frac{3}{4}$-)1-$1\frac{1}{2}$ mm broad, with entire margins; androecium of 5(-6) stamens 1-$1\frac{1}{4}$(-$1\frac{1}{3}$) mm long,and 5-10 staminodes, the outer staminodes without vestiges of staminal glands; gynoecium of (3-)4-8 carpels, the stigmatic column of apparently free, obtuse filaments, exserted to apices of stamens.

Ripe infructescences borne usually among persisting leaves, (2-)3-4 cm long; pedicels (4-)5-8(-10) mm long, hardly expanded under fruiting hypanthia; fruiting hypanthium globose to ellipsoid-globose, (4-)5-7(-8) mm long × (3-)4-5(-6) mm thick, thinly lignified, with walls $\frac{1}{4}$ - $\frac{1}{3}$ mm thick; hairs on ripe nutlet bodies 2-3 mm long; styles of ripe nutlets $2\frac{1}{2}$-3 mm long.

Detailed Description

Small to medium-sized trees (2-)5-20 m high; bole ca 5-20 cm diameter breast height, coppicing, sometimes suckering spontaneously; crown umbrageous, loosely corymbiform to broadly cylindrical, much shorter than to sometimes as long as bole, the leaves ± horizontal. Bark 3-4 mm thick when dry, outer surface smooth or slightly roughened with fine pustules, mid grey, inside deep sulphureous yellow, drying browner. Wood not examined*. Branchlet stems closely to ± loosely branched, the ultimate 4-6 internodes (1-)2-4(-4½) cm long × 2(-4) mm thick on leader stems, 1-1½ mm thick on lateral stems, occasionally sparsely grey-white pustuled below, drying pale to olive grey, generally glabrous, the penultimate internodes sometimes very sparsely hispid-strigose; shaded and sapling branchlet stems with ultimate 4-6 internodes up to 5½ cm long × (1-)1½-2(-2½) mm thick, drying blackish, generally glabrous. Petioles straight, divergent, (3-)4-6(-7) mm long × (¾-)1-1¼(-1½) mm thick, drying dark brown to black, glabrous, or sometimes sparsely hispidulous-strigillose on younger petioles. Leaf blades variously elliptic to ovate, very rarely obovate, (4-)5-8(-12) cm long × (1½-)2-4(-6) cm broad, broadly or narrowly cuneate at the base, shortly and narrowly acuminately mucronate obtuse, rarely quite acute, at the

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* To collect one adequate wood sample for study would have required the destruction, or gross disfiguration leading to possible death, of one of the few known surviving trees of this rare species.

apex; margins very deeply and distantly coarsely crenate-serrate; texture thinly to quite coriaceous, the upper face conspicuously lined with ± prominent nerves, infrequently vein reticulum; colour dull to very glossy dark green on upper face, paler but glossy on lower, in dry leaves pale greyish or brownish green on upper face, usually browner on lower; nervation with midrib planate to very slenderly prominulous on upper face, on lower with (4-)6-8(-10) slender but distinctly prominent main nerves ± straight and diverging widely from the midrib, the vein reticulum almost as conspicuously prominent as nerves; generally glabrous, rarely with a few hispid-strigose hairs at base of midrib on lower face of younger leaves; leaf blades on shaded and sapling branchlets larger and broader, with somewhat incurving cuneate bases, more closely crenate-serrate, less recurved margins, almost chartaceous to thinly coriaceous, nerves and vein reticulum more prominent on upper face, ± glabrous. Bark without odour, fresh stems and leaves very weakly aromatic.

Inflorescences borne at ultimate 1-3 leaf nodes among persisting leaves, ± congestedly thyrsiform, $2\frac{1}{2}$-4 cm long, generally glabrous, bearing (3-)5-13(-25) flowers. Primary peduncles 1-3 cm long, the base internode ($\frac{2}{3}$ -)$\frac{3}{4}$-1 mm thick, the distal internodes often tetragonous, generally glabrous or nodes sometimes very sparsely strigillose, (1-)2-3 (-4)-noded, with subterminal 1(-2) nodes usually single flowered; accessory axillary flowers frequent, solitary; bracts of primary peduncle 1-2 mm long × $\frac{2}{3}$ mm broad, sparsely strigillose abaxially, glabrous adaxially, occasionally foliose up to 4 cm long; secondary peduncles

$\frac{1}{2}$-$1\frac{1}{2}$ cm long, glabrous or occasionally very sparingly strigillose, 1-2-noded; bracts of secondary peduncle usually more ovate, shorter, and broader than those on primary peduncle; pedicels 3-5 mm long × $\frac{1}{3}$ mm thick, terete or slightly compressed, sometimes gradually expanded under hypanthium, sparsely strigillose. Mature flower buds $1\frac{1}{2}$-$1\frac{3}{4}$ mm long × $1\frac{1}{2}$-$1\frac{3}{4}$ mm thick, uniformly sparsely whitish strigillose, the vesture often densest on the abaxial midnerve of the outer pair of perianth bracteoles.

Open flowers. Hypanthium 1 mm long × $1\frac{1}{2}$ mm thick, rather sparsely sordid white strigillose, occasionally bearing outer pair of perianth bracteoles a little below rim; rim ± flat, $\frac{1}{3}$ mm broad. Perianth pale greenish white, 11-12-partite in 3(-4) whorls, the outer 2 whorls of opposite, rarely three, bracteoles, the inner 1 (-2) whorls comprising 7-8 tepals; outer pair of perianth bracteoles ovate-deltate to depressed ovate, 1-$1\frac{1}{2}$ mm long × 1-$1\frac{1}{2}$ mm broad, usually sparsely strigillose abaxially, the hairs sometimes confined to the mid nerve; inner perianth bracteoles circular to circular-elliptic, 2-$2\frac{1}{4}$ mm long × $1\frac{1}{2}$-2 mm broad, with entire margins, sparsely strigillose abaxially; tepals lanceate to elliptic, $2\frac{1}{2}$-3 mm long × ($\frac{3}{4}$-)1-$1\frac{1}{2}$ mm broad, rather thick, with entire margins, obscurely 3-nerved. Androecium pale green, 2-3-seriate; 5(-6) stamens 1-$1\frac{1}{4}$(-$1\frac{1}{3}$) mm long × $\frac{3}{4}$-1 mm broad × $\frac{1}{4}$ - $\frac{1}{3}$ mm thick, rarely partly aborted; filaments broad and short, $\frac{1}{4}$-$\frac{1}{2}$ mm long below staminal glands × $\frac{2}{3}$(-$\frac{3}{4}$) mm broad, usually sparsely strigillose adaxially; staminal glands depressed elliptic,peltate, $\frac{1}{3}$ mm long × $\frac{1}{2}$ mm broad; anthers compressed, depressed cubical, $\frac{1}{2}$ mm long × $\frac{2}{3}$ - $\frac{3}{4}$ mm broad; 5-10 staminodes often enveloped in pubescence of hypanthium rim, oblong-cylindrical, rarely squat batilliform, $\frac{2}{3}$ - $\frac{3}{4}$ mm long × $\frac{1}{4}$ mm thick, the base markedly thicker than apex, glabrous, rarely very sparsely strigillose abaxially, densely strigillose adaxially, without vestiges of staminal glands. Gynoecium of (3-)4-8 carpels*; styles exserted 1-1$\frac{1}{4}$ mm beyond hypanthium rim in a cylindrical-conical column; stigmatic column of apparently free, obtuse filaments, ca $\frac{1}{4}$-$\frac{1}{2}$ mm long, exserted to apices of stamens.

Ripe infructescences borne at ultimate 2-5 leaf nodes among leaves on branchlets, (2-)3-4 cm long, glabrescent, rarely very sparsely strigose in parts. Primary peduncles ($\frac{1}{2}$-)1$\frac{1}{2}$-3(-4) cm long, of the same thickness and form as in inflorescence, usually completely glabrescent; secondary peduncles of the same dimensions and form as in inflorescence, completely glabrescent; pedicels (4-)5-8(-10) mm long, of the same form as in inflorescence, hardly expanded under fruiting hypanthia, quite glabrescent. Fruiting hypanthium globose to ellipsoid-globose, (4-)5-7(-8) mm long × (3-)4-5(-6) mm thick, contracted at the rim or a little below into a short obscure neck, levigate, glabrescent with occasional hairs persisting, thinly lignified, with walls $\frac{1}{4}$ - $\frac{1}{3}$ mm thick; hypanthium chamber broadly rounded at the base, hispid or often almost glabrous below the rim, coarsely sordid brown hispid-hirsute with rather curling or crisped hairs**

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* The number of carpels and their form has, as a rule, been affected severely by insect infestation and gall formation in all specimens examined.

** Variations brought about by insect infestation.

towards the base among nutlets. Nutlets* elongating in maturing hypanthium to maintain the exsertion of the style apices beyond the rim as in flower, often partly to completely immersed in several or single large expanded masses of tissue** covered completely by short, sordid brown, crisped or curled hairs ca 1-2 mm long; bodies of ripe nutlets ellipsoid, relative small, 2 mm long × $\frac{3}{4}$-1 mm thick, the straight or curled hairs 2-3 mm long; styles of ripe nutlets relatively short, $2\frac{1}{2}$-3 mm long, somewhat expanded at base into body of nutlet, the apical ± $\frac{1}{2}$-1 mm glandular-hispidulous.

10-20-noded young plants ca 50-80 cm high, the ultimate 4-6 internodes strongly compressed, hardly tetragonous, 8-13 cm long × 2-3 mm thick on leader stems, $1\frac{1}{2}$-$2\frac{1}{2}$ mm thick on lateral stems, smoothly striate, drying blackish, glabrous or sparsely stramineous strigillose about ultimate internodes, the nodes on leader stems broadly compressed, up to 1 cm broad; cotyledons caducous; subsequent leaf pairs with petioles 4-7 mm long × ± 1 mm thick, very sparsely strigillose, early glabrescent, and leaf blades ovate, 5-7 cm long × $2\frac{1}{4}$-4 cm broad, with broadly obtuse, rarely cuneate bases, acuminate mucronate acute apices, crenate-serrate, rather planate margins, quite chartaceous texture, dull dark green colour on upper face, drying blackish, planate or hardly prominulous midrib on upper face, conspicuously prominulous nerves and vein reticulum on both faces, as in leaves of mature trees, early glabrescent, the early leaves with midribs sordid stramineous strigillose.

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* Partly unaffected by insect infestation only in McBarron 12959 in the series examined, and described from that collection.

** Galls, or the result of insect infestation.

The species is named after Mr. L.A.S.Johnson, senior botanist at the National Herbarium of New South Wales and one of the collectors of the type, whose interest in the taxonomy of the genus Daphnandra is revealed by many detailed notes on interspecific relationships on relevant collections held in the National Herbarium of New South Wales*.

Vernacular names: none recorded.

Series of specimens examined: 7 collections, comprising 1 with both flower buds and open flowers, 4 with near or fully mature fruiting hypanthia, and 1 of a young plant. Two of the collections were taken from the same tree at different dates (Schodde 5167 and 5183).

Geographic Distribution (map 10)

Daphnandra johnsonii is confined to the Illawarra district, central east New South Wales, and is so far known only from four localities in a small area between Kiama, Macquarie Pass, and Minnamurra Falls, 34°35′ - 40′S:

Yellow Rock creek, Albion Park; Spring creek, 1 mile west of Kiama; Kiama; Minnamurra Falls Reserve.

Ecology (figure 58)

Solitary or in loose colonies, D. johnsonii is a small subcanopy, rarely canopy, tree of the rainforest midstage or margins and secondary

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* In order to ratify the originality of my own treatment, it is necessary to point out that my own taxonomic conclusions on the species and their characters and inter-relationships are largely at variance with those reached by Johnson.

growth, between sea-level and 150 m altitude. Like other species such as *D. apatela* and *D. micrantha,* it prefers the rocky, well-drained, but permanently moist sites along the lower sides of gullies near creeks. Despite several recorded occurrences (Johnson and Constable: NSW 52310, Judd: NSW 67901, and Schodde 5167, 5183), it does not appear to favour forest margins or secondary growth, otherwise it might be expected to be more frequent and widespread than it is in such an extensively cleared district as the Illawarra. Its infrequent persistence in such sites, always adjacent to creeks, appears to reflect rather its limited ability to regenerate from suckers after forest clearing.

