STUDIES ON THE MORPHOLOGY, ONTOGENY AND EMBRYOLOGY
OF THE FLOWERS OF HEDYCARYA ARBOREA J.R. et G.Forst.
(SUBFAMILY MONIMIOIDEAE) AND LAURELIA NOVAE-ZELANDIAE
A.Cunn. (SUBFAMILY ATHEROSPERMOIDEAE) OF THE FAMILY
MONIMIACEAE.

Volume 1 - TEXT

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Male flower - Laurelia novae-zelandiae X 8

PHOTO M.D.KING

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ABSTRACT

The inflorescences, flowers and the vascularization of floral parts of Hedycarya arborea and Laurelia novae-zelandiae were described and comparisons made with other members of the family in an attempt to determine the basic types of inflorescences, flowers and floral vascularization in the family.

The vegetative, inflorescence and floral meristems of the two genera were compared. It was concluded that the vegetative apices of both had the tunica-corpus configuration typical of many other woody Ranales and other orders. The inflorescence apices were quite similar to the vegetative ones. The young floral apices are in a state of transition from a tunica-corpus to a mantle-core configuration and older floral apices had the mantle-core configuration, which is typical of the floral apices of many woody Ranales. Unusual features of the floral apices of Hedycarya and Laurelia were the lack of a pronounced rib meristem and the occurrence of relatively frequent divisions within vacuolate cells of the core.

The ontogeny of the stamens of Hedycarya and Laurelia was described and comparisons were made. In both genera the microsporangium developed in a similar fashion: in Hedycarya 5-6 wall layers are formed inside the epidermis; in Laurelia there are 3-5 layers. Both genera had a typically thickened endothecium and a tapetum of the secretory type in which the tapetal cells become binucleate during the first meiotic division of the pollen

mother cells. In Hedycarya the meiotic divisions of the pollen mother cells are of the successive type in which walls form by means of centrifugal cell plates. Pollen grains remain in permanent tetrads in this genus. In Laurelia wall formation at the end of meiosis is of a modified simultaneous type, which may not have been hitherto described in the literature. Pollen grains are not in permanent tetrads. When the first division occurs in each microspore in Hedycarya, all four cells of a tetrad are at the same stage of division and the generative cell is cut off towards the distal face of the grain. Each microspore is in the two celled condition when shed. It was deduced that the generative cell is cut off against what represents a radial wall of the grain (with reference to the tetrad stage) in Laurelia. Pollen is shed in either the two or three celled condition. Comparisons were made with the development of microsporangia and male gametophytes in other woody Ranales.

A study was made of the ontogeny, structure and function of the staminal appendages of Laurelia. It was found that the appendages function as nectaries, the nectar being predominantly sucrose. After a discussion of the various theories as to the morphological nature of the staminal appendages of the Laurales, it was concluded that they are morphologically staminodes.

The carpels of Hedycarya and Laurelia have a basically similar ontogeny in which, as in the Lauraceae, the terminal stigmatic region develops from a solid terminal meristem in contrast to

many woody Ranales in which the stigma consists of crests which surround the external part of the cleft of the carpel. The ovules of Hedycarya and Laurelia resemble those of most other woody Ranales in being bitegmatic, crassinucellate and ^aantropous with a monosporic 8-nucleate embryo sac of the Polygonum type. Both linear and T-shaped megaspore tetrads were found in the two genera.

Laurelia has pseudocarps which develop after anthesis and enclose plumose achenes, but in Hedycarya the fruits are drupes.

It was concluded that Laurelia and Hedycarya belong to two subfamilies which have been separated from each other for a long time and have undergone considerable evolution in different directions. It was also concluded that the Monimiaceae are closely related to the Lauraceae.

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MATERIALS AND METHODS

Collections were made for 2 years (1963-4) at monthly intervals or less and later (1965-6) at more infrequent intervals, from a single Laurelia tree (a remnant of native bush) on the property of Mr and Mrs Bublitz, 19 Oriental Street, New Plymouth and from a male plant and a female plant of Hedycarya growing on the fringes of native bush adjoining the Bublitz property.

Supplementary collections were made at sporadic intervals from a Laurelia at Pakuratahi Forks, S.E. Tararua Range. Flowers were collected from trees on the western side of Lake Ponui, Western Wairarapa district in late October and early November 1966. Additional material of Hedycarya was obtained from Wilton's Bush, Wellington and from the western side of Lake Wairarapa at infrequent intervals.

Unless otherwise stated, descriptions apply to the New Plymouth material.

The material was fixed and preserved in formalin-acetic-alcohol, aspirated with a vacuum pump as soon as possible after collection and after some months transferred to 70% ethanol to avoid any possible hardening of tissues due to prolonged storage in f.a.a. It was embedded in Gurr's 56°C m.p. paraffin wax by the tertiary butyl alcohol method of Johansen (1940) and sectioned with a Spencer rotary microtome at 5-12 μ thickness, according to the stage of development. Sections of vegetative buds were stained in safranin and fast green; other sections were stained in

Heidenhain's iron haematoxylin according to the rapid method of Darlington and La Cour (1960) and mounted in Canada balsam.

Both genera had floral bracts and bracteoles, peduncles and pedicels, perianth parts, portions of the stamens, carpels (excluding the stigmatic surfaces) and the floor of the receptacle, covered with long trichomes which become thick-walled as they mature. During sectioning some of the trichomes were deflected by the microtome knife causing damage to the sections. In order to obtain satisfactory sections, most of the mature trichomes had to be removed with the aid of a scalpel and dissecting microscope before the material was embedded. To simplify this procedure, parts no longer required for study were excised e.g. mature perianth segments. The dense covering of trichomes on sub-mature and mature carpels could not be cut off without removing some of the underlying tissues and it was found less time-consuming to dissect out and embed the ovules, once sufficient stages in carpel growth had been sectioned. This laborious and painstaking task seemed preferable to attempting to soften the trichomes by chemical means, which would tend to macerate the material. Mauritzon (1935) also found it necessary to remove hairs when studying the embryology of the carpel of Peumus (Monimiaceae). The trichomes prevented the sectioning of whole inflorescences except at a very young stage in development. Approximately 100 buds of each sex, of each genus, were sectioned in order to obtain reasonably complete stages in the growth of flowers to anthesis.

Information from sections was supplemented by the dissection of material under a Zeiss Opton dissecting microscope at magnifications of up to 160 times.

Preserved flowers were cleared in sodium hydroxide to reveal their vasculature by the method of Bailey and Nast (1943b).

Drawings of dissections were made with the aid of a Carl Zeiss camera lucida with built-in polarizing filters.

Photomicrographs were taken on Ilford Pan F 35 mm. film (a) under ordinary light with an Asahi Spotmatic camera mounted without lens to a Leitz Laborlux microscope (b) under ordinary light and phase contrast with a Carl Zeiss Photomicroscope.

All photographs were taken by the author unless otherwise stated.

The method used for testing for sugars in the exudate from the staminal appendages of Laurelia is described in the appendix.

I collected the following material from Australia and Tasmania in order to compare the flowers of Laurelia and Hedycarya arborea with those of some other members of the Monimiaceae:-

Atherosperma moschata Labill. (syn. Atherosperma moschatum Labill.)

Male and carpellate flowers and flower buds were collected from trees of this monotypic genus in Mount Field National Park, Tasmania on 21-8-65.

Doryphora sassafras Endl. Flowers and flower buds were collected from trees of this monotypic genus growing near Bowens Creek, Blue Mountains, New South Wales on 29-8-65.

Hedycarya angustifolia A. Cunn. Flowers and flower buds were collected from male and female trees on Mount Wilson, Blue Mountains, New South Wales on 29-8-65.

CHAPTER 1

INTRODUCTION

There has been renewed interest in the morphology of the woody Ranales in recent decades, following the finding of apparently primitive leaf-like stamens and carpels within the group, which began with the discovery of Degeneria (Bailey and Smith, 1942; Smith, 1949; Swamy, 1949). This led Bailey, Smith, Swamy, Nast and co-workers at Harvard University to a detailed re-investigation of the comparative morphology of many families within the woody Ranales, including the Monimiaceae. They found primitive types of wood anatomy, phloem structure, nodal anatomy, embryo development and pollen (some of these primitive features had been known in this group for some time) and stages in the phylogenetic development of more advanced types. In addition they discovered phylogenetic stages in the development of the leaf-like stamens, carpels and perianth parts leading to the more conventional flowers in the woody Ranales and other orders. References to, and summaries of, this work can be found in Eames (1961). These investigations were mostly based on studies of adult material, frequently re-expanded from herbarium specimens.

Subsequently more detailed studies have been made by a number of botanists, frequently on individual species or small groups of related genera. These studies, which were often ontogenetic in nature, using properly preserved material, in general confirmed

and extended the earlier work. They included studies on the structure and development of shoot apices of certain woody Ranales (Gifford, 1950); studies on the stamens, pollen, carpels, floral apices and vegetative shoots of the Magnoliaceae (Canright, 1952 a & b, 1960, 1963; Tucker, 1960, 1961, 1962, 1963); studies on the ontogeny of inflorescences and ontogeny and vascularization of flowers of the Winteraceae (Tucker, 1959; Sampson, 1963; Tucker and Gifford, 1964, 1966 a & b); studies on the ontogeny of the leaf and vegetative axillary bud of one of the Winteraceae (Gifford, 1951 a & b); on the morphology of the Lactoridaceae (Carlquist, 1964); on the flowers of the Nymphaeaceae (Moseley, 1958, 1961, 1965); on the pollen morphology of some ranalean families (Canright, 1963) and on the morphology of leaves, apices and flowers of two members of the Lauraceae (Kasapliligil, 1951).

There has been an increasing acceptance during this century that the Ranales and their allies are the most primitive angiosperms (Moseley, 1965). However, the Ranales are undoubtedly a heterogeneous assemblage, which as Eames (1961) states, are held together by the possession of several primitive characters and "the families seem to be an assortment of relic types, representing several ancient lines rather than a single basic stock. Archaic characters have been retained but are combined with well, even highly, advanced structure".