It has only been recorded from soil developed on basalt (Johnson and Constable: NSW 52310, Schodde 3475).

Phenology

The dates on the single flowering and several fruiting collections available are merely sufficient to indicate that flowering and fruiting apparently occur successively in austral spring and summer months.

Infraspecific Variation

Even though the series of collections examined is too small to permit generalisations on variability, the species appears to be morphologically rather uniform.

Taxonomic Notes and Typification

Daphnandra johnsonii is a very rare species. Until 1953 apparently only a single specimen had been collected, by W.H.Harvey from Kiama in

1856, so that neither lack of reference to it in the literature nor lack of recognition of its very distinctive characters is surprising. Both Anderson (1956) and Evans (1963), the only authors to have treated it previously, have maintained it in *Daphnandra micrantha*, which was then confused with *D. apatela*.

Although the collectors' names differ on the labels of the type collection in various herbaria, as indicated in the type citation above, L.A.S.Johnson (pers.comm.) has affirmed that all three collectors (Johnson, Constable, and Hayes) were present together to take flowering specimens from the same tree on the same date. The sheet in herb. CANB, though not as ample in material as those in some other herbaria, carries the most complete collection data on its label, and has therefore been designated the holotype.

Galls and Miscellaneous Observations

Galls occurred extensively in three out of the four available collections with mature fruit, and in the only collection with flowers. The infestation, which causes the carpels to concresce in large masses of callus tissue densely enveloped by short, brown, crisped hairs, appears to be of the same kind* in each. Larval cases of insects were observed in the gall tissue; they have not been identified. It is at least as

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* Such an infestation of the carpels has not been recorded in other species of the genus, except *D. apatela* and *D. tenuipes*, in which it is rare.

likely as not that the disturbance of the local environment by farming will bring about an intensification of gall infestation on the few surviving trees of the species.

There can be no doubt that the survival of the species is seriously threatened. Only a dozen or so trees are presently known to occur in small remnants of disturbed gallery and gully rainforests in a confined area ca 50 miles square near Kiama in the southern Illawarra district, a region given over to dairy farming and almost entirely cleared of natural forest. All of these trees, except for the three or four in the small Minnamurra Falls Reserve, may be lost with little further encroachment on the surviving pockets of forest by pastoral interests. It has been mentioned that severely or regularly disturbed forest does not appear to be the preferred habitat of the species. Seedlings have been observed only in the Minnamurra Falls Reserve, though suckering has been recorded elsewhere.

Chemistry

No information has been published. Non-phenolic alkaloids isolated in a cursory examination of a small quantity of leaf and bark material (Schodde 3475) were tenuipine, nortenuipine, and two hitherto unknown alkaloids in <u>Daphnandra</u> (Bick, pers. comm.). The formulae and characteristics of tenuipine and nortenuipine are described under <u>D. tenuipes</u>.

Uses

No uses have been recorded.

6. *Daphnandra apatela* Schodde, sp.nov.

Daphnandra micrantha auctt.[non (Tul.)Benth.]: Benth., Fl.Austral. 5(1870)285 p.p.; F.Muell., Syst.Cens.Austral.Pl. 1(1882)3 p.p.; F.M.Bail., Synops.Queensl.Fl. (1883)422; C.Moore, Cens.Pl.N.S. Wales (1884)58 p.p.; F.M.Bail., Queensl.Woods (1886)65; Bancroft, J.Proc.Roy.Soc.N.S.Wales 20(1887)70; id., Proc.Roy.Soc.Queensl. 4(1887)16; F.M.Bail., Queensl.Woods (1888)95; Hobein, Bot.Jb. 10(1888)72 p.p.?; Maiden, Useful Nat.Pl.Austral. (1889)167,414; F.Muell., Sec.Syst.Cens.Austral.Pl. 1(1889)5 p.p.; Pax, Pflzfm. 3,2(1889)103 p.p.?; F.M.Bail., Cat.Pl.Queensl. (1890)39; Moore & Betche, Handb.Fl.N.S.Wales (1893)15; Solereder, Syst.Anat. Dicot. (1899) [transl. Boodle, Fritsch, & Scott 2(1908)701?]; F.M.Bail., Queensl.Fl. 4(1901)1295, 1296; Perk. & Gilg, Pflzr. 4(1901)75 p.p., f.20 H-K; Maiden & Betche, Proc.Linn.Soc.N.S. Wales 28(1903)911; Dixon, Pl.N.S.Wales (1906)31; Guilfoyle, Austral.Pl. (1911)130,462; Maiden, For.Fl.N.S.Wales 5(1911)51; Perk., Pflzr. 49(1911)44; Petrie, Proc.Linn.Soc.N.S.Wales 37(1912) 152; F.M.Bail., Compr.Cat.Queensl.Pl. (1913)430; Maiden & Betche, Cens.N.S.Wales Pl. (1916)80 p.p.?; Baker, Hardwoods Austral. (1919)332; Maiden, For.Fl.N.S.Wales 7(1921)368 p.p., f.259 A-G, pl.?; White & Francis, Queensl.Ag.J. (1922)230, f.52, 53; Perk., Gattung. Monim. (1925) f.36 H-K; Francis, Austral. Rain-For.Trees (1929)23,94,f.55,56; Welch, J.Proc.Roy.Soc.N.S. Wales 62(1929)354,363 et seq., f.3; Garratt, Trop.Woods 39(1934)19, 30,43,41, f.III.1, f.IV.1; Fraser & Vickery, Proc.Linn.Soc.N.S. Wales 63(1938)148,174, table 1; Hurst, Poison Pl.N.S.Wales (1942) 122; Bick & Whalley, Univ.Queensl.Pap. I,28(1946)1, I,33(1948)1; Bick & Todd, J.Chem.Soc. (1948)2170,2171; Webb, C.S.I.R.Bull. n.232(1948)109; Bick, Ewen & Todd, J.Chem.Soc. (1949)2767; H enry, Pl. Alkaloids ed.4,(1949)326; Bick & Todd, J.Chem.Soc. (1950)1606; Metcalfe & Chalk, Anat.Dicot. 2(1950)1142,1144, f.275D; Money, Bailey & Swamy, J.Arn.Arbor. 31(1950)392, f.II. 27-28; Francis, Austral.Rain-For.Trees ed.2,(1951)28,49,109,401, f.56,57; Bick, Taylor & Todd, J.Chem.Soc. (1953)695 et seq.; Kulka in Manske & Holmes, Alkaloids 4(1954)218,221,240; Anderson, Trees N.S.Wales ed.3,(1956)223 p.p.; Baur, Austral.J.Bot. 5(1957) 224; Kulka in Manske, Alkaloids 7(1960)443,452;Hutchinson,Gen.Fl. Pl.1(1964)112.

Atherosperma micranthum auctt.[non Tul.]: F.Muell., Pl.Colon.Vict. 1(1860)24 p.p.; [Benth., Fl.Austral. 5(1870)285 p.p. pro syn. *Daphnandrae micranthae*]; F.Muell., Fragm. 10(1877)106 p.p.?

Arbor altitudinis mediae (10-)15-25(-30) m alta, cortex interior lignumque in vivo luteo-eburneus vel luteolus, folia matura in sicco plerumque subgriseo-viridia, cum costis supra pallidis, peranguste prominulis, raro ad planas, et marginibus vadose crenato-serratis,raro ad crenulatas, flores relative parvi, cum hypanthiis subtiliter strigilloso-tomentosulis, et tepalis interioribus (2-)2½-3(-4) mm longis, viridi-albis, ad margines subtiliter fimbriatis, raro integris, et hypanthia fructificantia uroeolata vel raro subcylindrica, (7-)8-15(-20) mm longa × $(1\frac{1}{2}-)2-4(-6)$ mm crassa, ad basim cum parietibus ligneis, $(\frac{1}{4}-)\frac{1}{3} - \frac{2}{3}(-\frac{3}{4})$ mm crassis. Ab omnibus speciebus *Daphnandrae* combinatione horum characterum differt.

TYPUS: R.Schodde 5123, Clay road, Doyles River State Forest —— holotypus in CANB (168894), isotypi in A, AD, B, BH, BO, BRI, CANB, CHR, CONC, E, FI, G, K, L, LAE, MEL, NSW, P, PNH, PRE, SGO, SING, UC, US, W, WELT.

Figures 35, 37B.

Diagnosis

Average tree height 15-25 m; inner bark ± pale yellowish cream; ultimate branchlet stems sparsely to densely hispidulous-strigillose, rarely almost glabrous; petioles straight, (3-)5-8(-12) mm long; crown leaf blades narrowly to ± broadly lanceate, infrequently elliptic, $(2-)4\frac{1}{2}-10(-14)$ cm long × $(\frac{3}{4}-)1\frac{1}{2}-3\frac{1}{2}(-5\frac{1}{2})$ cm broad, ± coriaceous, drying ± pale grey-green, less often blackish, rarely olive, with margins closely crenate-serrate, midrib ± prominulous or lineate on upper face, ascending nerves ± obscurely lined on upper face, generally glabrous, or sparsely hispidulous-strigillose towards base of blade on lower face.

Inflorescences borne among, rarely below persisting leaves, ± congestedly thyrsiform, $(\frac{1}{2}-)1\frac{1}{2}-4\frac{1}{2}(-7\frac{1}{2})$ cm long, ± sparsely hispidulous-strigillose, bearing (3-)11-23(-35) flowers; pedicels $(\frac{1}{2}-)1\frac{1}{2}-4(-7)$ mm long.

Open flowers with hypanthium sparsely to densely strigillose; perianth pale green to whitish, (8-)10-11(-13)-partite, the inner tepals

(2-)$2\frac{1}{2}$-$3\frac{1}{2}$(-4) mm long x ($\frac{1}{2}$-)1-$1\frac{1}{2}$(-2) mm broad, with finely fimbriolate, rarely almost entire margins; androecium of (3-)4-5(-6) stamens ($\frac{2}{3}$ -)± 1 (-$1\frac{1}{4}$) mm long, and (3-)5-7(-9) staminodes, the outer staminodes without vestiges of staminal glands; gynoecium of (3-)4-6(-9) carpels, the stigmatic column narrowly obtuse or conical, exserted to near apices of stamens or slightly beyond.

Ripe infructescences borne usually among, occasionally below persisting leaves, ($1\frac{1}{2}$-)$2\frac{1}{2}$-5(-6) cm long; pedicels (2-)3-5(-9) mm long, ± conspicuously expanded under fruiting hypanthia; fruiting hypanthium slenderly, less often broadly urceolate, (7-)8-15(-20) mm long x ($1\frac{1}{2}$-)2-5 (-6) mm thick, lignified, with walls ($\frac{1}{4}$-)$\frac{1}{3}$ - $\frac{2}{3}$(-$\frac{3}{4}$) mm thick; hairs on ripe nutlet bodies (5-)7-8(-10) mm long; styles of ripe nutlets (4-)5-10 (-12) mm long.

Detailed Description

Medium-sized, sometimes tall trees (10-)15-25(-30)* m high, young trees in open sites often flowering when < 3 m high; bole ca (10-)20-60 (-70) cm diameter breast height, rarely coppicing and suckering spontaneously; crown corymbiform to slightly cylindrical, ca $\frac{1}{3}$ - $\frac{2}{3}$ x length of bole, rarely almost as long as bole, the leaves ± horizontal. Bark (2-)3-4(-5) mm thick when dry, outer surface either slightly roughened with fine pustules or finely flaking, pale to mid grey and grey-brown, often washed blackish, inside rather pale yellowish cream, rarely pure cream or more deeply yellow, drying pale to dirty brownish cream.

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*Up to 30 m high, according to White and Francis (1922), and Francis (1929, 1951).

Wood pale to rather deep yellowish cream or pale greyish, the yellow wash sometimes retained.* Branchlet stems ± closely branched, the ultimate 4-6 internodes ($\frac{3}{4}$-)1$\frac{1}{2}$-4$\frac{1}{2}$(-8)cm long x (2-)4-6(-7) mm thick on leader stems, 1-2$\frac{1}{2}$ mm thick on lateral stems, often coarsely striate and sparsely grey-fawn to off-white pustuled below, drying variously brown, olive-brown, olive-grey, or grey-fawn tinted yellowish or reddish, infrequently blackish, sparsely to densely hispidulous-strigillose, rarely almost glabrous, the vesture more extensive, denser, sometimes longer, and more strigose on penultimate internodes of leader stems; shaded and sapling branchlet stems with ultimate 4-6 internodes (1-)2-5$\frac{1}{2}$(-10) cm long, not slenderer, more sparsely pubescent or extensively glabrescent. Petioles straight, divergent, very rarely incurved towards the stem, (3-)5-8(-12) mm long x ($\frac{1}{2}$-)$\frac{3}{4}$-1(-1$\frac{3}{4}$) mm thick, drying pale yellow to olive-brown, infrequently dark brown or blackish, sparsely to rather densely hispidulous-strigillose, or variously glabrescent, rarely glabrous, hardly less pubescent on shaded and sapling branchlets. Leaf blades narrowly to broadly lanceate, infrequently elliptic, very rarely ± ovate, (2-)4$\frac{1}{2}$-10(-14) cm long x ($\frac{3}{4}$-)1$\frac{1}{2}$-3$\frac{1}{2}$(-5$\frac{1}{2}$) cm broad, narrowly, rarely broadly cuneate or obtuse,

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*According to wood samples: Pullen 3761, Schodde 3536, 5123. There is some confusion in the literature about the colour of presumably dry wood of this species. Bailey (1888, 1913) and Francis (1929, 1951) describe it as bright (glossy) yellow, Baker (1919) as pale canary, and Welch (1929) as greyish-yellow to yellow. Bailey (1886) earlier states that the dry wood is a greyish colour, and Maiden's observation (1889, p.414) that the wood is yellowish when fresh but becomes dirty looking "with age" is consistent with my own.

occasionally slightly oblique at the base, attenuately, often slightly acuminately mucronate obtuse to acute at the apex which is often curved away from the axis of the stem; margins conspicuously closely crenate-serrate; texture rather thinly to quite coriaceous, the upper face very finely or obscurely lined with prominulous nerves, rarely with vein reticulum; colour rather glossy mid to dark green on upper face, duller and paler on lower, brighter in shoot leaves, in dry leaves usually pale grey-green, less often blackish, rarely olive on upper face, similarly coloured or slightly darker on lower; nervation with midrib planate to usually prominulous, often lineate on upper face, rarely shallowly impressed towards the petiole, often drying pale cream-yellow to pale brown, on lower with (4-)5-7(-8) slender but conspicuously prominent main nerves ascending from the midrib, the vein reticulum usually more finely prominulous than nerves, sometimes obscure; generally glabrous, or very sparsely sordid off-white to brownish hispidulous-strigillose towards base of blade on lower face, eventually glabrescent, the hairs denser, more persistent on midribs of younger leaves; leaf blades on shaded and sapling branchlets more ovate, (3-)5-12(-14) cm long × (1¼-)2-4(-5½) cm broad, with shorter acuminate apices, broader cuneate bases, more deeply and extensively crenate-serrate, often less recurved margins, chartaceous to thinly coriaceous, often blackish when dry, nerves and vein reticulum usually more prominulous on both faces, usually more sparsely pubescent. Bark with a faint harsh or rather astringent odour, and stems and leaves often faintly and sweetly aromatic when crushed*, the odour usually evanescing in these parts when dried.

Inflorescences borne at ultimate (1-)2-6(-8) leaf nodes among, rarely below persisting leaves, ± congestedly thyrsiform, with the flowers often appearing clustered, $(\frac{1}{2}-)1\frac{1}{2}-4\frac{1}{2}(-7\frac{1}{2})$ cm long, sparsely, rarely densely off-white to grey-white or sordid stramineous hispidulous-strigillose, exceptionally ± glabrous, bearing (3-)11-23(-35) flowers. Primary peduncles $(\frac{2}{3}-)1\frac{1}{2}-3\frac{1}{2}(-6\frac{1}{2})$ cm long, the base internode $(\frac{2}{3}-)\frac{3}{4}-1$ mm thick, the distal internodes often tetragonous, usually sparsely off-white to dirty grey-green or sordid stramineous strigillose, rarely glabrescent, with hairs often densest on base internode, (1-)3-5(-6)-noded, with subterminal 1-2(-4) nodes usually single-flowered; accessory axillary flowers occasional, sometimes frequent, usually solitary; bracts of primary peduncle $(1\frac{1}{4}-)1\frac{1}{2}-2\frac{1}{2}(-3)$ mm long × $\frac{2}{3}-\frac{3}{4}$ mm broad at base nodes, $(\frac{3}{4}-)1-1\frac{1}{2}(-2)$ mm long × $\frac{2}{3}-\frac{3}{4}$ mm broad at distal nodes, uniformly sparsely to rather densely off-white to sordid pale grey hispidulous-strigillose abaxially, ± glabrous adaxially, very infrequently foliose up to $1\frac{1}{2}$ cm long, with serrate margins; secondary peduncles $(\frac{1}{4}-)\frac{1}{3}-1(-1\frac{1}{2})$ cm long, more slender, and either similarly to more sparsely strigillose or earlier

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* L.A.S.Johnson, ms. in herb.NSW, records that the leaves of this species are much more aromatic than those of *D. tenuipes*. This is not confirmed by my own experience of both species in the field. It is noteworthy that one collection of *D. apatela* (Schodde 5114) gave off a strong and persisting odour of liquorice after it had been dried.

glabrescent than primary peduncle, 1-2(-3)-noded; bracts of secondary peduncles usually more ovate-deltate than those on primary peduncle, $(\frac{1}{2}-)\frac{3}{4}-1(-2)$ mm long × $\frac{1}{2}-\frac{3}{4}$ mm broad; pedicels $(\frac{1}{2}-)$ 1-4(-7) mm long × $\frac{1}{4}-\frac{1}{3}$ mm thick, terete or slightly compressed, sometimes expanded under hypanthium, ± sparsely strigillose, sometimes completely glabrous. Mature flower buds $1-2(-2\frac{1}{2})$ mm long × $(\frac{3}{4}-)1-2$ mm thick, sordid whitish strigillose, rarely almost glabrous, the vesture usually densest on the hypanthium.

Open flowers. Hypanthium $(\frac{1}{2}-)\frac{3}{4}-1\frac{1}{3}(-1\frac{2}{3})$ mm long × $(\frac{1}{2}-)\frac{2}{3}-1\frac{1}{4}(-1\frac{2}{3})$ mm thick, sparsely to rather densely sordid whitish to greyish or stramineous strigillose, very rarely almost glabrous, occasionally bearing outer pair of perianth bracteoles below rim to near base; rim poorly-defined, ± $\frac{1}{4}$ mm broad. Perianth pale green to whitish or yellowish green, the inner petaloid tepals brightest, (8-)10-11(-13)-partite in 3(-4) whorls, the outer 2(-3) whorls of ± opposite bracteoles, the inner 1-2 whorls comprising (4-)6-7(-8) tepals; outer pair of perianth bracteoles ovate-deltate to depressed ovate, circular, or oblong-elliptic, $(\frac{2}{3}-)\frac{3}{4}-1\frac{1}{4}(-1\frac{1}{2})$ mm long × $(\frac{1}{2}-)\frac{3}{4}-1(-1\frac{2}{3})$ mm broad, usually uniformly sparsely strigillose abaxially, the hairs sometimes concentrated along the midnerve, rarely almost absent; inner 1(-2) pairs of perianth bracteoles circular to obovate, or depressed oblong-elliptic, sometimes rounded trullate, rarely ± elliptic, $(1-)1\frac{1}{2}-2(-2\frac{1}{4})$ mm long × $(1-)1\frac{1}{2}-2(-2\frac{1}{4})$ mm broad, with entire, rarely obscurely fimbriolate margins, usually more sparsely strigillose abaxially than outer perianth bracteoles; tepals narrowly to broadly lanceate, sometimes narrowly ovate, rarely almost linear or elliptic, (2-)$2\frac{1}{2}$-$3\frac{1}{2}$(-4) mm long × ($\frac{1}{2}$-)1-$1\frac{1}{2}$(-2) mm broad, with finely to obscurely fimbriolate, rarely almost entire margins towards the apex, rather conspicuously 3- or 5-nerved, with ± obscure vein reticulum. Androecium entirely pale green or green-cream, (2-)3-seriate; (3-)4-5(-6) stamens ($\frac{2}{3}$ -)±1(-$1\frac{1}{4}$) mm long × ($\frac{2}{3}$ -)$\frac{3}{4}$-1(-$1\frac{1}{4}$) mm broad × $\frac{1}{4}$ - $\frac{1}{3}$ mm thick, never aborted*; filaments broad and short, $\frac{1}{4}$ - $\frac{1}{3}$ mm long below staminal glands × ($\frac{2}{3}$ -)$\frac{3}{4}$(-1) mm broad × $\frac{1}{4}$ mm thick, generally strigillose adaxially; staminal glands depressed elliptic,peltate, rarely almost circular peltate, $\frac{1}{4}$ - $\frac{1}{3}$ mm long × $\frac{1}{3}$ - $\frac{1}{2}$(- $\frac{2}{3}$) mm broad; anthers compressed,depressed cubical, ($\frac{1}{3}$ -)$\frac{1}{2}$ - $\frac{2}{3}$ mm long × ($\frac{2}{3}$ -)$\frac{3}{4}$(-1) mm broad × $\frac{1}{4}$(- $\frac{1}{3}$) mm thick; (3-)5-7(-9), frequently 6 staminodes broadly to very broadly oblong or somewhat batilliform, ($\frac{1}{2}$-)$\frac{2}{3}$ - $\frac{3}{4}$(-1) mm long × ($\frac{1}{4}$-)$\frac{1}{3}$ - $\frac{1}{2}$(- $\frac{2}{3}$) mm thick, the base hardly thicker than apex, sometimes with an obscurely prominent abaxial midnerve, sparsely, rarely densely strigillose,or glabrous abaxially, rather densely strigillose adaxially, without vestiges of staminal glands. Gynoecium of (3-)4-6(-9) carpels**; styles exserted $\frac{1}{4}$ - $\frac{2}{3}$(-1) mm beyond hypanthium rim in a slender cylindrical to rather conical column; stigmatic column short, often curling, narrowly obtuse or conical, ($\frac{1}{4}$-)$\frac{1}{3}$ - $\frac{1}{2}$ mm long, exserted to near apices of stamens or $\frac{1}{4}$ mm beyond.

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* According to those examined in all specimens studied.

** The carpels are sometimes insect-infested and fused into enlarged ellipsoid strigose structures ca 2-3(-4) mm long.

Ripe infructescences borne at ultimate (1-)2-6(-9) leaf nodes usually among, occasionally below leaves on branchlets, ($1\frac{1}{2}$-)$2\frac{1}{2}$-5(-6) cm long, sparsely strigillose to entirely glabrescent. Primary peduncles of the same dimensions and form as in inflorescence, more sparsely haired or glabrescent; secondary peduncles ($\frac{1}{3}$ -)$\frac{1}{2}$-$1\frac{3}{4}$(-3) cm long, of the same form as in inflorescence, generally glabrescent; pedicels (2-)3-6(-9) mm long, of the same form as in inflorescence, usually rather conspicuously expanded under fruiting hypanthia, more coarsely haired or glabrescent. Fruiting hypanthium slenderly, less often broadly urceolate, rarely subcylindrical, (7-)8-15(-20) mm long × ($1\frac{1}{2}$-)2-5(-6) mm thick, narrowed into a neck ca ($\frac{1}{2}$-)$\frac{1}{3}$(-$\frac{1}{4}$) × length of hypanthium, levigate or finely rugulose-pusticulate or finely striate, rather glossy mid to dark green, glabrescent, rarely sparsely strigillose in parts, lignified, with walls ($\frac{1}{4}$-)$\frac{1}{3}$ - $\frac{2}{3}$(-$\frac{3}{4}$) mm thick; hypanthium chamber narrowly rounded at the base, densely sordid off-white to stramineous hispid immediately below the rim, longer and sparser hirsute, rarely almost glabrous on the neck, either denser or sparser darker brown silky hirsute towards the base among nutlets. Nutlets elongating in maturing hypanthium to maintain or slightly increase the exsertion of the style apices to 1-2 mm beyond the hypanthium rim; bodies of ripe nutlets ellipsoid to narrowly ellipsoid, (4-)5(-6) mm long × ($1\frac{1}{4}$-)$1\frac{1}{2}$-2(-$2\frac{1}{2}$) mm thick, the hairs (5-)7-8(-10) mm long; styles of ripe nutlets (4-)5-10(-12) mm long, slightly but usually ± conspicuously expanded at base into body of nutlet, the apical ± $\frac{1}{2}$ mm often glabrous.