Introduction to present study

I was attracted to a study of floral morphology within the

Monimiaceae in that this family appeared an interesting one, on the fringes of the woody Ranales. It possessed considerably more advanced floral structure than Pseudowintera of the Winteraceae, which I had studied previously (Sampson, 1961, 1963). Furthermore, two genera, Hedycarya and Laurelia, were readily accessible as they occur within the native flora of New Zealand. The genera are in different subfamilies and seemed at least superficially quite dissimilar in floral structure. An additional consideration was that there have been few studies on floral morphology within the family, but a recent comparative study of the morphology and relationships of the various genera in the family by Money, Bailey and Swamy (1954) provided a good basis from which a detailed study of the floral ontogeny, morphology and embryology of the two genera could be made.

Money et al. (1950) concluded that "the Monimiaceae is a key family in understanding and in interpreting the morphology, not only of the Lauraceae, Gomortegaceae, and Hernandiaceae, but also of the Chloranthaceae and probably other dicotyledonous families". The Monimiaceae has long been considered closely related to the Lauraceae and in the latter family a number of studies have been made on floral development in various genera (see Sastri, 1958). These studies included, in addition to those of a primarily embryological nature, a Ph.D. study of the apices and flowers of two genera (Kasapligil, 1951). Kasapligil paid particular attention to the vascular anatomy of the flowers and

to the nature of their staminal appendages which have been variously interpreted. This work was of great interest to me, as Laurelia possessed apparently analagous staminal appendages and the considerable embryological studies in the Lauraceae provided a basis whereby comparisons could be made with the embryology of Hedycarya and Laurelia.

Previous relevant studies in the Monimiaceae

(a) Perkins and Gilg (1901) and Perkins (1911) had provided a detailed description of the genera and species in the Monimiaceae, as part of "Das Pflanzenreich". These descriptions totalled almost 200 pages.

(b) Heilborn (1931) described the embryology of the female plant of a species of Siparuna, a genus which Money et al., (1950) placed together with two other genera, in a separate subfamily, the Siparunoideae. Heilborn's results indicated a unique and anomalous type of embryology (see Chapter 6).

(c) Mauritzon was attracted by the unusual results of Heilborn and therefore studied the embryology of the female flower of Peumus, a genus which Money et al., (1950) included, together with Hedycarya and some other genera, in the subfamily Monimioideae. Mauritzon's (1935) results indicated nothing very unusual in the embryology of Peumus.

(d) Money et al's (1950) study compared the leaves, stem anatomy, nodal anatomy and flowers of the various genera of the family and the authors made some taxonomic changes including the

removal of some genera from the family.

Aims of the present study

(a) To describe and compare the structure of the inflorescences and flowers of Hedycarya and Laurelia, including the vascularization of floral appendages and to make comparisons where possible with other members of the family and of related families in an effort to interpret the relative stages of evolution of the various floral parts, compared to other woody Ranales.

(b) To describe and compare the vegetative, inflorescence and floral meristems of the two genera and to make comparisons with similar studies on other ranalean genera.

(c) To describe and compare the ontogeny of the stamens and the development of the microsporangia and male gametophytes of the two genera and to interpret these results in relation to similar studies on other woody Ranales.

(d) To study the ontogeny, structure, function and morphological nature of the staminal appendages of Laurelia and to make comparisons with Kasapligil's studies on the staminal appendages of Laurus and Umbellularia of the Lauraceae.

(e) To describe and compare the ontogeny of the carpels of Hedycarya and Laurelia and to interpret their nature in the light of the trends of carpel specialization which Bailey and Swamy (1951) have proposed for the woody Ranales.

(f) To describe and compare the development of the megasporangia and female gametophytes of the two genera and to

interpret the results in relation to studies on related genera.

(g) To assess the relationships of the Monimiaceae in view of the results obtained from this thesis.

Distribution of Hedycarya and Laurelia

Hedycarya is a genus of 25 species (Willis, 1966) which occur mainly in New Caledonia but also in Australasia, Fiji, Samoa and the Solomon Islands (Allan, 1961; Perkins and Gilg, 1901; Perkins, 1911). Laurelia comprises 2 (Willis, 1966) or 3 (Perkins, 1911; Money et al., 1950) species one of which occurs in New Zealand and the other one or two in Chile. Hedycarya arborea, the sole New Zealand species of the genus, occurs throughout the North and South Islands and on Three Kings Island, in lowland to montane forest (Allan, 1961). Laurelia novae-zelandiae occurs in lowland semi-swamp and gully forest and is distributed throughout the North Island and extends to latitude 42° on the east and 46° on the west of the South Island (Allan, 1961).

Laurelia (aff. novae-zelandiae) pollen appeared in the fossil record of New Zealand in the Waitakian Stage (middle Oligocene), according to Couper (1960). Berry (1935) recorded that macro-fossils of Laurelia have been found from Tertiary strata in South America and Seymour Island. Hedycarya has not been recorded in the fossil flora of New Zealand. Four species of this genus have been recorded from the Oligocene and Miocene of Europe and a fifth from the Tertiary of Australia (Berry, 1935).

CHAPTER 2

THE INFLORESCENCES AND FLOWERS

Introduction

Hedycarya arborea is dioecious (Allan, 1964). Allan described Laurelia as being dioecious to polygamous, defining the latter term as "bearing unisexual and bisexual flowers on the same plant". Hermaphrodite flowers of Laurelia novae-zelandiae have been described as being similar to the female, but with "some or all of the outer row" of stamens perfect (Cheeseman, 1925). Male flowers lack rudiments of carpels.

I have examined 20 Laurelia trees in various localities (New Plymouth, Pakuratahi Forks, Lake Ponui and Kapiti Island) and all were polygamous. All plants had many more male flowers than other types. Inflorescences were either wholly male or mixed, never of wholly female and/or hermaphrodite flowers in the several hundred inflorescences which I examined. Some trees had a ratio as high as approximately 100 male flowers to every 1 female or hermaphrodite flower. It is possible that a larger sampling might reveal male trees but it does not seem likely that trees exist with only female and/or hermaphrodite flowers. Thus, results indicate that this species is not truly dioecious.

The female and hermaphrodite flowers are very similar in structure and present a problem in terminology. Both contain staminodes which become progressively reduced towards the centre

of the flower. The hermaphrodite flowers have in addition, external to the staminodes, one or more functional stamens. Similarly, in the related monotypic Atherosperma moschata, it has been noted that the so-called female flowers have "the outer row consisting of staminodia, and often (in Tasmania) developing perfect anthers in 2 or 3 of them" (Rodway, 1903). Not infrequently in Laurelia, one or more of the outermost staminodes in the female or hermaphrodite flowers undergo dehiscence but their pollen sacs contain abortive pollen. Sometimes too, in the stamens of male and hermaphrodite flowers, one of the two pollen sacs is full of abortive pollen and this sac may or may not undergo dehiscence. It is concluded that there is an unstable transition stage in the evolution from an hermaphrodite to a female flower. Hermaphrodite flowers were of greater abundance than female ones. For example 38 out of 50 carpellate flowers, chosen at random, had one or more functional stamens. Money et al., described the flowers of Laurelia sempervirens (Ruiz & Pav.) Tul. and erroneously those of L. novae-zelandiae, as being invariably unisexual. They found that the flowers of Laurelia serrata Phil. had "in addition to functional carpels, two or more stamens with sporangia that contain fully developed pollen". They examined limited material and I would think it possible that all 3 species have both hermaphrodite and female flowers. For simplicity, I will in general refer to both the female and hermaphrodite flowers as carpellate.

	Hedycarya arborea	Laurelia novae-zelandiae
	MALE FEMALE	MALE FEMALE
Perianth primordia initiated	April - June	March - April
Stamen primordia initiated	May - July	April
Carpel primordia initiated	July	April - May
Sporogenous tissue within stamens	July - September	May - July
Megaspore mother cell within ovules	September	August
Microsporogenesis	September	July - Mid September
Megasporogenesis	Late September - October	Late August - September
Division of microspore nucleus	October	Late September
1, 2 & 4 - nucleate embryo-sacs	November	October
Flowering begins	Late October	Mid October
Fruits (<i>Hedycarya</i>) and pseudocarps (<i>Laurelia</i>) initiated the previous year approach their maximum size.	May - September	January - April
Ripe fruits (<i>Hedycarya</i>) and dehiscing pseudocarps (<i>Laurelia</i>) which were initiated the previous year.	October - November	May - November
Formation of next year's inflorescences begins	October	September

Perianth primordia initiated

Stamen primordia initiated

Carpel primordia initiated

Sporogenous tissue within stamens

Megaspore mother cell within ovules

Microsporogenesis

Megasporogenesis

Division of microspore nucleus

1, 2 & 4 - nucleate embryo-sacs

Flowering begins

Fruits (*Hedycarya*) and pseudocarps (*Laurelia*) initiated the previous year approach their maximum size.

Ripe fruits (*Hedycarya*) and dehiscing pseudocarps (*Laurelia*) which were initiated the previous year.

Formation of next year's inflorescences begins

TABLE I - STAGES IN THE DEVELOPMENT OF HEDYCARYA & LAURELIA FLOWERS AT NEW PLYMOUTH 1963-4

Stages in flower development

Table I summarizes stages in floral development. The three trees were growing within 50 yards of one another and occupied similar habitats with respect to slope, aspect, altitude and presumably soil type, thus enabling meaningful comparisons to be made. No significant differences were noted in the times at which particular events occurred from one year to the next. For example collections of Laurelia on 29-8-63 and 29-8-64 both contained some carpellate flowers with megaspore mother cells at prophase I and some male flowers with stamens undergoing microsporogenesis. Similarly, collections of Hedycarya on 21-10-63 and 17-10-64 contained some female flowers with megaspore mother cells at prophase I and some male flowers in which the unicellular microspores were dividing. Furthermore, in Laurelia, no significant differences were found in the times at which various events occurred in the stamens of male flowers compared with those of hermaphrodite flowers. On 28-9-64 for example, some male and some hermaphrodite flowers had stamens with microspores undergoing their first division.