Pseudo-infructescences of galls occasionally present, the galls globose, 3-5 mm in diameter, rugose-pusticulate, fawn to dark brown, rarely greyish, borne on a system of stipes, comprising primary stipes (≡ infructescence peduncles) (½-)1½-3(-5) cm long, usually glabrous, with several nodes giving off secondary stipes (≡ infructescence pedicels) which bear the galls.

15-25-noded young plants ca 50-100 cm high, the ultimate 4-6 internodes strongly compressed, hardly tetragonous, 2-6(-12) cm long x 2-5 mm thick on leader stems, 1-2 mm thick on lateral stems, smoothly striate, drying black or olive-black, off-white to sordid stramineous hispidulous-strigillose, more sparsely haired or glabrescent below, the nodes on leader stems broadly compressed, up to 2½ cm broad, densely pusticulate about the base of lateral branchlets; cotyledons caducous; subsequent leaf pairs with petioles 5-8 mm long x 1(-1½) mm thick, variably hispidulous-strigillose, and leaf blades broadly lanceate to ovate, (3-)5-13 cm long x (1¼-)2-4½(-5) cm broad, with broadly obtuse or slightly cuneate bases, attenuately, often slightly acuminately mucronate acute apices, ± deeply serrate-crenate, very slightly recurved margins, chartaceous to thinly coriaceous texture, slightly glossy, rather dark green colour on upper face, drying blackish (early leaves), or pale grey-brown or grey-green (later leaves), planate or sometimes finely prominulous midrib on upper face, prominulous nerves and vein reticulum on both faces, pubescence similar to that on younger leaves of mature trees.

The epithet apatela is derived from ἀπατηλός, meaning deceptive or misleading, and alludes to the fact that the species has been mistaken for Daphnandra micrantha by all previous revisers.

Aboriginal name: Tdum dambie (Clarence river —— Maiden 1921).

Vernacular names: Bitter wood (Maiden 1911), Butter wood (Welch 1929), Canary sassafras (Francis 1929, 1951, Garratt 1934), Grey sassafras (Welch 1929), Light yellow wood (Maiden 1889, 1921, Guilfoyle 1911, Anderson 1956), N.S.W.Satin-wood (Guilfoyle 1911), Satin wood (Maiden 1889, Moore and Betche 1893, Dixon 1906, Maiden 1921, Welch 1929, Anderson 1956, C.Moore: NSW 67891), Socket wood (Maiden 1921, White and Francis 1922, Francis 1929, 1951, Welch 1929, Hurst 1942, Webb 1948, Anderson 1956), Yellow box (Welch 1929), Yellow sassafras (Welch 1929, Metcalfe and Chalk 1950, Hutchinson 1964), Yellow wood (Maiden 1911, Baker 1919, Maiden 1921, Welch 1929, Rudder: NSW 67929). The most widely used names are Socket wood (in allusion to the swollen socket-like joints of the limbs), Yellow wood (because of the colour of the timber), and Satin wood (because of a sheen to the timber).

Series of specimens examined: 94 collections, comprising 15 with inflorescence buds, 24 with flower buds, 33 with open flowers, 19 with near or fully mature fruiting hypanthia, and 2 of young plants.

Geographic Distribution (map 10)

Daphnandra apatela occurs in the coastal regions and adjacent ranges of south-east Queensland and north-east New South Wales, from the Gympie district to the Newcastle district, $26^{\circ}20' - 33^{\circ}$S:

Queensland. Gympie; Amamoor; Imbil; Mt.Glorious, D'Aguilar range; Pine river; Draper's Crossing, near Brisbane; "Moreton Bay"; Enoggera; Enoggera creek (3 mile scrub); Upper Brookfield, near Brisbane; Brookfield; Mistake range; Mt.Mistake (Bailey's Timber vale); Mt.Cordeaux, Cunningham Gap; Tambourine mountain; Emu Vale (Forest Reserve 399); Macpherson range, near Emu Vale; Mt.Mitchell; Sarabah range, ca 12 miles south of Canungra; Border of Lamington National Park, O'Reilly's road; Killarney.

New South Wales. Tweed river; Acacia Creek via Killarney; Tooloom scrub; Cox's road, Toonumbar State Forest; Kyogle subdistrict; Moore Park, near Kyogle; Wilsons creek, Lismore district; Whian Whian; Red Scrub, Whian Whian State Forest; Newrybar; Casino district; Worani, Richmond river; Monaltree, Richmond river; Clarence river; Chapmans Plains, south-east of Clouds Creek; between Blicks river and Clouds Creek; Cascade; Dorrigo; Bundagen; Urunga; Oakes State Forest; Styx river; McLeay river; Hubeys creek, McLeay river, Moona river, Walcha; Forestry camp, Mt.Boss State Forest, north-west of Wauchope; Clay road, Doyles River State Forest, west of Wauchope; Ellenborough Falls; below Rowley's Trig, Dingo State Forest, west of Wingham; Murrurundi; Blandford, near Murrurundi; 8 miles S.W. of Murrurundi; Wingham; Wingham brush; Craven State Forest; Barrington; Mount Woolooma, Belltrees; near Upper Chichester, N.N.W. of Dungog; Upper Williams river; Williams river valley,near Barrington House; Allyn river valley;

Bungwahl-Bulahdelah road; Bulahdelah; Patersons river; Blackbutt reserve, New Lambton.

D. apatela, by far the most widespread species of Daphnandra, has a more-or-less continuous distribution throughout its range. The Gympie and Newcastle districts represent its northern and southern limits respectively because of unsuitable habitat beyond.

Ecology (figures 50, 55, 56, 57)

Often in loose colonies and less frequently solitary, D. apatela is a medium-sized tree of rainforest margins and secondary growth between sea-level and 1130 m altitude. It occurs less often within the shade of a tall rainforest than other species of the genus, such as D. melasmena and D. repandula. At the northern end of its geographic range, it is confined to cool montane forest at altitudes between 600 and ± 1130 m. In southern parts, indeed throughout New South Wales, it is most common between the altitudes of 200-800 m in hill rainforest, and rarely occurs above 900 m.

Like other species of the genus, it prefers wet, often rocky gullies, and is an important and characteristic element of rainforest seres in such sites, particularly towards the heads of gullies (Schodde 5120, 5123, Webb 2008). It also occurs somewhat less frequently on alluvial plains, as in the "Big Scrub", Richmond river, at Chapmans Plains, north of Dorrigo (Schodde 3541), and in the Wingham brush (Schodde 5114). It shows a marked preference for the red soils developed from basaltic rocks (Schodde 3541, 3543, 3577, 5114, and Story 6930), but may not be confined to them.

Phenology

Flowering and fruiting is seasonally regular throughout the geographic range of the species. Inflorescence buds appear and develop in early austral winter months, sometimes a little later (May-June, rarely to August), flower bud expansion occurs from August to late October in spring, flowers open between late August and late October, flowers mature and fruiting hypanthia commence to elongate between October-December, and the fruiting hypanthia ripen during January to dehisce in February and March in late summer. As a rule, trees at higher altitudes and from northern localities flower and fruit a little later than their counterparts at lower altitudes and more southern localities (cf. Schodde 5114, 5136, and C.T.White 13117). The period from flower opening to dehiscence of the fruiting hypanthia is five to six months. Flower buds and mature flowers were never found together with near mature fruiting hypanthia on any collection of. Daphnandra repandula.

It is noteworthy that several collections from Emu Vale, Mount Tambourine, and Acacia Creek in the region of the New South Wales-Queensland border are in flower bud and open flower in the unseasonal period between February and May in the late austral summer and autumn (Dunn 69, Francis: BRI 052053, Saunders: BRI 052059), and in fruit in July in winter (Shirley 1).

Infraspecific Variation

Apart from the usual differences between the vegetative parts of saplings and shaded branchlets and the canopy branchlets of mature trees, which are enumerated in the formal description, variation, usually of a clinal nature, occurs in a number of characters in mature trees as described below.

1. Stem and leaf pubescence. In northern forms, the ultimate stems and the leaves are generally more sparsely puberulous and more extensively glabrescent. The hairs are often confined to the ultimate 1-2 stem internodes or lateral branchlets, and sometimes entirely absent. In southern forms, by contrast, the pubescence often extends over the ultimate 6-10 stem internodes. The density and extensiveness of pubescence on saplings and shaded branchlets as a rule follows this geographic trend, though not so markedly,

2. Leaf form. The leaf blades of northern forms average slightly broader lanceate, $4\frac{1}{2}$-9 cm long x $1\frac{1}{2}$-$3\frac{1}{2}$cm broad, with shorter narrower obtuse apices and more cuneate bases than in southern forms, in which they are narrower, averaging 5-10 cm long x $1\frac{1}{2}$-3 cm broad, and have quite attenuate apices and more obtuse bases. The blades in some southern collections are strikingly narrow, being for example 6-14 cm long x $1\frac{1}{4}$-3 cm broad in Schodde 3197 from the Williams river. It also appears that in northern forms, the blades are often slightly more coriaceous, with the upper face smoother and the nerves and vein reticulum more generally obscure.

3. Bract size. Notwithstanding individual variation, the bracts on the primary peduncles of northern forms average longer, (1-)1½-2½(-3) mm long, than those in southern forms, which are (¾-)1-2(-3) mm long. The bracts are all more-or-less identical in shape.

4. Pedicel length. The length of pedicels in the terminal dichasia varies from (¾-)1-3 mm long in northern forms to (1-)2-4 mm long in southern forms. In infructescences, this trend is maintained, with those in northern forms 2-4½(-9) mm long, shorter than those in southern forms, (3-)4-6(-7) mm long.

5. Flower pubescence. Flowers, particularly the floral hypanthia, are often more densely strigillose in northern than in southern forms. There is also some indiscriminate variation in the density of pubescence, and two collections —— Hayes: COFFS, from Bundagen, and Crawford: MEL 3205, from Moona river, Walcha —— have almost glabrous flowers reminiscent of those of D. melasmena. Both these collections have respectively blackish-green and dull olive-green crenulate leaves that also resemble those of D. melasmena rather than D. apatela, and indicate the possibility of introgression between the two species.

6. Floral hypanthium and petaloid tepal size. The floral hypanthia at the northern and southern geographic limits of the species appear to be generally larger, ¾-1⅓(-1⅔) mm long × (⅔ -)¾-1¼(-1⅔) mm broad, than those towards the centre of the range in the region of the New South Wales-Queensland border-Richmond river, which are (½-)⅔ - 1 mm long × (½-)⅔ - 1 mm broad. Variation in the size of the inner petaloid tepals follows the

same trend, with these at the northern and southern limits $(2-)2\frac{3}{4}-3\frac{1}{2}(-4)$ mm long x $(\frac{3}{4}-)1-1\frac{1}{4}(-2)$ mm broad, whereas those from the central region, generally smaller, are $(2\frac{1}{4}-)2\frac{1}{2}-3(-3\frac{1}{4})$ mm long x $(\frac{1}{2}-)\frac{3}{4}-1(-1\frac{1}{4})$ mm broad.

7. Petaloid tepal margins. Northern forms have the margins of the tepals generally more distinctly fimbriolate than southern forms, in which the margins are occasionally almost entire.