The following points are relevant to the Table:-

(a) Some range of developmental stages of stamens and carpels may be present at one time, although not within a single flower, except during the time when primordia are being successively initiated. For example some Laurelia flowers collected on 14-7-63 had stamens in which the sporogenous tissue was still dividing

whereas others had stamens undergoing microsporogenesis.

(b) Floral development continues throughout the winter, in contrast to those temperate climate plants with flowers which are quiescent during the middle of winter e.g. Drimys lanceolata (Tucker and Gifford, 1966a).

(c) During October three stages are present on Laurelia and female Hedycarya trees:- open flowers, mature fruits from the previous year's flowers and young buds of the following year's flowers.

(d) Perianth primordia are initiated somewhat earlier in the male Hedycarya flowers although the female flowers begin flowering about two weeks before the males. However the ovules are not mature at anthesis and immature (4-nucleate) embryo sacs were not found until mid-November at which time male plants were in full flower.

(e) It is stated in the Table that formation of the next year's inflorescences begins in September (Laurelia) and October (Hedycarya). These dates need qualification as they refer to the time at which the inflorescence buds are visible in the axils of leaves which have recently expanded from the bud stage (PLATE 1, fig. 1, uppermost pair of spreading leaves). Actual initiation of inflorescence primordia, in the axils of leaf primordia within the bud, would have occurred at an earlier date.

Structure of inflorescences

Allan (1961) described the inflorescences as "axillary cymes

or racemes". Neither of these terms, in their usual sense, accurately describes the inflorescences. In both genera the inflorescence arises in the axil of a leaf, or rarely leaf-scar, and consists basically of an axis bearing a number of decussately arranged pedicellate flowers, each of which arises in the axil of a bract*. The axis terminates in a flower (PLATE 1, fig. 2) which may, or may not, be subtended by a bract or pair of bracts. Some inflorescences are compound, with a secondary axis arising in the axil of one or more of the lower bracts (PLATE 2, fig. 1). Each of these secondary axes usually consists of two flowers forming a monochasium (PLATE 2, fig. 2) ^{at lower left} or three flowers, forming a dichasium (PLATE 2, fig. 1). Sometimes a secondary axis resembles the primary axis and bears several pairs of decussately arranged flowers and terminates in a flower. Most bracts abscise shortly before anthesis, although the lowest pair may be more persistent.

The following variations were noted in the structure of inflorescences:-

- (a) One or both of the lowest (proximal) pair of bracts, and rarely bracts elsewhere, may not subtend a flower or inflorescence.

* Bract is used in the sense of a reduced leaf-like structure which subtends an inflorescence or flower or is present on the flower stalk or on the floral receptacle below the perianth parts. Many writers regard a bract as a leaf (whether reduced or not) in the axil of which a flower arises and a bracteole (prophyllum) as similar to a bract but arising on the flower stalk itself (e.g. Rendle, 1930; Willis, 1955; Lloyd, 1950).

Such a bract usually subtends a vegetative bud. This bud invariably remains dormant and wilts before the time of anthesis. On occasions a bract is completely barren. Although they are usually at the base of the inflorescence, the lowermost bracts may arise some distance (up to 8 mm.) from it (PLATE 2, fig. 3 - inflorescence at right). They are usually inserted so that they are decussate to the subtending leaf and stem to which it is attached, but are sometimes inserted in the median plane of the subtending leaf and stem.

(b) The terminal flower is often ebractate, with one or more bracts inserted on its pedicel* or at the base of the floral receptacle. Rarely other flowers are ebractate, in the sense that they do not arise in the axil of a bract although a bract or bracts are often present on the pedicel or at the base of the receptacle. On occasions, in both genera, there appears to be a gradation between bracts and perianth parts with transitional appendages being inserted on the receptacle external to the perianth parts.

(c) In Hedycarva the ultimate and penultimate pairs of flowers

* It is sometimes difficult to judge precisely where the inflorescence axis ends and the pedicel of the terminal flower begins, in a nearly mature inflorescence. In PLATE 1, fig. 2, the terminal flower at first glance does not appear to arise in the axil of a bract, for the bract scar is at "s". However it would appear from a difference in texture of the "stalk" above and below "s", that the pedicel does begin above "s". In other words, in this instance the inflorescence axis has extended appreciably beyond the level of insertion of the ultimate pair of pedicels. In other instances it would appear that the inflorescence axis does not grow appreciably above the level of insertion of the ultimate pair of flowers.

are frequently not separated by an internode, but the level of insertion of the penultimate pair of flowers is slightly below that of the other pair (PLATE 2, fig. 2).

(d) In Laurelia a lateral branch is formed when the vegetative bud in the axil of a leaf (PLATE 1, fig. 2) breaks dormancy. A leaf has either a vegetative or an inflorescence bud in its axil but not both. It was observed in two herbarium specimens of L. serrata that when a lateral branch is formed, the first pair of leaves are smaller than the others (PLATE 62). This feature was occasionally found in L. novae-zelandiae. As stated, the inflorescence axis may itself bear one or more bracts which subtend a vegetative bud, but this remains dormant. In both Hedycarya arborea and H. angustifolia some leaves bear both a young lateral branch and an inflorescence in their axils - the inflorescence being situated closest to the petiole.

(e) A few aberrant inflorescences were found, noteworthy among which was that of a female Hedycarya plant with four pairs of decussately arranged flowers subtended by bracts which became progressively larger and more leaf-like. The ultimate (5th) pair of bracts resembled miniature toothed leaves and each subtended a vegetative bud and the axis terminated in an apical vegetative bud similar to that at the tip of a shoot. The axis had therefore undergone reversion from a floral to a vegetative shoot.

(f) In some Hedycarya inflorescences a pair of flowers or

(INSERT)

Medycarya

There were from 3 to 15 flowers per inflorescence. The inflorescence with three flowers had been formed at the end of the flowering season. It comprised a lowermost pair of fertile bracts with a sterile pair above and terminated in a single flower which was subtended by a third pair of bracts. The commonest number of flowers per inflorescence was 7, for both male and female plants.

secondary inflorescence axes are not inserted directly opposite one another (PLATE 2, fig. 2).

(g) In a few mixed inflorescences of Laurelia, the axis terminated in a pair of flowers.

Hedycarya - see insert at left
Laurelia

There were from 5 to 20 flowers per inflorescence. A diagram of a male inflorescence with 20 flowers is shown in PLATE 3, fig. 4. The commonest number of flowers per inflorescence was 7 for male and 9 for mixed inflorescences. In the mixed inflorescences, the main axis, and secondary axes where present, invariably terminated in a male flower (PLATE 3, figs. 1-3, 5-7). The carpellate flower or flowers are usually inserted immediately below the terminal flower of the main or secondary axis (PLATE 3, figs. 2, 3, 5-7). In one case however the single carpellate flower was one of the penultimate pair (fig. 1). In another case one of the ultimate pair and one of the penultimate pair of flowers were carpellate. The ratio of male : carpellate flowers varied somewhat but in general male flowers predominated. Out of 50 mixed inflorescences chosen at random, 76% contained predominantly male flowers, 2% had the same number of male and carpellate flowers and 22% had predominantly carpellate flowers. Ratios varied from 8 male ; 1 carpellate (fig. 1) and 1 : 1 (4 male and 4 carpellate) to 3 male : 14 carpellate (fig. 7). The commonest ratio found in the New Plymouth material was 5 male : 4 carpellate (32% of the 50 inflorescences).

Conclusions

The terminal vegetative meristem of a shoot and the inflorescence apical meristem are homologous in that they initiate in acropetal succession decussately arranged leaves (vegetative meristem) or bracts (inflorescence meristem) in the axils of which arise buds. These are inflorescence or vegetative buds (vegetative meristem) and flower buds or secondary inflorescence buds (inflorescence meristem). The two meristems differ in that the vegetative is indeterminate and theoretically unlimited in the number of leaves it can give rise to, whereas the inflorescence meristem (and any secondary inflorescence meristems it may produce) is determinate. The inflorescence meristem is transformed into a floral meristem which grows into the terminal flower of the primary or secondary inflorescence axis. Although the order of initiation of the flower buds is acropetal, flowering begins at approximately the same time for all the members of an inflorescence. Flowers of an individual inflorescence open within one or two days of each other and a flower in any position on the inflorescence may be the first to open.

These inflorescences would not come within the common usage of racemose which is usually defined in texts as an indeterminate inflorescence consisting of an axis bearing flowers in acropetal succession. Nor could they be described as cynose which is generally defined as a determinate inflorescence displaying sympodial growth "in which each successive branch ends in a flower

after bearing one or more bracteoles, from whose axils the branching is continued" (Willis, 1955). Thus "the first formed flower limits apical growth of the main axis of the inflorescence" (Eames, 1961).

The inflorescences resemble the racemose type in being basically monopodial and the cymose type in being determinate. Secondary inflorescence axes when they do not resemble the main axis, appear to be of the monochasial or dichasial type. The resemblance to these types is strengthened in that the terminal flower is often ahead of the other flower or flowers in its development, for a time (see monochasium at lower left in PLATE 2, fig. 2).

Eames (1961) has criticised as "unsatisfactory" and "morphologically inaccurate" the way in which the order of development of flowers is used to distinguish the major types of inflorescences. He noted that many inflorescences are intermediate in type, with racemose forms which have a terminal flower and added that a single genus may have both determinate and indeterminate inflorescences. Carlquist (1961) has praised the work of Rickett (1955) in delimiting and redefining inflorescences. According to this classification the inflorescences of Laurelia and Hedycarya would be of the racemose type. After an historical survey of various definitions in which he pointed out inconsistencies in their application to actual inflorescences, Rickett concluded that the important distinction between racemose and cymose inflorescences

	<i>Hedycarya arborea</i>		<i>Laurelia novae-zelandiae</i>	
	MALE	FEMALE	MALE	CARPELLATE
Perianth parts per flower	7 - 11 (8)	4 - 8 (6)	4 - 9 (5)	5 - 9 (7)
Functional stamens	18 - 64		7 - 13 ■ (10)	0 - 6 (2 & 4)
Staminodes	0			13 - 24 (15)
Functional carpels		7 - 22 (13)		8 - 12 (10)
Sterile carpels		3 - 16 (9 & 12)		0
Length of pedicel	5 - 18 mm.	6 - 16 mm.	5 - 9 mm.	2 - 4 mm.
Flower diameter at anthesis	9 - 16 mm.	4 - 7 mm.	5 - 12 mm.	6 - 10 mm.
Length from base of primary inflorescence axis to base of floral receptacle of terminal flower *	2.1 - 6 cm.	2 - 3 cm.	1.6 - 4.5 cm.	1.6 - 5 cm.

* Range found in 25 samples of each type of inflorescence

NOTE: 1. Figures in brackets indicate the most common number of parts per flower.

2. 50 flowers of each type were chosen at random and used to compile all but the last ~~line~~ of this table.

TABLE 2 - STRUCTURE OF FLOWERS OF HEDYCARYA & LAURELIA COLLECTED AT NEW PLYMOUTH

was whether they were monopodial or sympodial. I would concur with these views and it can be seen that Hedycarya and Laurelia would conform to Rickett's definition of racemose as - a monopodial inflorescence composed of a central axis along the sides of which arise pedicellate flowers or small flower-clusters, usually arising in the axils of bracts; flowering is commonly but not necessarily acropetal, and the axis may or may not be terminated by a flower.

Inflorescences of other members of the family will be discussed later in the chapter.

Structure of the flowers

Floral structure is summarized in Table 2. The carpellate Laurelia flowers are readily distinguished from the males even in bud stage because they are perigynous with an urceolate receptacle, whereas the male flowers are hypogynous* (PLATE 1, fig. 2; PLATE 2, fig. 1). Male and female Hedycarya flowers can also be distinguished from an early stage in development. The female flowers (PLATE 4, fig. 2) have relatively small perianth segments, which do not overlap one another much in the bud. The male perianth parts are larger and not as tapered. They overlap considerably in the bud stage and the male flower has a concave receptacle with the tips of the tepals curving downwards into the central concavity (PLATE 2, fig. 2) in marked contrast to the female flower. The inflorescences differ in that the male ones are more erect.

*This is also true for Atherosperma, but a pair of bracts enclose each flower bud and mask these features.

In both genera the perianth parts are not differentiated into sepals and petals. These tepals are larger than the bracts, but as stated intermediate forms are often found. Bracts and tepals are rather similar in colour and texture except that the tepals are less pubescent on their inner (adaxial) surfaces, which are a lighter shade of green or greenish-white (PLATE 5, fig. 1; frontispiece). The tepals persist into the fruit stage and can be seen ("t") on mature pseudocarps of Laurelia (PLATE 6, fig. 1) and below fruits of Hedycarya (fig. 2).

In Laurelia the two outermost tepals are usually opposite each other and decussate to the subtending bract and inflorescence axis. The remaining tepals are arranged in a spiral of about $1\frac{1}{2}$ turns. In some flowers all of the tepals are arranged in two whorls. In the bud stage part of each tepal overlaps part of the adjacent one (imbricate aestivation), apart from the two outer tepals where the tip of one tepal may overlap the tip of the other.

In Hedycarya the outermost four tepals are arranged in decussate fashion although one of the inner pair may not be exactly opposite to its partner. The remaining tepals are arranged in a whorl. In some cases only the outermost pair of tepals are inserted outside the others and the latter are in a whorl. At maturity the tepals usually appear to be in a single whorl (PLATE 5, fig. 2). Some flowers have one or more reduced tepals inside the others, arranged in a second whorl (PLATE 5, fig. 3, "p").

The female flowers of Hedycarya commonly have fewer tepals than the males in contrast to Laurelia (Table 2). In Hedycarya too, the female flowers are of smaller diameter* (Table 2). In Laurelia the male and carpellate flowers are of similar diameter but as shown in the Table the carpellate flowers have shorter pedicels. The pedicels of male flowers are equal to the combined length of the pedicels of carpellate flowers and the urceolate receptacle. This seems to be slight evidence for regarding the urceolate receptacles of carpellate flowers as axial in nature (see on).

The stamens of Hedycarya are arranged without great precision along a spiral of approximately 3-4 turns. The outermost carpels in the female flower are sterile and reduced in size and structure (e.g. "c" in PLATE 12, fig. 3). They occupy a single whorl or sometimes two whorls. They are solid structures without a locule. Some carpels were found internal to these, in some flowers, with a structure somewhat intermediate between the sterile and fertile carpels. They possessed an ovule but this was reduced in size. One such ovule had reached the megaspore mother cell stage but did not develop further. Internally the fertile carpels are arranged along a spiral of about 3 turns.

The stamens in the male flower of Laurelia are arranged in a spiral of 2-3 turns (PLATE 5, fig. 4). The stamens (where present) followed by staminodes in the carpellate flower are

* Measured from petal-tip to petal-tip when the flower is fully open.

arranged in a spiral of about 3 turns (PLATE 5, fig. 5). It seems surprising that the carpellate flower should contain a greater total number of stamens and staminodes, than the male flower does of stamens (Table 2). The carpels are arranged in a spiral of approximately $1\frac{1}{2}$ turns. A single teratological flower was found in which functional stamens and staminodes were present as in a carpellate flower but the flower lacked carpels.

Vascularization of floral parts

Laurelia:- bracts and tepals

No significant differences were found in the vasculature of bracts subtending male flowers on the one hand and carpellate flowers on the other; nor between tepals of male and carpellate flowers; nor between functional stamens of male and carpellate flowers. The bracts (PLATE 7, figs. 9 & 10) have a more complex vascular supply than the tepals (figs. 1-8). Each bract has a number of fine central strands* which do not branch and a number of lateral traces, more (fig. 9) or less (fig. 10) adjoining the central strands. The lateral traces are branched and in some bracts (fig. 10) they anastomose.

The vascularization of tepals varied considerably. For example figs. 3-8 illustrate the vasculature of 6 tepals from a

* It should be noted that in this and other illustrations only the tracheary elements of the xylem are illustrated. The techniques used did not render visible other elements of the vascular bundles. Thus in fig. 9 for example, what appears to be a number of fine central vascular strands is in fact just the water conducting elements of the xylem and each strand is one or more tracheary cells in width.

single carpellate flower. No two of these have the same vascularization. There were two basic patterns; (a) a single median trace (figs. 1, 6) or group of traces, with lateral branches; or (b) a single median trace or traces, with lateral branches, plus a lateral trace which may or may not branch, on either side of the median trace (figs. 2-5, 7, 8). An unusual feature of tepal vascularization was the presence of isolated vascular strands near the periphery of the tepal. They were present in all tepals examined. Figs 1 and 2 of PLATE 8 are photomicrographs of an isolated vascular strand found within the dotted portion of fig. 1, PLATE 7. Kasapligil found on occasions one or two isolated traces within the sepals and petals of Umbellularia. He concluded that they might possibly represent a reduction series from a three-trace to a one-trace condition in the sepals and petals (see figs. 14-22 of his paper). He did not find isolated traces near the margins of the perianth parts analagous to those in Laurelia. I, like Kasapligil, did not make a detailed study of the isolated strands to determine whether they were connected to other strands via undifferentiated procambium. Such a study would be time-consuming as procambium is not visible in clearings and one would have to make a three-dimensional reconstruction from serial sections. I would suggest that tepals have been derived from bracts in Laurelia and that the isolated strands represent traces which have been partly lost during the derivation of the tepals from the more extensively

vascularized bracts. Kasapligil noted that isolated traces have been found in floral organs of a number of dicotyledons. I have not been able to find in the literature other examples of isolated peripheral traces in perianth parts.

Hedycarya:- bracts and tepals

No differences were found in the vasculature of bracts of male inflorescences on the one hand and female on the other. The larger bracts (PLATE 7, fig. 19) had a median group of unbranched traces and two lateral branched traces. This basic pattern of central unbranched traces and lateral branched ones is similar to that found in Laurelia, but simpler. No anastomosing traces were seen. Smaller bracts had a more reduced vasculature (figs. 20, 21) with reduction to a single median strand and the smallest bracts were not vascularized.

The tepals too were less complex in their vascularization than in Laurelia. The smaller size of tepals of female flowers was reflected in their simpler vascularization. Figures 11-18 illustrate tepals of female flowers and figs. 14-18 are from a single flower. Most tepals had a single unbranched median strand (figs. 11, 16-18) thereby resembling small bracts. Some contained a pair of strands; one on either side of the mid-line (fig. 13); others a median and a lateral strand (fig. 12). Sometimes the median strand branched (figs. 12, 14, 15). In some cases it seems clear from the size (larger), shape (notched apex) and venation (more traces) of a tepal that it has been formed

from the coalescing of two tepal primordia. The tepals of the male flowers are larger and usually have more veins than those of the female flower. They have 2-5 traces (most commonly 3) which may or may not branch (PLATE 5, fig. 2; PLATE 11).

Laurelia:- stamens and staminodes

There is considerable variation in stamen vascularization (PLATE 9, figs. 1-10). Stamens illustrated in figs. 3-7 were from a single male flower, yet no two have an identical vasculature.