8. Stamen and staminode numbers. Although the numbers of stamens and staminodes and their whorls do not vary gradually in any geographic direction, they are markedly fewer, comprising only 3-4(-5) stamens and staminodes per flower, in collections from extreme southern localities: Patersons river (R.Brown: K), Bungwahl-Bulahdelah (Rupp: NSW 67883), and Murrurundi (Cambage 1778). Collections with the greatest number of staminodes per flower (9), however, are from Dingo State Forest (Schodde 5120) near Wingham, and Doyles River State Forest (Schodde 5123) west of Wauchope, only a little north of Bulahdelah and Murrurundi.

9. Stamen and staminode size. Stamens in northern forms appear to be generally a little larger, $(\frac{4}{5}-)1-1\frac{1}{5}(-1\frac{1}{4})$ mm long x $\frac{3}{4}-1(-1\frac{1}{4})$ mm broad, than in southern forms, in which they are ~~$(\frac{2}{3}-)\frac{3}{4}-1(-1\frac{1}{5})$ mm long x~~ $(\frac{2}{3}-)\frac{3}{4}-1(-1\frac{1}{5})$ mm long x $(\frac{2}{3}-)\frac{3}{4}-1(-1\frac{1}{4})$ mm broad. The variation appears to be brought about largely by differences in the size of the anthers, which vary clinally from $\frac{1}{2}-\frac{2}{3}$ mm long x $(\frac{2}{3}-)\frac{3}{4}(-1)$ mm broad in northern localities to $(\frac{1}{3}-)\frac{1}{2}(-\frac{2}{3})$ mm long x $(\frac{2}{3}-)\frac{3}{4}$ mm broad in southern areas. Staminodes also appear to be slightly longer, and a little narrower, in northern forms ($(\frac{2}{3}-)\frac{3}{4}(-1)$ mm long x $(\frac{1}{4}-)\frac{1}{3}$ mm thick), than in southern forms ($(\frac{1}{2}-)\frac{2}{3}-\frac{3}{4}$ mm long x $(\frac{1}{4}-)\frac{1}{3}-\frac{1}{2}(-\frac{2}{3})$ mm thick).

10. Carpel numbers. The carpels appear to be more consistent in number (5-6(-7)) in northern forms than in southern forms, in which they are not only more variable, but also apparently average fewer per flower, (3-5(-9)). This pattern of variation parallels in large degree that in the numbers of stamens and staminodes per flower.

11. Infructescence length. The length of mature infructescences is perhaps generally shorter in northern forms ((1½-)2½-4(-5) cm long) than in southern forms ((2½-)3½-5(-6) cm long). Variation in the lengths of primary infructescence peduncles is consistent with this trend.

12. Fruiting hypanthium form. Perhaps the most striking variation in a clinal sequence is exhibited by the shape and size of the fruiting hypanthium. The hypanthium varies from rather short and broadly urceolate, (7-)8-12(-15) mm long x (1½-)3-5(-6) mm thick, in northern forms, to longer and slenderer urceolate, (7-)10-15(-20) mm x (1¾-)2½-3½(-4) mm thick in southern forms. The usually fewer nutlets per hypanthium and usually longer nutlet hairs (length 9-10 mm compared with 6-8 mm) in southern forms would appear to be consistent with the narrower and longer form of the fruiting hypanthia.

Because of its extensive range of some 500 miles in a north-south direction, it is not surprising that Daphnandra apatela is more variable than the other species of the genus (with the possible exception of D. repandula), nor that the variation is generally clinal, with character gradients running in a north-south direction without any marked discontinuities.

In this connection, Bick, Taylor, and Todd (1953) in a survey of the alkaloids of D. apatela* have found that though micranthine, daphnoline, and daphnandrine occurred in varying proportions in samples from Wauchope and Toonumbar in the southern and central parts of the range of the species, micranthine was the dominant, if not sole alkaloid present in more northern samples from Queensland.

Taxonomic Notes

As explained under Daphnandra micrantha, all previous authors have confused D. apatela with that species, notwithstanding that both are more closely related to different species in the genus than to each other. It is unfortunate that, as a result of incorrect application of the epithet micrantha, the new name apatela has had to be given to this most well-known and widely used species of Daphnandra.

The name Artheocarpus acuminata or Aetheocarpus acuminatus used by Robert Brown in his manuscripts and herbarium labels refers to this species.

Galls

The carpels,and to a degree the hypanthia in the flowers of Daphnandra apatela,are distorted occasionally by insect infestation, as described in the formal description. The pseudo-infructescences of galls formed are quite different in appearance from the structures produced by insect infestation in D. johnsonii and D. tenuipes.

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* Under the name Daphnandra micrantha.

Chemistry

Under the name of D. micrantha, the alkaloids of D. apatela have been studied in some detail by Bancroft (1886, 1887a), Pyman (1914), Bick and Todd (1948), Bick, Ewen, and Todd (1949), Bick and Todd (1950), and Bick, Taylor, and Todd (1953). They have been reviewed by Henry (1949) and Kulka in Manske (and Holmes) (1954, 1960). Pyman established that the bark contained 6% total alkaloids. Three major alkaloids, micranthine, daphnandrine, and daphnoline have been isolated, which, according to Bick, Taylor, and Todd (l.c.) vary in presence and proportion between different localities,and possibly at different times of the year,throughout the geographic range of the species (see above).

Micranthine, the dominant alkaloid in northern forms, is colourless, has the formula $C_{34}H_{32}O_6N_2$ (Bick and Todd 1950), and contains one methoxy- and one methylimino-group. It is one of the small group of bisbenzylisoquinoline alkaloids containing a phenodioxin system (Bick and Todd 1950), and three diphenyl ether linkages. According to Pyman (l.c.), it has a melting point of 190-6°C.

Daphnandrine is also a colourless alkaloid, has the formula $C_{36}H_{38}O_6N_2$ (Pyman l.c., Bick, Ewen, and Todd l.c.), and contains three methoxy-groups and one methylimino-group. It has weak phenolic properties, and shows reactions of the secondary amine (Bick, Ewen, and Todd l.c.). According to Pyman (l.c.), it has a melting point of 280°C.

Daphnoline also occurs as a major alkaloid of Doryphora aromatica, and its characteristics are treated under that species.

Uses

The pharmacological action of the three known alkaloids of D.apatela has been examined by Bancroft (1887a, b) and Dale (quoted by Pyman 1914). It is of the same kind in all three, with that of daphnandrine the weakest, and similar to that of the alkaloids in D. repandula, causing great oedematous infiltration of the subcutaneous tissues and loss of sensibility when injected locally into warm-blooded animals. The alkaloids also act as a depressant on the central nervous system and, when administered intravenously, cause vasodilator circulatory depression. Bancroft reported using a tincture of the bark in the treatment of heart cases with apparently good results. The bark has also been reputedly much used as a tonic by sawyers (Maiden 1889, 1921). According to Hurst (1942), there appear to be no field reports of poisoning by this species.

The timber, being light, easily worked, and taking polish well, has been used occasionally in general indoor and cabinet work (F.M.Bailey 1888, 1901, 1913, White and Francis 1922, and Anderson 1956). It has an average lateral hardness of 475 kg (Welch 1929). Its pale yellow colour after being dressed does not often appear to be permanent, and its lack of durability and general weakness* make it of little use for ourdoor and construction purposes. Welch (1929), Garratt (1934), Metcalfe and Chalk (1950), and Francis (1951) record that it is nevertheless suitable

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* cf. Baker 1919.

for plywood, turned articles, bush stocks, door knobs and tool handles, case material, toys, flooring, lining, interior fittings, broom handles, and furniture generally. But because the species rarely grows to an economically millable size, it is not as a rule sought or used by the timber industry in Australia.

XV. REVIEW OF FOSSIL RECORDS

An enumeration and review of fossil forms attributed to the Atherospermataceae has been prepared to permit assessment of the phytogeographic origins and affinities of the family on as broad a basis as possible. Under the term "assessment" in the lists of **fossils** is given my opinion on whether or not the taxa are attributable to the Atherospermataceae or its present-day genera. The reasons for such opinions are discussed below.

Atherosperma berwickense Deane, Rec.Geol.Surv.Vict. 1(1902)26, f.VII.1-3; Duigan, Proc.Roy.Soc.Vict. 63(1951)47; Rüffle, Geol.Jahrg. 1(1965)79.

Form: leaves

Site: Berwick, Victoria, Australia

Age: Eocene

Assessment: not Atherospermataceae

Atherospermoxylon Kräusel, Abh.Bayer.Akad.Wiss., math.-naturw.Abt., N.F. 47(1939) f.3 E-L [n.v.]; Müller-Stoll & Mädel,Trans.Geol.Soc.S.Africa 65(1962)98,99; Buchheim in Melchior, Syllab.Pflzfm. ed.12,2(1964)122.

Form: woods

Site: Egypt

Age: Lower Oligocene

Species: Athercspermoxylon aegyptiacum Kräusel, l.c.; Müller-Stoll & Mädel, l.c.

Assessment: probably authentic

<u>Daphnandra obliqua</u> Deane, Rec.Geol.Surv.Vict. 1(1902)27, f. VI.2; Duigan, Proc.Roy.Soc.Vict. 63(1951)48; Rüffle, Geol. Jahrg. 1(1965)79.

Form: leaf

Site: Berwick, Victoria, Australia

Age: Eocene

Assessment: not Atherospermataceae

<u>Daphnandra selwynii</u> Deane, Rec.Geol.Surv.Vict. 1(1902)17, f.I.5; Duigan, Proc.Roy.Soc.Vict. 63(1951)48; Rüffle, Geol.Jahrg. 1(1965)75.

Form: leaf

Site: Pitfield, Victoria, Australia

Age: early Tertiary (Eocene)

Assessment: not Atherospermataceae

<u>Laurelia</u> Juss.: Lesquereux, U.S.Geol.Surv.Monogr. 17(1892)108; [Ettingshausen, Neuholl., Char.der Eoc.Eu., pp.88-90, f.126,131,138-140 [n.v.]?]; Berry, Proc.U.S.Nat.Mus. 73,22(1928)21; Berry, Bot.Gaz. 96(1935)751,754; Berry, Geol.Soc.Amer.spec.pap. 12(1938)16,34,75; Oliver, Svensk.Bot.Tidskr. 49(1955)15,16; Couper, N.Zeal.Geol.Surv.Palaeont.Bull. 32(1960)31; Fleming in Gressitt, Pacif.Basin Biogeogr. (1963)372, f.2. Forms, localities,

and ages indicated under species below.

Laurelia amarillana Berry, Proc.U.S.Nat.Mus. 73,22(1928)21, f.V.3; Berry, Amer.Mus.Novit. n.536(1932)1-10 [n.v.]; Berry, Bot.Gaz. 96(1935)754; Berry, Geol.Soc.Amer.spec. pap. 12(1938)30,76; Rüffle, Geol.Jahrg. 1(1965)80.

Form: leaves

Site: upper Rio Chalia, prov.Santa Cruz, Argentina; prov. Chubut, Argentina

Age: Deseado formation, Eocene-Oligocene (Chubut); Lower Miocene (Santa Cruz)

Assessment: authentic, resembling present-day Laurelia

Laurelia giuñazui Berry, Bot.Gaz. 96(1935)752, f.2; Berry, Geol.Soc.Amer.spec.pap. 12(1938)17,75, pl.19; Rüffle, Geol. Jahrg. 1(1965)80.

Form: leaves

Site: Rio Pichileufu ca 30 miles east of Lago Nahuel Huapi, Argentina

Age: early Miocene

Assessment: authentic, resembling present-day Laureliopsis

Laurelia insularis Dusén, Wiss.ergeb.Schwed.Südpolar-exped. 3,3(1908)4,20,24, f.I.5; Cockayne, Veg.N.Zeal. ed.3,(1958) 426; Rüffle, Geol.Jahrg. 1(1965)79.