The ear-like, stalked, vascularized staminal appendages of Laurelia and some other genera in the family, which are inserted two per stamen on the filament, have been termed "staminodes" by Money et al., (1950). In Laurelia and in some of the Lauraceae at least, the appendages function as nectaries (see Chapter 5). To avoid confusion with the sterile stamens (i.e. staminodes) of the carpellate flower and in order to use a non-committal term, I shall follow Kasapligil and call the appendages staminal glands in Laurelia. Isolated traces were found in some stamens near the base of the stamen (figs. 3 and 10). Isolated strands were found too in some staminodes (figs. 12 and 14) but situated at a higher level. Kasapligil found isolated strands in some stamens and staminodes of Umbellularia and Laurus. They were not completely analagous to those in Laurelia. In Umbellularia an isolated strand was only found in some of the cases in which one or two of the four pollen sacs had aborted. A vascular tissue was developed in place of the sterilized pollen sacs and

this tissue may or may not be connected to another trace. In the stamens of Laurus the isolated strands occur whenever a staminal gland is reduced in size and its vasculature appears as an isolated tissue. Kasapligil (1951) found that undifferentiated procambium did connect the xylem of such a staminal gland to a lateral vascular trace of the filament. He did not state whether this was invariably so.

Two basic vascularization patterns were found in stamens of Laurelia:- (a) There is a central strand (or strands) without lateral branches which passes through the connective and terminates near the tip of the stamen. The strand may or may not bifurcate near its tip (compare figs. 1 and 2 of PLATE 9). Where there are two or more central strands, these fuse for some of their length (figs. 4, 5, 7, 9, 10) and usually separate near the tip of the stamen and may then bifurcate (e.g. fig. 5, trace at right). Kasapligil too, found that the central vascular tissue in Umbellularia stamens consisted of a single thick trace or a number of thinner traces and made the logical conclusion that the single thick trace has resulted from the fusion of thinner traces. Where there is a single lateral trace to a gland, it usually divides before entering it (figs. 1 and 2 - trace to gland at right). Where there is more than one lateral trace to a gland, these traces may (fig. 1, trace to gland at left) or may not, fuse (fig. 7).

(b) One or both staminal glands may be vascularized by a lateral

branch from the central strand (fig. 6, trace to gland at left) of group of strands (fig. 3, trace to gland at right). Figure 25 of Money et al's paper shows a stamen of Laurelia in which both glands are vascularized by lateral branches of a central strand. In this illustration the extent of prolongation of the connective beyond the anthers has been exaggerated.

Variations within the two basic types were as follows:-

- (i) In some cases a strand enters the base of the filament but soon terminates (figs. 7, 9). Such a strand sometimes originates as a branch of the central strand (fig. 6).
- (ii) In a number of stamens, a strand passes towards the bottom of a pollen sac and terminates at varying distances from it. Such a strand may either be a discrete lateral one (figs. 2, 4) or it may originate as a branch from a strand to a gland (figs. 9, 10 - trace to gland at right).
- (iii) Frequently a glandular trace extends into the filament to a level beyond the level of insertion of the gland and then bends downward abruptly and passes into the gland (e.g. fig. 3). A glandular trace may bend sharply even when it does not extend above the level of insertion of the gland (figs. 8, 10). This type of trace has not been described for stamens of Laurus or Umbellularia. It presents a problem in interpretation. The conservatism of vascular traces has been established in some cases e.g. in Eames' (1931) classic study of the inferior ovary in the Ericales. If the bent strands in Laurelia represented a

conservative condition, this might indicate that the glands were once inserted at a higher level.

Figures 16 and 17 illustrate the vascularization within the staminal glands. Sometimes one but in general two, strands enter the gland and each strand divides a number of times, usually dichotomously, to produce a somewhat dendritic vascular pattern. Similar but more extensive vasculature occurs in Laurus and Umbellularia (Kasapligil, 1951). An unusual feature in Laurus, not found in the other genera, was that the glands of the staminodes of carpellate flowers had a more abundant vascular supply than did those of stamens.

Figure 11 illustrates a transitional stage between a stamen and staminode. This particular organ underwent dehiscence but contained abortive pollen. Its reduced staminal glands were not vascularized. In this situation therefore the hypothesis of conservatism of vascular strands would not apply. The reduced gland shown in fig. 12 is however vascularized. Applying the hypothesis of conservatism again, it could be argued that the two lateral traces of the staminode illustrated in fig. 13 represent traces to formerly existent glands. However they reach rather a high level in the staminode; higher than one would normally find glands, although it should be recalled that glandular traces in some stamens bend downwards. On the other hand the traces may represent a pair of lateral traces analogous to those terminating near the bases of pollen sacs in some functional stamens. The

simplest staminode which I examined, is illustrated in fig. 15. In no instance was a staminode found with a single unbranched median trace thereby differing from the simplest ones in Umbellularia (Kasapligil, 1951). In contrast to the stamens, no staminodes of Laurelia were found in which a median strand or strands bifurcated near the tip of the organ.

Kasapligil concluded on evidence from vascular anatomy and from transition forms, that the staminode of Umbellularia represents only the filament portion of modified stamens. This does not appear to be true for Laurelia. It would seem that the distal part from where the staminode broadens, has been derived from the anther portion of the functional stamen.

A comparison of PLATE 7, figs. 1-8 and PLATE 9, figs. 1-10, reveals that some stamens resemble many tepals in having a median strand or group of strands and a lateral strand (or group of strands) on each side of the mid-vein.

Hedycarya:- stamens

Each stamen is vascularized by a median strand or group of aggregated strands which pass through the connective. The vascular tissue terminates at the level of the distal tip of the pollen sacs and does not extend into the prolonged part of the connective beyond the pollen sacs. Some stamens are vascularized by two strands or two groups of strands which may (PLATE 11, "a") or may not ("b") originate from independent parts of the vascular system of the torus. In PLATE 12, fig. 1, two strands can be

seen at the procambial stage entering a young stamen from different directions. The two strands aggregated near the centre of the stamen (not shown in the section illustrated). As can be seen in the section, the strand has bifurcated near its tip.

Laurelia:- carpels

There is little fluctuation in details of carpel vascularization. A single dorsal and a single ventral trace enter each carpel. These two traces may or may not both come from a single trace in the torus. The ventral (adaxial) trace is short and unbranched and passes through the ventral wall of the carpel until it reaches the funicle of the single anatropous ovule. It enters the funicle and terminates in the chalazal region of the ovule (PLATE 10, figs. 8, 9). The thicker dorsal (abaxial) trace passes through the dorsal wall of the carpel where it bifurcates twice. The strands terminate a short distance below the stigmatic region of the carpel - which commences above "s-t" in figs. 8 and 9. Money et al., in fig. 38 of their paper, illustrated a carpel of Laurelia sempervirens. Its vascularization resembles that of L. novae-zelandiae except that the dorsal trace does not branch.

Hedycarya:- carpels

These show some variation in vascularization. There is a ventral trace or aggregated traces and a dorsal trace or aggregated traces. In contrast to Laurelia, the dorsal trace or traces pass into the stigmatic region (above "s-t" in PLATE 10, fig. 2) where there is profuse branching. Two main types of vascularization

were noted:-

(1) A single unbranched ventral trace passes through the ventral wall of the carpel, enters the ovule via the funicle and terminates in the chalazal region (fig. 6). It therefore resembles the condition in Laurelia, although the ovule of Hedycarya has its micropyle directed upwards.

(ii) Before entering the ovule, the ventral trace forms one (figs. 1, 2, 4) or two (figs. 3, 5) lateral branches. These may or may not (fig. 1) extend through the ventral wall of the carpel to a level above that of the ovular trace. In some carpels one or both of the lateral branches fuse with the dorsal trace system in the stigmatic region. The carpel shown in fig. 3 illustrates this condition. It is drawn as seen from the adaxial side and the two lateral traces can be seen on either side of the median ovular trace ("o"). In fig. 2 it can be seen that the lateral branch of the ventral trace has split into a number of small branches at its tip. In one carpel the ventral strand split into two lateral traces and a median ovular trace. The ovule trace, just before it passed into the funicle of the ovule gave off a small branch which passed upwards through the ventral wall of the carpel for a short distance.

As shown in figs. 1-6, there is variation in the complexity and extent of ramification of the dorsal strand. In many instances a branch from the dorsal complex extends downwards through the ventral side of the carpel wall towards one of the two lateral

branches of the ventral strand, as with "d" in fig. 3. In many carpels one or a pair of upwardly extending ventral strands do not quite reach one or a pair of downwardly extending dorsal strands. In fig. 1 a branch of the dorsal strand extends towards the short lateral ventral strand and another branch of the dorsal strand extends downwards towards the position where the second lateral ventral branch would be, if it were present. It would seem likely therefore that the ventral trace system has become reduced and wholly or partially detached from the dorsal system during the phylogenetic development of the carpel.

Money et al., in fig. 34 of their paper illustrate a carpel of Hedycarya dorstenioides in which both the lateral branches of the ventral strand have fused with branches of the dorsal strand. This occurs infrequently in H. arborea.

The carpels of Laurus and Umbellularia have a single anatropous ovule with the micropyle pointed upwards as in Hedycarya and are in general vascularized by a dorsal and a ventral (ovular) trace (Kasapligil, 1951). As in Hedycarya this dorsal trace terminates near the tip of the carpel. It may or may not branch dichotomously near its tip. Such branches when present are less extensive than in Hedycarya. Some teratological carpels of Umbellularia have supernumerary traces. In some of these carpels one or more of the traces is isolated, although connected to other traces by means of undifferentiated procambium. The ventral trace is unbranched within the carpel wall and in contrast to Hedycarya

and Laurelia, is profusely branched at its tip, within the ovule.

Origin of vascular strands to floral appendages

The rather complicated and varied vasculature of the floral receptacles was not studied in great detail. Most attention was given to the male flowers of Hedycarya arborea, to permit comparison with Melville's (1963) study of the vasculature of the male flower of Hedycarya angustifolia.

Plate 11 illustrates part of the vasculature of the male flower of Hedycarya arborea. For simplicity the vascular supply to the bases of stamens depicted by broken lines, rather than by dotted lines, is omitted. The following features can be seen in the PLATE:-

- (a) The tepals may ("P") or may not ("Q") be vascularized by strands which originate from a single strand in the torus.
- (b) As already stated, each stamen may or may not be vascularized by strands from independent parts of the torus. Some stamens (e.g. "ST" in PLATE 11) are vascularized by a single trace from the torus.
- (c) In general, each stamen is vascularized by a strand or strands which originate from a strand or strands which also supply the tepals. An exception is the vascular supply to the stamen labelled "S".

The vasculature of the other flowers does not differ greatly from that described above. In female Hedycarya flowers each sterile carpel has a single trace which may originate from a strand

supplying a tepal or bract. Each fertile carpel is vascularized by dorsal and ventral strands which may or may not arise from independent parts of the torus. In male Laurelia flowers too, the traces to each stamen may or may not originate from independent traces in the torus, and may or may not originate from a strand supplying a tepal. In carpellate flowers the dorsal and ventral traces of each carpel may originate from the same or different traces in the torus.

If PLATE 11 is compared with fig. 56 of Melville's paper, which illustrates the male flower of Hedycarya angustifolia, the following differences emerge:-

- (1) Although the vein pattern within the tepals is similar in both species, the vascular supply to each tepal of H. angustifolia originates from a single strand in the torus.
- (ii) In H. angustifolia there is only a single trace to each stamen which invariably originates from a trace supplying a tepal.

Such differences seem surprising within a single genus, especially as the flowers of the two species seemed of a similar morphology, including the presence of sterile outermost carpels in female H. angustifolia flowers. I therefore decided to clear and examine male flowers of H. angustifolia which I had collected in New South Wales in order to check Melville's results. I found, as Melville indicated, that the vascular supply to each tepal originated from a single strand. Most stamens were vascularized by a single trace or group of traces which originated

from a single trace to a tepal. However a few stamens were each supplied by two groups of traces originating from different vascular strands in the torus, as in many stamens of H. arborea.

I found in cleared carpels of H. angustifolia that the dorsal trace passed into the stigmatic region and branched as in H. arborea, except that there were no branches from this complex which extended downwards on the ventral side of the carpel. No ventral ovular trace could be seen within the carpels despite the fact that they had been removed from flowers which had recently undergone anthesis. Material was therefore sectioned at this stage and it was found that the ventral trace was present but the cells of the trace were still at the procambial stage. No supra-ovular traces were observed, in contrast to H. arborea. In young cleared fruits of H. angustifolia* the ventral ovular (seed) trace could be clearly seen but although 30 fruits from three flowers were examined, no supraovular traces were found. There have been records of other plants in which the ventral carpellary trace or traces mature after the dorsal one(s); for example in Michelia of the Magnoliaceae (Tucker, 1961); in Drimys lanceolata (Tucker and Gifford, 1964) and in Lactoris (Carlquist, 1964). I also found this feature in carpels from cleared flowers of Doryphora sassafras and Atherosperma moschata. In these genera the ovular trace was not visible at anthesis but was visible in young cleared fruits of Atherosperma. No fruits of Doryphora

* Obtained from Mt. Wilson, Blue Mountains N.S.W., through the courtesy of Mr. J. Waterhouse, Botany Department, University of New South Wales.

were available for me to investigate.

Melville (1963) stated that in the male flower of Hedycarya the basal halves of the petals are fused, with the stamens being attached to the upper surface of this fused part. This is a difficult statement to prove or disprove. In the ontogenetic development of the male flowers of the two species under consideration (H. arborea and H. angustifolia) the tepal and stamen primordia appear as independent protuberances from a concave and flattened floral apex (PLATE 27, fig. 11). The situation was not encountered in which the stamens are initiated as protuberances on the adaxial surface of a hollow cylinder, with the latter clearly representing the phylogenetically fused bases of the tepals. The problem therefore hinges on whether the concave floral apex is in fact a somewhat sunken receptacle (axial theory) or whether its more distal part consists of the fused bases of the tepals and stamens (appendicular theory). The vascular anatomy of the flowers seems to neither prove nor disprove either theory. Although I favour the axial theory in this case, I must conclude that until a thorough comparative ontogenetic study is made of the flowers of other species of Hedycarya and related genera, the problem remains open. McLean and Ivimey-Cook (1956) have described and illustrated the male and female flowers of Tambourissa which Money et al., place in the same subfamily as Hedycarya. In Tambourissa the flowers of both sexes are cup shaped and the carpels are actually sunken into the inner surface of the "cup". McLean

and Ivimey-Cook concluded that this cup in Tambourissa "does not bear the aspect of a combination of organs, but rather that of a genuine receptacular cupule".

This brings us to a consideration of the nature of the urceolate hypanthium* of the perigynous carpellate flower of Laurelia. Has the perigynous cup formed by adnation of tepals to stamen and staminode bases or has it formed in an axial manner by the invagination of the receptacle? Eames (1961) has pointed out that there have been only a few cases in which the cup has been formed by sinking of the receptacle e.g. in Cactaceae. However it is tempting to conclude that the hypanthium in Laurelia has formed in this manner, for the following reasons which are in addition to the slight evidence given on page 23.

(i) There is a ring of vascular bundles in the hypanthium, as in the pedicel. There is no fusion of tepal and stamen or staminodal traces within the hypanthium such as occurs in some members of the Ericaceae where there has been adnation of appendages (Eames, 1931). Any fusion of traces from different appendages occurs at the tip of the hypanthium.

(ii) If the region above the hypanthium is considered, the tepals and functional stamens are of similar size and shape to those in the male flower, in which no hypanthium is present.

Nonetheless this problem too should remain open until a thorough study is made of related flowers in the family.

* This term is used according to Eames' (1961) definition of it (p.249).

Discussion

The inflorescences

Perkins and Gilg (1901) illustrated four inflorescences of Laurelia sempervirens. Each consists of two pairs of decussately arranged flowers. The absence of a solitary terminal flower seems surprising in view of its almost invariable presence in L. novae-zelandiae. I have not been able to obtain flowering material of L. sempervirens to check Perkins' and Gilg's observations. However their illustrations of plants known to me are of a high order of accuracy.

There is considerable diversity in inflorescences within the family. They vary from the enormous number of flowers in the decussate - paniculate inflorescences of Kibara (Perkins and Gilg, 1901); to the dichasial cymes of varying complexity in Macropheplus (ibid); to the type in Hedycarya and Laurelia. The simplest are the three-flowered cymes of Doryphora and the single-flowered inflorescences of Atherosperma (PLATE 13, figs. 1, 2). Ehippiantha of the subfamily Monimioideae also has solitary flowers in the leaf axils (Perkins and Gilg, 1901).

From descriptions of genera in the family in Perkins and Gilg (1901) and Perkins (1911) I would conclude that the basic type of inflorescence has a decussate phyllotaxy, homologous to that of the leaves. Cymose inflorescences would seem to be derived from this type by reduction, with intermediate forms being present in a number of plants including the N.Z. species of Hedy-

carya and Laurelia. It seems clear that solitary flowers of some plants in which the flowers terminate a shoot may represent a primitive condition, as in Magnolia and Eupomatia (Eames, 1961; McLean and Ivimey-Cook, 1956). However in the words of Eames "Solitary axillary flowers are commonly surviving units of axillary clusters". This latter would seem to apply to Atherosperma. Its solitary flower could have been derived from the three-flowered dichasial cyme of the related Doryphora by suppression of the pair of flowers. It could be argued on the basis of an ebractate peduncle up to 1 cm. long in Doryphora that this proximal sterile part of the inflorescence has arisen by suppression of flowers, presumably with a decussate phyllotaxy. In this genus the opposite pair of flowers are bractate and the pedicel of the terminal flower arises in a pair of caducous bracts. Now in Atherosperma the flower is subtended by a pair of bracts which are inserted at the distal end of the flower stalk, in such a way as to resemble sepals ("br" in PLATE 13, fig. 2). If each of these bracts once subtended a pedicel in the ancestor of the present day Atherosperma, (as in Doryphora), and such a pedicel has been suppressed, then the flower stalk of Atherosperma would be morphologically a peduncle.

The mixed inflorescence of Laurelia novae-zelandiae is an unusual type. I can find no reference to other plants with mixed inflorescences in which male flowers are followed by carpellate ones, followed by a terminal distal male flower. A few other

genera in the Monimiaceae have mixed inflorescences e.g. some species of Siparuna (Perkins and Gilg, 1901; Perkins, 1911), but these are not comparable. I have no information as to whether mixed inflorescences occur in the other two species of Laurelia. Presumably after the male flowers have been initiated in L. novae-zelandiae, including the terminal flower, there is an internal chemical change which leads to the production of the sub-terminal female flower(s). At present little is known of the physiological factors governing sex expression in plants. Experiments in some monoecious plants in the Cucurbitaceae have shown that the proportion of female flowers in a mixed inflorescence can be increased by spraying the plants with certain auxins (Heslop-Harrison, 1957, 1959).

The flowers

There are transitions between bisexual and unisexual flowers in the family (Money et al.). The intermediate stages, e.g. in those carpellate flowers of Laurelia and Atherosperma which have one or more functional stamens, indicate that unisexuality is a derived condition. It is of interest that all genera with bisexual flowers in the subfamily Atherospermoideae - Daphnandra, Doryphora (PLATE 13, fig. 3), Dryadodaphne and Neumaron, have staminodes. They are analagous to the staminodes in the carpellate flowers of the remaining genera - Atherosperma and Laurelia. The most perfect bisexual flowers occur in Hortonia angustifolia and H. floribunda of the subfamily Hortonioidae, which usually lack

any staminodes (Money et al.). The flowers of the subfamily Monimoideae, which includes Hedycarya, are invariably unisexual and the flowers of each sex lack any rudiments of the other sex, except in the female flowers of Peunus which bear three-lobed staminodes (Money et al.).