Form: leaf

Site: Seymour island, Antarctica

Age: Eocene-Oligocene (cf. Berry 1935,1938)

Assessment: authentic, resembling present-day *Laurelia* and *Laureliopsis*

Laurelia cf. *novae-zelandiae* A.Cunn.: Couper, N.Zeal.Geol. Surv.Paleont.Bull. 22(1953)40, f.V.44,45 "Laurelia cf. novae-zealandiae", 32(1960)36,47, f.V.5,6 "Laurelia aff. novae-zelandiae".

Form: pollen grains

Site: New Zealand generally

Age: Middle Oligocene (Waitakian stage) to present day

Assessment: authentic, probably referable to present-day *Laurelia novae-zelandiae*

Laurelia primaeva Lesquereux, U.S.Geol.Surv.Monogr. 17(1892)108, f.XX.8; Rüffle, Geol.Jahrg. 1(1965)79.

Form: leaf

Site: Arkansas, U.S.A.

Age: Dakota formation, Middle Cretaceous

Assessment: doubtfully Atherospermataceae

Laurelia rediviva Unger, Denkschr.Akad.Wiss.Wien,math.-nat. 25(1866)72, f.XXIV.4-9 [n.v.]; Ettingshausen, Sitz.Ber. Akad.Wiss.Wien 61(1870)839; Pax, Pflzfm. 3,2(1889)105; Perk. & Gilg, Pflzr. 4(1901)11; Perk., Gattung.Monim.

(1925)13; Rüffle, Geol.Jahrg. 1(1965)79.

Form: leaves, fruit (fide Rüffle, l.c.)

Site: Radoboj, Croatia

Age: Miocene (fide Berry 1935, 1938)

Assessment: not Atherospermataceae

Laurelia tertiaria Engelhardt, Abh.hessische geol.Landesanst. 7, 4(1922)51, f.XII.1 [n.v.]; Rüffle, Geol.Jahrg. 1(1965)80.

Form: leaves

Site: Messel, Germany

Age: Upper Eocene (fide Berry 1935, 1938)

Assessment: not Atherospermataceae

Protoatherospermoxylon Mädel in Muller-Stoll & Mädel, Trans. Geol.Soc.S.Africa 65(1962)99, 100; Buchheim in Melchior, Syllab.Pflzfm.ed.12,2(1964)122.

Form: woods

Site: east Pondoland, South Africa

Age: Upper Senonian, Upper Cretaceous

Species: Protoatherospermoxylon kraeuselii Mädel, l.c., f.1b [nom.invalid.: I.C.B.N. 1966, art.38].

P. renniei Mädel, l.c., f.3.

P. resiniferum Mädel, l.c. [nom.invalid.: I.C.B.N. 1966, art.38].

P. triseriatum Mädel, l.c., f.4.

P. umzambicum Mädel, l.c., f.la,c [nom.invalid.: I.C.B.N. 1966, art.38].

All species of same age, from same site.

Assessment: authentic, not referable to present-day taxa

There can be little doubt that the fossil wood described by Kräusel (1939) as Atherospermoxylon and by Müller-Stoll and Mädel (1962) as Protoatherospermoxylon is attributable to the Atherospermataceae. The fossils comprise impressions of narrow vessel members with scalariform perforation plates and pitting and a tendency to form radial multiples, relatively narrow rays, frequent to ± absent oil cells, fibre tissue septate only in parts, and wood parenchyma that is either absent or diffuse when present. Illustrations of transverse and tangential sections of the fossil wood of Protoatherospermoxylon given by Müller-Stoll and Mädel virtually confirm the relationship.

Müller-Stoll and Mädel (l.c.) infer that Atherospermoxylon from early Tertiary deposits resembles living members of the family rather closely. Its wood parenchyma is said to be extremely scanty (diffuse) or perhaps absent, oil cells are usually absent, and the rays narrow, never more than 5 cells wide. Without having seen Kräusel's descriptions, I am unable to determine which of the two present-day tribes Atherospermoxylon resembles most.

The wood of Protoatherospermoxylon, from earlier Upper Cretaceous deposits, is rather different from that of living members of the family, particularly in its ubiquitous wood parenchyma (chapter IV,2), its rays which, though mostly narrow, may be up to 13 cells wide, and its abundant oil cells, most of which occur within the parenchyma. Of the two present-day tribes, it resembles the wood of the Laurelieae more closely, judging from the overall size of the rays and vessel members, and the occurrence of oil cells which today are found only in Dryadodaphne, and perhaps Daphnandra and Doryphora. To suggest, however, that it may represent an ancestral form of that tribe could be misleading. Reference has already been made in chapters IV.2 and V of the way in which it apparently represents an evolutionary link between the family and Monimiaceae.

Five species of Protoatherospermoxylon, all from the same deposits, have been described by Mädel (in Müller-Stoll and Mädel l.c.) on the basis of differences in ray width, the frequency of tyloses, and the association of vessel members in radial multiples. These differences are difficult to assess. Some, such as the association of vessel members, are equivalent to those characteristic of present-day genera; others, for example the frequency of tyloses, may be insignificant and represent only local variation in individuals of a species.

Fossil leaf impressions have been referred to the family on the basis of shape, size, texture, marginal indentations, and venation patterns. It is to be expected that these characters are more plastic and more easily modified than those of the secondary xylem; they may occur in a wider range of families. Only fossil leaf forms bearing a very close resemblance to living genera in all of the characters are therefore considered to be possibly authentic. Those differing markedly from all living forms in any one character are regarded as doubtful because of the uncertainty that they do in fact represent ancestral types. For these reasons, it is considered unlikely that *Atherosperma berwickense* and *Daphnandra obliqua* from Eocene beds at Berwick, Victoria (Deane 1902c), and *Daphnandra selwynii* in beds of similar age at Pitfield, Victoria (Deane 1902b), belong to the Atherospermataceae.

Deane's illustrations of *Atherosperma berwickense* (f.VII.1-3) show a leaf form quite unlike the leaves of living *Atherosperma*, particularly in its serrate-crenate leaf margins. Though it resembles the leaves of *Doryphora sassafras* more in shape and marginal indentations, its size is smaller and the pattern of tertiary venation different. Rüffle (1965) has suggested that other fossil leaves referred to *Fagus** and *Lomatia* by

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* In connection with references to "*Fagus*" in this chapter, attention is drawn to Cranwell's note (in Gressitt 1963) that most records of *Fagus* from the southern hemisphere fossil record are disputable. Its characteristic pollen, which would confirm the macrofossil evidence, is lacking from all known deposits. Oliver (1950) transferred to *Nothofagus* the New Zealand fossil species described as *Fagus*. Whether all southern hemisphere records of fagaceous plants referred to *Fagus* belong instead to *Nothofagus* or related extinct forms is still uncertain but apparently not unlikely.

Deane (1902c) belong to this species, but the converse seems more likely.

In the case of the two species of "*Daphnandra*", Rüffle (l.c.) has already pointed out that their leaves could belong to a single species; they certainly belong to the same genus (Deane 1902c). The leaf forms, as illustrated in Deane (1902b, f.I.5 and 1902c, f.VI.2), differ from all living members of the Atherospermataceae in having fine marginal crenations that extend to the very base of the blades. They differ from *Daphnandra* also in their broadly obtuse apices, small size, and lateral nerve branching.

There are, nevertheless, illustrations of other leaf impressions from the Eocene beds at Berwick (Deane 1902c) that very closely resemble the leaf form of living *Daphnandra* and *Doryphora* species in shape, size, and marginal crenations. They are illustrated in figures 4-7, plate V in Deane (1902c), and are referred to *Lomatia*. These leaves are recorded associated with others attributed to *Commersonia*, *Fagus*, *Hedycarya*, *Lomatia*, *Mollinedia*, *Nephelites*, *Tristanites*, and, in quantity, *Eucalyptus*. This association, according to Deane (1902a), suggests that at that time in southern Victoria, the same two vegetation formations, rainforest and open (sclerophyll) forest with eucalypts and proteaceous plants, occurred together as they do now.

The leaf records from the northern hemisphere are also all doubtful, according to Berry (1928, 1935, 1938) and Rüffle (l.c.). They are *Laurelia primaeva* from Middle Cretaceous beds in Arkansas, *L. rediviva* from Miocene beds in Croatia, *L. tertiaria* from Upper Eocene beds in

Germany, and a species of *Laurelia* described by Ettingshausen from Lower Miocene beds in Bohemia (fide Berry 1935, 1938). Berry (l.c.) has suggested that *L. rediviva* belongs to Ternstroemiaceae.

Lesquereux's figure of the leaf impression of *L. primaeva* resembles the leaf of *L. sempervirens* more closely than that of any other living member of the Atherospermataceae in its general form and undulate blade margins. It differs in its broadly ovate shape. Furthermore, its large number of lateral nerves often linked by tertiary veins close to the midrib (cf. *L. novae-zelandiae*), and pattern of lateral nerve branching, are anomalous in the family. Rüffle (l.c.) has perhaps correctly observed that *Ficus? undulata* Lesquereux from the same fossil flora as *Laurelia primaeva* belongs to the latter species. It is larger, with more deeply and distantly undulate margins, but does not resemble closely the leaves of any living member of the Atherospermataceae in its general form.

The remaining three fossil leaf impressions referred to the family, namely *Laurelia amarillana*, *L. guiñazui*, and *L. insularis*, are from southern America and Antarctica. They appear to be correctly placed.

The description and particularly figure of the leaf of *L. amarillana* (Berry 1928) resembles closely the leaf form in living *Laurelia*, especially *L. sempervirens*, in its elliptic blade with shallowly crenate margins and open tertiary venation. In the Deseado beds of Eogene age in Chubut province, Argentina, *L. amarillana* is associated with leaf impressions referred to *Fagus* and *Nothofagus*. It has been therefore regarded as an element of the small and coriaceous-leaved Eogene "Fagus flora", which appears to have been widespread at the time in Antarctica and southern South America, north at least as far as latitude 41°S, under moist cool temperate climatic conditions (Berry 1938). The species is also recorded from Lower Miocene beds at Rio Chalia, Santa Cruz province, Argentina, which are believed to be contemporaneous with those at Rio Pichileufu, Argentina, from which *L. guiñazui* is known, and the Concepción-Arauco coal measures in Chile. There it is associated with leaves attributed to the genera *Adiantum*, *Bignonites*, *Fitzroya*, *Hydrangea*, *Laurophyllum*, *Peumus*, and *Sterculia* in a more mesophytic stream-valley rainforest flora of tropical and subtropical affinities. This flora apparently extended at least as far south as latitude 51°S in South America at the time, and is thought to indicate a warm humid (subtropical) environment (Berry 1928, 1938). *L. amarillana* is the only fossil species that has been recorded from both the Eogene temperate "Fagus Flora" and the Lower Miocene subtropical valley forest in southern South America (Berry 1938).

Notwithstanding Rüffle's comment (l.c.) that they agree with *Siparuna* or *Mollinedia*, the leaf impressions figured as *Laurelia guiñazui* (Berry 1935, 1938) bear an almost perfect resemblance in form and marginal serrations to those of living *Laureliopsis philippiana*. The only discordant features in the fossil leaves are the more conspicuous venation, and perhaps larger leaf size. These characters are of little taxonomic consequence in living members of the family, reflecting only the more moderate environment of sheltered situations.

Common genera in the rich Lower Miocene fossil flora at Rio Pichileufu (41°S), from which *L. guiñazui* is recorded, have been identified as *Cassia*, *Cupania*, *Myrica*, and *Sterculia* (Berry 1938); the largest families are Sapindaceae, Lauraceae, Myrtaceae, and Rubiaceae, in that order. The flora is thought to represent a mesophytic stream-valley rainforest association growing under a moist subtropical climate (Berry 1938). Only a few of the angiosperm genera, including *Laurelia*, are recorded as temperate genera indicative of a non-tropical environment.