Perianth. In Trimenia* of the Trimeniaceae, a family closely related to the Monimiaceae, the immature stamens and carpel are invested by 5-25 pairs of decussately arranged scale-like appendages. They are deciduous prior to anthesis and leave the stamens and carpel devoid of a perianth (Money et al.). The lowermost pairs of appendages differed from the uppermost ones in shape and Money et al., concluded that there was an intergradation between bracteoles and tepals but that there were no morphological boundaries between them. If such a flower is primitively simple then it would appear to illustrate a stage in the derivation of tepals from bracteoles, which themselves represent modified leaves (Eames, 1961). It has been noted that in Hedycarya and Laurelia occasional appendages occur which are intermediate in structure between bracts and tepals.

Money et al., stated that the tepals in the family have a fundamentally decussate arrangement with transitions to cyclic. I have mentioned a further trend to spirally arranged tepals in some flowers of Laurelia.

An advanced feature of the perianth in some genera is in its

* Perkins and Gilg included this genus in the Monimiaceae.

differentiation into sepals and petals e.g. in Daphnandra. Another advanced feature in some genera is the presence of a constant number of perianth parts per flower. For example Doryphora has 6 tepals per flower (PLATE 13, fig. 3).

Perianth vascularization. It has already been noted that the vascularization of the tepals in Hedycarya and Laurelia seems to be derived from that of the bracts by reduction. Assuming that such bracts have been derived from leaves, or at least had a common ancestor with the leaves, it seems surprising that they do not show a close resemblance to the leaves in their venation. The leaves in the family are typically dicotyledonous with a thick mid-vein and pinnately arranged lateral veins. These laterals in Laurelia, Hedycarya and Atherosperma at least, give off branches which form a reticulate venation with some of the veinlets having free endings. I decided to examine cleared bracts and tepals of Doryphora and Atherosperma to determine whether they showed a closer resemblance to leaves in their vasculature. The following results were obtained:-

(a) The most primitive type of bract venation occurs in Atherosperma*. There is a mid-vein and pinnately arranged laterals. Branches of the laterals form a network which is less extensive than that of the leaves. Some of the veinlets have free endings. It would appear that the type of bract venation in Laurelia arose when the larger, lower lateral veins became disconnected from the

* This is argued on the assumption that the most primitive type of venation is that which most closely resembles the leaf venation.

mid-vein during evolution of the bract.

(b) The most primitive type of tepal venation was found in Doryphora*. There is a mid-vein and lateral veins are inserted in pinnate fashion on the distal two-thirds of the mid-vein. The laterals usually branch dichotomously one, two or three times. In some tepals a few of the lateral veinlets anastomose but not extensively enough to form a network. In addition there are one or two dichotomously branched lateral veins on each side of the mid-vein, which are free from the mid-vein. They vascularize the lower part of the tepal. Bracts of Doryphora have a similar venation. There is then in this genus, in the tepals and bracts, an intermediate stage in the derivation of a palmate-parallel vascularization system from a pinnate one. Bailey (1956) noted that venation of perianth parts "tends in many cases to be pseudo-palmate even where the leaves have a typical pinnate venation". The tepal venation of Atherosperma (PLATE 13, figs. 1, 2) resembles that described for the male flowers of Hedycarya.

The above results support Hiepko's (1965a and b) conclusion that the perianth parts of the woody Ranales are bracteoid in nature, at least for the Monimiaceae. In contrast to this, some members of the herbaceous Ranales are considered to have petals which have been derived from stamens by sterilization, e.g. some of the Nymphaeaceae (Hiepko, 1965; Moseley, 1958).

* This is argued on the assumption that the most primitive type of venation is that which most closely resembles the leaf venation.

Staminal appendages and valvular dehiscence. The stamen of Hedycarya with its four decurrent pollen sacs which dehisce by two longitudinal slits; its simple vascularization and lack of a filament, contrasts markedly with the stamen of Laurelia with its two pollen sacs, valvular dehiscence, varied vascularization and short filament. The stamens of Laurelia more closely resemble those of Umbellularia and Laurus of the Lauraceae. There is however a link between the stamens of Laurelia and Hedycarya in that the stamens of Peumus and Monimia of the subfamily Monimioideae to which Hedycarya belongs, possess staminal appendages (Money et al.). Such stamens resemble those of Hedycarya in having longitudinal anther dehiscence and from illustrations in Money et al.'s paper and in Perkins and Gilg (1901) it seems likely there are also four pollen sacs per stamen. Money et al., stated that flowers of the Monimioideae (except Peumus and Monimia) and the Siparuneeae "have lost all vestiges" of the paired staminal appendages. They presumably therefore consider these plants once had the appendages and therefore the presence of appendages on the stamens represents the more primitive condition in the family. The occurrence of paired staminal appendages and valvular anther dehiscence in the Laurales (sensu Hutchinson, 1959) can be summarized as follows*:-

* Compiled from information and illustrations in Money et al., (1950); Perkins and Gilg (1901) and Hutchinson (1959, 1964).

MONIMIACEAE

- Hortonioidae - staminal appendages; longitudinal-slit dehiscence; probably four pollen sacs.
- Monimioideae - staminal appendages in Monimia and Peumus only; longitudinal slit dehiscence; probably four pollen sacs in all genera.
- Atherospermoideae - staminal appendages; valvular dehiscence; two pollen sacs in some, most likely all, genera.
- Siparunoideae - no staminal appendages; valvular dehiscence; probably two pollen sacs.

LAURACEAE

Staminal appendages; valvular dehiscence; two or four pollen sacs.

GOMORTEGACEAE

Staminal appendages; valvular dehiscence; probably two pollen sacs.

HERNANDIACEAE

Staminal appendages; valvular dehiscence; probably two pollen sacs.

There is thus in the Laurales a widespread occurrence of staminal appendages and valvular dehiscence, but the two characters do not always occur together. Valvular dehiscence also occurs in the Berberidaceae and in some of the Hamamelidaceae. Hutchinson (1964) concluded that this character in the Berberidaceae did not signify a close relationship to the Laurales, "probably being nothing more than parallelism". As the Hamamelidaceae too does not seem to be related to the Laurales in most of its features, I would think it likely that valvular dehiscence arose by parallel evolution in this family too.

Morphology and vascularization of stamens. Recent investigations in the woody Ranales have led to the suggestion that the most primitive angiosperm stamen is a three-trace leaf-like organ without differentiation into anther, connective and filament (see Eames, 1961). The stamens of the Monimiaceae are considerably advanced from this form, although Doryphora has a marked prolongation of the vascularized connective beyond the anthers (Money et al., fig. 29). It is questionable whether this long tapered extension is a primitive feature as it apparently is in Belliolum of the Winteraceae (Bailey and Nast, 1943a), or a secondary modification as has been suggested for stamens of certain species of Magnolia (Canright, 1952). There is a slight prolongation of the connective beyond the anther in Hedycarya and Laurelia.

In Laurus, Umbellularia and Laurelia, as noted, and in Doryphora (personal observation) the vascularization of the stamens, including their appendages, is so varied as to make it difficult to discern any basic type. In these genera the vascular supply to the appendages may or may not be independent of that to other parts of the stamen. All genera had some stamens which contained isolated vascular strands. In Doryphora such strands occurred within the leaf-like appendages. In contrast to the stamen illustrated in fig. 29 of Money et al., many stamens had appendages in which the vascular trace underwent varying degrees of dichotomous branching. This branching, coupled with the occurrence of

isolated strands in positions where one would expect parts of dichotomous branches to be, suggests that the condition in which the appendage is vascularized by an unbranched strand is a derived one. I found too that one or both of the lateral strands, present in the stamen illustrated by Money et al., are absent in some stamens. Some other stamens had the strand to an appendage fused to another lateral one, as illustrated in fig. 57C of Melville's (1964) paper. The staminal appendages of Atherosperma are inserted at the base of the stamen and their vascular supply is invariably independent of that to the rest of the stamen. In general, the appendages lose part and finally all of their vascularization as they are reduced in size on the stamens and staminodes of Peumus and Doryphora (Money et al.,) Laurus and Umbellularia (Kasapligil) and in Laurelia. As already noted, there are exceptions to this in Laurelia.

If each staminal appendage is a staminode, as claimed by Money et al., then some of the stamens of Laurelia, Umbellularia, Laurus and Doryphora are three-veined if one ignores traces to staminal appendages and may therefore represent the putative primitive vascular condition of the Ranalean stamen.

Melville (1963) has interpreted the stamens of the Laurales in the light of his Genophyll theory, which takes some account of the Telome theory. He has based his interpretation on the vascularization of the flower and takes little consideration of the morphology of individual stamens. According to this

interpretation (shown in part in fig. 65 of Melville's paper) each stamen of Doryphora, Laurelia and Umbellularia is equivalent to a segment of the male flower of Hedycarya. This segment consists of a tepal and the stamens which are borne on what Melville interprets as the fused inner part of the tepal. Ten such epiphyllous stamens are shown in the figure. By reduction and partial sterilization the superficially similar stamens of Laurelia, Doryphora and Umbellularia have evolved by processes which are not identical for all genera nor even for all stamens within a single flower (as in his description of Umbellularia). I find no merit in this theory for the following reasons:-

(a) Superficially similar stamens, even within a single species, because they have a varied vascularization are regarded as having evolved in different ways from one another. By implication, if this were true, morphological similarities between certain stamens on a single flower would be due to parallel evolution because their vascularization was different. This seems to stretch the arm of coincidence to the breaking point.

(b) I have stated how the stamens of Peumus and Monimia provide a link between the Atherospermoideae and Monimioideae in that they appear to resemble stamens of Hedycarya except that they bear the vasculated staminal appendages. With this link it seems that the stamens of Hedycarya on the one hand and Laurelia on the other could be derived one from the other without the complicated processes which Melville has proposed.