The leaf impression of *Laurelia insularis*, as figured in Dusén (1908), resembles most closely the leaves of either *Laurelia sempervirens* or *Laureliopsis philippiana* among living species, on account of its serrate but not too sharply toothed margins, and obscure nerving with little discernible tertiary venation. As in *L. guiñazui*, the leaf is rather larger than in the living species. Associated leaf impressions in the Seymour island beds have been attributed to *Araucaria*, *Caldcluvia*, *Drimys*, *Fagus*, *Iliciphyllum*, *Knightia*, *Laurophyllum*, *Lomatia*, *Mollinedia*, *Myrica*, *Nothofagus*, and a number of ferns (Dusén l.c.). According to Berry (1938), these deposits are of Eocene-Oligocene age and of a flora apparently contemporaneous with the Eogene "Fagus flora" of Patagonia.

Fossil pollen attributable to the Atherospermataceae has so far been found only in New Zealand. There can be little doubt that the grains recorded by Couper (1953, 1960b) belong to the family*, as they have

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* Couper's comment that the grains figured (l.c.) are in distal view indicates he has the wrong conception of grain orientation.

the characteristic encircling depression, two furrows, and finely reticulate sculpturing. Whether they are of a *Laurelia* and have particular affinities with *L. novae-zelandiae*, as suggested by Couper (l.c.), is less certain but not unlikely. Grains from post Tertiary deposits have actually been recorded as *L. novae-zelandiae* (Couper 1960b). Though they resemble those of *Doryphora sassafras* and *Atherosperma moschatum* in their ellipsoidal shape more than those of *Laurelia* as described here, they are almost identical in form and sculpturing with grains of *L. novae-zelandiae* figured by Cranwell (1953).

Laurelia pollen has been recorded as rare from a number of New Zealand deposits from the Middle Oligocene (Waitakian Stage) to the present day. Pollen of other groups found in those deposits in which *Laurelia* first appears have been referred to *Nothofagus* subsect. *Bipartitae*, *Triorites* (Casuarinaceae), *Nothofagus* subsect. *Quadripartitae*, and Podocarpaceae. The former two appear to have been common in the flora of the time, whereas the latter two were minor elements. It has been assumed that such an association indicated a moist subtropical climate, rather warmer than that prevailing in New Zealand at the present time. According to Oliver (1955), the flora of the period (Middle Oligocene-Lower Miocene) had almost attained its present day composition concomitantly with the disappearance of the characteristic, often deciduous elements of the Cretaceous and Lower Tertiary floras in New Zealand, such as *Acer*, *Cinnamomum*, *Sassafras*, and *Ginkgo*.

But the fossil pollen record may not indicate the time of arrival of Laurelia in New Zealand with accuracy. For example, fossil pollen could antedate the advent of Laurelia if it had been blown in from some other source. Or, the pollen would postdate the arrival if the thin-walled grains present in earlier beds had disintegrated. [Erdtman (1952) and Cranwell (in Gressitt 1963) have drawn attention to the fact that the pollen record of a number of ranalean families, such as Winteraceae and Lauraceae, is poor and relatively recent, not because the taxa are young, but apparently because of the fragility and erodibility of their pollen grains.]

No fossilised flowers or fruits appear to have been recorded.

Summary

The fossil evidence bearing on the history of the family may be summarised as follows.

So far, verifiable fossils have been found only in the southern hemisphere, except for the occurrence of preserved wood in Egypt in Lower Oligocene beds (Kräusel 1939). This suggests that the family may have always been a southern one. South Africa-Egypt is the only one of the equable southern continental masses where the family has no living representatives today. The absence of unequivocal fossil forms from Australia has no real significance.

The fossils date from the Upper Cretaceous (Upper Senonian) to the present time. On this evidence, the family does not appear to be of great antiquity. But the lack of earlier fossils has little meaning in view of the scantiness of the fossil record and its well-known inability to shed much light on the origin of angiosperm groups.

The rarity of atherospermataceous remains in fossil beds after Senonian time also suggests that the family was never a common or dominant element in the floras of the times, except possibly in the Senonian in South Africa (cf. Müller-Stoll and Mädel l.c.). If the ecology of living species of the family is any indication, former members would have grown in moist riverine environments suitable for the development of fossil beds. If at all dominant or common, they might be expected to have been preserved in quantity.

All macro-fossil material so far found has been from beds of Upper Cretaceous and Eocene to Lower Miocene age. Comparison of their form with those of living genera gives some conception of the rate and direction of evolution in the family. The wood of Upper Cretaceous forms is rather distinct, according to its characters described above and evaluated in chapter IV.2. Lower and Middle Tertiary forms, on the other hand, appear to resemble living members of the family rather closely in wood, leaf, and pollen characters; all have been referred to Laurelia, with the single exception of that species ascribed to the fossil genus Atherospermoxylon.

The climatic regimes and plant associations which fossil leaf forms are purported to indicate differ in a number of ways from those in which atherospermataceous plants occur now. Laurelia amarillana, the fossil form most like living species of *Laurelia*, has been recorded from two different floras. One, the small-leaved Eogene *Nothofagus* flora, apparently grew under cool temperate conditions similar to those in which *Nothofagus* in south-east Australia and New Zealand is found today. The other, a large-leaved flora, has overwhelming floristic affinities with the present day tropical and subtropical rainforest of southern central America (Berry 1928). The two living species of *Laurelia*, however, occur in subtropical rainforests that are not floristically related to either the extant temperate-latitude *Nothofagus* forests, or the subtropical-tropical rainforests of southern central America.

Laurelia guiñazui, which seems to be related to *Laureliopsis* rather than *Laurelia*, apparently occurred in the same large-leaved subtropical forest flora as *L. amarillana*. *Laureliopsis* today is associated with the temperate *Nothofagus* forests of southern Chile. The few genera recorded with *L. guiñazui* in the Rio Pichileufu beds with which *Laureliopsis* and other genera of the family are floristically associated today were *Araucaria*, *Coprosma*, *Drimys*, *Embothrium*, *Eucryphia*, *Fitzroya*, *Lomatia*, and *Podocarpus*.

Laurelia insularis, on the other hand, is recorded from the small-leaved Eogene *Nothofagus* flora. Forms attributed to *Nothofagus* subsect. *Bipartitae* are also represented (cf. Auer 1958, Cranwell in Gressitt 1963). As has been implied in chapter IX, this group of *Nothofagus* nowadays represents a subtropical facies of the southern hemisphere *Nothofagus* forest.

The above conclusions are based on two assumptions. First, that the leaf fossils and their floristic associates have been identified correctly. Second, that the leaves have not been transported far, either by wind or water, from their sources to the site of fossilisation.

If these assumptions are correct, the fossil evidence places interpretation of the geographic and floristic affinities of the family in something of a dilemma. It suggests that the presence of all living members of the Laurelieae in subtropical rainforest of the type in which *Nothofagus* subsect. *Bipartitae* survives, and of all living members of the Atherospermateae in temperate rainforest associated with *Nothofagus* subsect. *Quadripartitae*, is historically recent and rather fortuitous. Yet the morphological features of living members of the two tribes, viewed against their present geographic and ecological occurrence, would seem to indicate that the tribes are of great antiquity, and that they have been fitted and confined to their respective subtropical and temperate environments for a considerable period of time. On the basis of high and varied chromosome numbers, Ehrendorfer et al. (1968) have also concluded that the family, as part of the Monimiaceae alliance, is a very ancient one. Because of the inevitable element of doubt about the identity of fossil forms and the homogeneity of fossil floras, it seems reasonable to maintain the latter view.

The apparent advent of *Laurelia* in New Zealand, as indicated by fossil pollen, in a flora dominated by *Nothofagus* subsect. *Bipartitae* reinforces the close affinity of the genus with *Nemuaron* and *Dryadodaphne*.

It is also consistent with the present occurrence of *Laurelia* in a southern subtropical rather than temperate rainforest flora.

XVI. PHYLOGENETIC AND PHYTOGEOGRAPHIC CONCLUSIONS

On the premise that a partial view of the evolutionary relationship between organisms provided by a phylogenetic interpretation of living forms is better than none at all (Crow 1926), a phylogenetic assessment of the genera and tribes within the Atherospermataceae is presented here. It is based on an a priori weighting of all characters studied in the family according to current evaluations of primitive and advanced features in living angiosperms (I.W.Bailey 1949, 1953, Money et al. 1950, Hutchinson 1959, 1964, Zimmermann 1959, Thorne 1963), modified by the observed relationships of these characters, singly and in combination.

The resulting determination of unspecialised and derived features is displayed in table IV, and discussed under pertinent sections in chapter IV. As a rule, trends in the modification of floral characters parallel those of xylary specialisation, strengthening the case for phylogenetic interpretation. Moreover, many characters invoke the so-called "biogenetic law". Examples are the derivation of single- or three-flowered inflorescences from thyrsiform types, introrse or extrorse anther dehiscence from latrorse, staminal glands from staminodes, lateral from terminal styles, and the occurrence of fibre tracheids in early wood and libriform (septate) fibres in late wood of several genera (Dryadodaphne, Nemuaron).

The conclusions drawn from table IV, and the phylogenetic, geographical, and ecological aspects discussed in the chapters dealing with the characters of both living and fossil Atherospermataceae are:

TABLE IV

Unspecialised characters	Laureliopsis	Atherosperma	Dryadodaphne	Nemuaron	Laurelia	Doryphora	Daphnandra	Derived characters
forest canopy trees	-	o	-	-	-	-	+	forest subcanopy trees
<5% of secondary xylem pores in radial multiples	-	-	o	o	-	-	+	<20% of secondary xylem pores in radial multiples
exclusively fibre tracheids	-	-	o	o	-	-	+	fibres predominantly libriform and septate
intervascular pit borders large and distinct	+	+	-	-	-	-	+	intervascular pit borders small and indistinct
multiseriate rays relatively heterocellular and narrow	-	-	o	o	o	+	+	multiseriate rays relatively isocellular and broad
oil cells in xylem rays	+	+	-	+	+	o?	o?	no oil cells in xylem rays
leader stem nodes unexpanded, with single terminal and paired lateral buds	-	-	-	-	-	-	+	leader stem nodes expanded, with numerous buds in serial arrangement
inflorescence buds stipitate	o	-	-	-	+	-	-	inflorescence buds ± sessile
inflorescence thyrsiform without accessory axillary flowers, 5-11-flowered with mediumsized flowers	-	+	-	-	-	+	+	inflorescence elaborate with accessory axillary flowers, or reduced to 3 or 1 flowers of large size
bracts small, early caducous	-	+	-	-	o	+	-	bracts large, enveloping flower buds and persisting until flowering
distal bracts ± tepaloid in texture and venation	-	+	+	+	+	-	+	bracts entirely herbaceous, distinct from tepals in texture and venation

Unspecialised characters	*Laureliopsis*	*Atherosperma*	*Dryadodaphne*	*Nemuaron*	*Laurelia*	*Doryphora*	*Daphnandra*	Derived characters
bracteoles subtending floral hypanthium	o	+	-	o	+	+	+	bracteoles absent or contiguous with perianth
flowers bisexual	o	+	-	-	+	-	-	flowers unisexual
arrangement of flower (perianth) parts cyclic	-	-	-	-	+	-	+	arrangement of flower (perianth) parts hemi-cyclic to spiral
flower (perianth) parts regularly 4-merous	-	-	-	o	+	+	+	flower (perianth) parts 3-merous or in irregular whorls
flower parts uniformly pale green	o	+	-, +	?	+	+	-, +	flower parts white or pigmented reddish
perianth and androecium borne within hypanthial cupule	-	-	+	+	+	+	+	perianth and androecium borne on ± well-defined flat to convex hypanthium rim or outside hypanthial cupule
tepals ± isomorphic	-	-, o	-, o	-	-, o	-	+	"tepals" differentiated into outer sepaloid and inner petaloid parts
texture of inner tepals sepaloid	o	+	-, o	o	+	+	+	texture of inner tepals petaloid
venation of inner tepals pinnate	-	+	o	o	+	-	+	venation of inner tepals palmate-parallel
staminal glands stamen-like, attached near base of filament	-	-	o, +	o, +	+	+	+	staminal glands variously peltate, planate deltate, wing-like, or cupular, attached along sides of filament

Unspecialised characters	*Laureliopsis*	*Atherosperma*	*Dryadodaphne*	*Nemuaron*	*Laurelia*	*Doryphora*	*Daphnandra*	Derived characters
apices of undehisced stamens rounded-truncate	-	+	o, +	o	o	+	+	apices of undehisced stamens prolonged, aristate, or broadly truncate
anther dehiscence latrorse	-	+	-, o	+	o	o	+	anther dehiscence extrorse or somewhat introrse
staminodes dimorphic	-	+	+	+	+	-	+	staminodes ± isomorphic
*cytokinesis of pollen mother cell of simultaneous type		-			+			cytokinesis of pollen mother cell of successive type
pollen grain colpi ill-defined, 1 or 2 per grain	-	+	-	-	+	+	-	pollen grain colpi well-defined, 2 per grain
stigmatic column coherent	o	+	-	o	-	+	-	stigmatic column stellate
style terminal	-	-	-	o	-	+	-	style subterminal or laterifixed
ovule placentation basal	-	-	o	+	-	-	+	ovule placentation sub-basal or sub-marginal
*supra-ovular vascular strand present		-			+			supra-ovular vascular strand absent
fruiting hypanthium cupular, with free woody appendages (staminodes) surrounding gynoecium	-	-	+	+	+	+	+	fruiting hypanthium cylindrical-urceolate, with all appendages fused into a wall enclosing gynoecium
fruiting hypanthium ribbed or scarred with vestiges of contributing perianth and androecium parts	-	+	+	+	-, +	-	+	fruiting hypanthium ± levigate

Unspecialised characters	*Laureliopsis*	*Atherosperma*	*Dryadodaphne*	*Nemuaron*	*Laurelia*	*Doryphora*	*Daphnandra*	Derived characters
dehiscence and valves of fruiting hypanthium corresponding with outer perianth parts	–		–	–	+	o	+	dehiscence and valves of fruiting hypanthium irregular
nutlet bodies uniformly hirsute	–	+	+	o	o	+	–	nutlet bodies unilaterally or entirely glabrous
styles elongate, persistent	–	–	–	+	–	+	–	styles aborted or caducous
ecological occurrence in primary rainforest	–	–	–	–	–	–	+	ecological occurrence in secondary rainforest

1. The genus in which the greatest number of unspecialised features are combined is Laureliopsis (Atherospermateae; Chile). It possesses the primitive form in all characters assessed, except for small indistinct borders to the intervascular pits in its secondary xylem and lack of oil cells in the xylem rays. These are relatively insignificant in comparison with its unspecialised features, notably its relatively narrow and heterocellular multiseriate rays, regularly tetramerous flower parts in cyclic arrangement, expansive concave hypanthium rim, pinnate tepal venation, rounded-truncate anthers with strictly latrorse dehiscence, ill-defined pollen grain colpi, stamen-like staminal glands, dimorphic staminodes, cupular fruiting hypanthium with vestiges of contributing perianth and androecium parts and elongated staminodes surrounding the gynoecium, and uniformly hairy nutlets.

Atherosperma, the genus most closely related to Laureliopsis, is more advanced in having single-flowered, strictly unisexual inflorescences, white flowers, palmate-parallel tepal venation, extrorse anther dehiscence, well-defined pollen grain colpi, isomorphic staminodes, a stellately-branched stigmatic column, and unilaterally glabrous nutlets.

2. The greatest number of derived features occur in Daphnandra (Laurelieae; Australia). Only in having small and early caducous bracts, bisexual flowers, rather ill-defined pollen grain colpi, a coherent stigmatic column, and uniformly hairy nutlets with persistent elongate styles can it be considered to be less specialized than other genera, such as Doryphora or Laurelia. Neither of the latter genera,

however, combine all of these characters in the derived condition. It can be argued, moreover, that because they are not so necessary for bud protection, the small, early caducous bracts are more of an advantage to *Daphnandra* than large flower-enveloping structures of the type found in *Doryphora* and *Atherosperma*.

Daphnandra is strikingly specialised in all features of its secondary xylem, and also in its small subcanopy tree size, elaborate inflorescence, irregular number of flower parts in hemicyclic to spiral arrangement, differentiated perianth, squat, truncate, extrorsely-dehiscing stamens with peltate staminal glands attached ataxially immediately below the anthers, and irregular or single-fissure dehiscence of the fruiting hypanthium. Many of these developments appear to be related to its adaptation to life in secondary rainforest growth.

3. In the Laurelieae, the genus having the greatest number of unspecialised characters is *Dryadodaphne* (New Guinea and north-east Australia). Its laxly thyrsiform inflorescence, paired bracteoles subtending the floral hypanthium, regularly tetramerous arrangement of flower parts, ± isomorphic tepals, latrorse to extrorse anther dehiscence, rather weakly modified staminal glands, relatively ill-defined pollen grain colpi, and isomerous dehiscence of the fruiting hypanthium, are evidence therefor.

Dryadodaphne is nevertheless more advanced than *Laureliopsis* in having a well-defined hypanthium rim, somewhat modified staminal glands, and a fruiting hypanthium in which all floral appendages have become fused into a levigate, thickly lignified wall enclosing the gynoecium. Many of its characters are intermediate or transitional between the unspecialised and derived condition. Examples are its 10% of xylem pores in radial multiples, semi-pinnate tepal venation, varied and, in *D. pterandrica*, weakly modified elongation of the anther connective, staminal glands of variable form, and sub-basal placentation. It also exhibits transitions between fibre tracheids and libriform wood fibres with septae, as discussed in chapter X. The oil cells in the xylem rays of several of its species, furthermore, would appear to represent an ancestral feature that it has been retained (cf. chapter IV.2).

Dryadodaphne links all other genera of its tribe.

4. Of the two tribes, the Atherospermateae is the less specialised in overall characteristics. This is exemplified by its secondary xylem with narrow vessels and relatively heterocellular rays, its undeveloped hypanthium rim, its ± regularly tetramerous and cyclic arrangement of perianth ~~flower~~ parts, its stamen-like staminal glands, and its unspecialised cupular fruiting hypanthium. Various modifications of these features occur in the members of the Laurelieae.

Similarities between the tribes in a number of characters appear to be the result of parallel evolution rather than of common origin. Examples are the reduced inflorescences with large flowers and flower bud-enveloping bracts in *Atherosperma* and *Doryphora*, the unisexual flowers in *Atherosperma* and *Laurelia*, the palmate-parallel tepal venation in *Atherosperma*, *Laurelia*, and *Daphnandra*, the extrorse anther dehiscence in

Atherosperma and *Daphnandra*, the stellately-branched stigmatic column in *Atherosperma* and *Doryphora*, and the unilaterally hairy nutlets in *Atherosperma* and *Dryadodaphne*. The first example is apparently related directly to environmental pressure.

5. The ecogeographic distribution of the tribe Atherospermateae is subantarctic and widely disjunct in south-eastern Australia and southern Chile-western Patagonia, in association with a temperate rainforest habitat. That of the Laurelieae is tropical montane-subtropical and more continuous on an arc from Australia through New Guinea, New Caledonia, and New Zealand to southern Chile, in association with a subtropical rainforest habitat. Overlap between the two tribes is limited to small areas at the extremities of their geographic ranges in south-east Australia and Chile.

6. The present centre of diversity in the family is in eastern Australia, where four of the seven genera are found, including the most specialised in both tribes. Three are endemic. They are related to each other through genera occurring entirely or largely outside Australia. That such diversification may have been promoted by more stringent historic environmental stresses can be inferred from the present ecological requirements of all species. Except for the species of *Daphnandra*, those in Australia (and New Zealand) are confined to damp everwet gullies and semi-swamp habitats, despite the availability of well-drained rainforested sites, whereas those in New Guinea and Chile are widespread on well-drained uplands and valley margins. *Daphnandra*, the

most specialised genus, apparently occurs beyond the confines of gully sides only because of its adaptation to life in rainforest seres.

7. In the Laurelieae, the less specialised genera (*Dryadodaphne*, *Nemuaron*) occur in montane environments in tropical latitudes, and the more advanced (*Laurelia*, *Doryphora*, and *Daphnandra*) in more temperate latitudes. This pattern is repeated for the less specialised species of *Daphnandra* and *Doryphora*, which are confined to mountain ranges in north-east Queensland, while more specialised forms in both genera are more widespread in southern regions.

There is, furthermore, a direct relationship between *Dryadodaphne* (New Guinea, north-east Australia), *Nemuaron* (New Caledonia), and *Laurelia* (New Zealand, Chile), in the order of their geographic distribution. Links between the other two genera, *Daphnandra* and *Doryphora*, are few, indirect, and forged by *Dryadodaphne*.

These relationships indicate the north-east Australia-New Guinea region as a centre of origin and diversification for living members of the tribe. Nevertheless, in the light of evidence presented below, it is unlikely that the Melanesian tropics represent the ancestral area of the tribe itself.

The close, presumably monophyletic relationship between *Dryadodaphne*, *Nemuaron*, and *Laurelia* suggests either earlier land continuity of one kind or another, or long distance dispersal between the regions in which they now occur, at some time(s) during their evolution. Because of the unlikelihood that atherospermataceous nutlets can be transported by wind for great distances (see chapter XIII), or that they are viable after immersion in sea water, the former alternative is the more likely. The present distribution of the two genera of the Atherospermateae leads to the same conclusion.

9. Because the Atherospermateae are primitive and confined to temperate rainforest in south-eastern Australia and Chile whereas the more specialised Laurelieae are more widespread in subtropical rainforest nearer the equator, it can be surmised first, that the ancestral environment for the family was a cool temperate ever-wet one, and second, that there has been a historic adaptation to warmer climates. *Daphnandra*, the most specialised genus, is the only member of the family found at all regularly near sea-level north of 20°S (*D. repandula*).

The presence of the least specialised genus in the Laurelieae (*Dryadodaphne*) closest to the equator does not alter these conclusions, because there it is confined to montane areas no warmer than those in which its more specialised congeners, *Daphnandra*, *Doryphora* and *Laurelia*,occur farther south. It is not unlikely that *Dryadodaphne* arrived in its present tropical habitat fairly recently, after the Middle Tertiary. This is indicated by evidence of two kinds. First, the central New Guinean cordillera,where the genus is now centred,was not raised from the sea until that time (cf. David 1950, chapter XV.). Second, there has been a historic contraction of the forests of *Nothofagus* subsect. *Bipartitae*, with which the genus is associated today, from a drying Australia to the New Guinea region during the late Tertiary (Couper 1960a). Only those forms particularly well adapted to sheltered everwet gully conditions can be expected to have survived in the relatively small rainforest refugia along the east coast of Australia. If their present-day ecological requirements are the same as in the past, it is not surprising that the above subsection of *Nothofagus* and the New Guinea forms of *Dryadodaphne* are absent, because they now show no particular preference for such habitat. On the other hand, the occurrence of the only Australian species of *Dryadodaphne* in semi-swamp gully forest in one small mountain range in north-east Queensland assumes special significance here.

The fact that the more specialised species of *Dryadodaphne* extend to lower altitudes than the single unspecialised one, *D. pterandrica*, is further evidence for adaptation to warmer environments in the family.

10. In summary, the Atherospermataceae are an ancient yet morphologically very coherent family. They were ~~It was~~ probably never more diverse than they are ~~it is~~ now, if the fossil record can be taken as indicative. They were ~~It was~~ formerly much more widespread on the southern continents, and survive today only in confined areas of suitable rainforest habitat bordering the southern Pacific ocean.

The overall pattern of relationships between the genera is partly reticulate. Ehrendorfer et al. (1968) have emphasised the role of historic hybridisation and consequent polyploidy in determining such reticulate patterns of relationship in woody ranalean plants. That there is no simple evolutionary sequence in morphological characters paralleling adaptation to warmer environments is not surprising because of the combined effects of historic geographic disjunctions and regional vicissitudes of environment in promoting divergent and convergent evolutionary trends in the family.

11. The genus Daphnandra, through its association with disturbed habitats and evolution of more specialised and perhaps more efficient flowering and fruiting mechanisms, occupies a wide range of habitats, and is varying and speciating. Such active expansion is not evident at present in the other genera. The processes of evolution associated here with the exploitation of new habitats have provided a framework and impetus for further diversification in the family.