Vascularization of carpels. It is now well established that the most primitive form of carpel in the woody Ranales appears to be the conduplicate type, in which two rows of ovules are vascularized by branches from a median dorsal trace and two marginal ventral traces. (See Eames (1961) for details.) It is possible that in its most primitive condition, the median trace is double in nature, in keeping with the theory that the two-trace unilacunar nodal pattern is the most primitive (Carlquist, 1961; Tucker and Gifford, 1964; Swamy, 1964). Bailey and Swamy (1951) and Eames (1961) have indicated how this type of carpel could be modified in various ways to give rise to the follicle and achene.

If, as seem likely, the uniovulate carpels of the Monimiaceae have been derived from the conduplicate type, then the downwardly directed branches of the dorsal trace in Hedycarya and the supraovular branches of the ventral trace, may represent traces to formerly existent ovules in the ancestors of Hedycarya et al. This hypothesis assumes of course, the conservatism of vascular traces. That the supraovular traces in Hedycarya are in general paired, suggests that the ovules in the ancestral carpel were in two rows, as in the conduplicate carpels of the Winteraceae, for example (Bailey and Nast, 1943b). Presumably too these paired traces were completely separate from one another in the ancestral carpel. In other words, the paired supraovular traces in Hedycarya are the result of incomplete fusion of two ventral traces.

Kasapligil suggested that the ventral trace in the carpel of Umbellularia represented the two fused marginal (ventral) traces, on the grounds that its double nature was evident from teratological specimens. In these, the trace bifurcated within the ovule. There are some uniovulate carpels within the woody Ranales which do have two ventral traces, for example, some carpels of Sarcandra (Swamy and Bailey, 1950). Eames (1961) noted that in "higher orders, solitary basal ovules may have two traces - one from each ventral vein".

It has been noted that Laurelia lacks a supraovular trace. Money et al., illustrated such a trace in the related Atherosperma (in their fig. 39). This affords a link between the carpels of Hedycarya and Laurelia and indicates that the ancestral carpel of Laurelia would have possessed a supraovular trace.

CHAPTER 3

VEGETATIVE, INFLORESCENCE AND FLORAL MERISTEMS

Introduction

The terminal buds of shoots of female Hedycarya and Laurelia trees were sectioned to permit comparison of vegetative, inflorescence and floral meristems. To my knowledge, this is the first study of meristems within the family.

Time did not permit a study of seasonal changes in the structure of the shoot apex. Buds were collected during the spring, at which time the apical meristems of the shoot were particularly active. Insufficient buds were sectioned to obtain a range of sizes for maximal and minimal plastochron stages and therefore the figures quoted refer to a limited number of samples. Terminal buds were not sectioned from male Hedycarya plants. It is of interest in this respect that Kasapligil found considerable differences in the shape of the vegetative apical meristems of male and female plants respectively, in Laurus. These apices did however have similar cytohistological zonation.

Terminal mixed buds

Longitudinal sections of terminal buds of Hedycarya and Laurelia are illustrated in figs 1 and 2 of PLATE 14. The shoot apex of Hedycarya is approaching maximal surface area and that of Laurelia is near minimal area. In fig. 1 the two outermost leaves of Hedycarya enclose young axillary meristems. It cannot

be determined at this stage whether these meristems will give rise to axillary vegetative buds or inflorescence buds. It is anticipated that they will in fact give rise to inflorescence buds which will flower the following spring, since the bud terminated a shoot which had borne flowers and not vegetative axillary buds, for several seasons. Similarly in fig. 2, a putative young inflorescence bud is in the axil of the lowermost right-hand leaf in Laurelia. The terminal mixed buds of the two genera do not contain bud scales, in contrast to Laurus and Umbellularia (Kasapligil).

The vegetative shoot apex

In both genera the vegetative apical meristem has a two-layered tunica (PLATE 15, fig. 1; PLATE 16, fig. 2). Two-layered tunics have been found in all woody Ranales so far investigated, with the exception of Notaphoebe (Lauraceae) which has a three-layered one (Gifford, 1954).

At maximal surface area the apex is convex and at minimal area approximately flat in both genera. In Hedycarya it is approximately 215μ wide* and 53μ high at maximal area (PLATE 15, fig. 1); in Laurelia it is $160\mu - 193\mu$ wide and $48\mu - 64\mu$ high at this stage. At minimal area the shoot apex is 90μ wide and slightly convex in Hedycarya and 46μ wide in Laurelia (PLATE 16, fig. 2). The apical meristem is thus somewhat larger in Hedycarya. The dimensions of these apices lie within the limits of maximal and

* Measurements are made at the adaxial level of insertion of the first visible pair of primordia.

minimal sizes recorded for the vegetative apices of 6 genera of the Lauraceae (Kasapligil).

At the maximal area phase, the apical meristems of the two genera are clearly divided into the cytohistological zonation characteristic of Umbellularia and Laurus (see fig. 96 of Kasapligil's paper) and other woody Ranales (Gifford, 1950) as well as many other dicotyledons (Gifford, 1954). In Laurelia and Hedycarya the central initial cells of the tunica and corpus do not have the markedly larger cells and "huge nuclei" characteristic of this zone in Umbellularia and Laurus (Kasapligil). As noted by Kasapligil and others (see Gifford, 1954) the cytohistological zonation was not very distinct near the minimal phase of plastochron (compare fig. 1, PLATE 15, with figs. 2 and 3 of PLATE 16). At this phase too, the inner (T2) tunica layer was less regular because of the occurrence of some periclinal divisions within it (PLATE 16, fig. 3). Gifford (1950) commented that if one used the term tunica in its strictest sense, as layers in which invariably anticlinal divisions occur, there would be only a single tunica in woody Ranales. However as the subjacent layer primarily divides anticlinally and therefore predominantly gives surface growth, I shall follow Gifford (1950) and others and refer to it as a second tunica layer. PLATE 16, fig. 1 illustrates a transverse section of the shoot apex of Hedycarya through the T2 layer. The youngest pair of leaf primordia are joined to this layer in the photo. It can be deduced from this section that

the apical meristem is approximately circular in cross section.

Initiation of primordia

Leaf, bract and tepal primordia are initiated in a similar way by periclinal divisions in the T2 layer on the flank of the vegetative, inflorescence or floral meristems. This method of origin, in which one (or more) subsurface layers of the meristem undergo periclinal division, is common in both dicotyledons and monocotyledons (Esau, 1953). In Hedycarya and Laurelia these divisions are followed by anticlinal divisions in the T1 (outer tunica) layer and anticlinal and periclinal divisions within the T2 and subjacent layer, to form a protuberant primordium (PLATE 16, figs. 2, 3; PLATE 20, fig. 1). The primordium grows for a time by general cell enlargement and division in varying planes (PLATE 17, fig. 1) but at a later stage sub-apical initials arise, as in Umbellularia (Kasapligil), Drimys winteri (Gifford, 1951; Tucker, 1959) and many other angiosperms, to form regular layers of cells. At a later stage too, marginal and adaxial basal meristems arise, as described for Drimys winteri by Tucker (1959) and Gifford (1951).

The inflorescence meristem

The inflorescence meristem arises in the axil of a leaf primordium when it is one of the third pair of primordia from the vegetative apex. The inflorescence meristem in Drimys winteri also arises in the axil of the third youngest primordium from the vegetative apex, but in this case the primordium is a bract,

not a leaf (Tucker, 1959). The meristem is initiated by anticlinal divisions in the T1 and T2 layers and periclinal divisions within the T2 and subjacent layer. A mound of tissue is formed which is separated from the surrounding vacuolating parenchyma by an arc of several layers of flattened meristematic cells which Schmidt (1924) called the shell zone (PLATE 17, fig. 2). At the stage shown in the figure and at subsequent stages, the meristem has two tunica layers, as in Drimys winteri (Tucker, 1959) and Umbellularia (Kasapligil). During the production of bracts, the inflorescence apex exhibits plastochron changes similar to those of the vegetative apices. Thus the inflorescence apex is flat near minimal area (PLATE 18, fig. 2; PLATE 19, fig. 1) and convex near maximal surface area (PLATE 19, fig. 2). The putative inflorescence bud of Laurelia which is shown in PLATE 14, fig. 2 and PLATE 18, fig. 1, has two pairs of bract primordia and differs from the other buds sectioned in the extent of the internode between the pairs of bracts. The lowest pair (one of which can be seen in part in PLATE 14, fig. 2) are inserted at the base of the inflorescence axis. This elongated internode can be contrasted with the more typical one of the inflorescence shown in section in PLATE 19, fig. 1, which bears three pairs of bract primordia. Part of one of the lower pair of bracts is on the left hand side of the photo. Presumably these early differences in internode length of different inflorescences foreshadow the observed differences in the length of basal internodes of various mature inflorescences (Chapter 2).

In Hedycarya the first pair of bracts were initiated when the female inflorescence was a convex mound 40μ high, with a width (measured across the leaf axil) of 150μ . These bracts were 115μ long and in the axil of the fourth youngest pair of leaves when the vegetative apical meristem was initiating the fifth pair of leaves.

The vegetative and inflorescence apices have similar cytological zonation, as seen by comparing approximately similar plastochron stages of vegetative and inflorescence meristems of Laurelia in fig. 1 of PLATES 17 and 19. The T2 layer in vegetative and inflorescence apices of Laurelia is somewhat more elongated vertically than this layer in the meristems of Hedycarya (compare PLATE 19, fig. 1 and PLATE 16, fig. 2 with PLATE 15, fig. 1 and PLATE 18, fig. 2). The dimensions of inflorescence and vegetative meristems were approximately similar to each other within each genus, as in Umbellularia (Kasapligil).

The floral meristem

The floral meristem of both genera arises in the axil of a bract primordium, circa 1000μ in length (Hedycarya) and circa 700μ in length (Laurelia), when it is one of the third pair of primordia from the inflorescence apex. Its initiation and early development is similar to that of the inflorescence meristem. PLATE 20, fig. 2 illustrates an early stage in the development of a floral meristem of Laurelia. One of the cells of the T1 layer of the young meristem is dividing anticlinally and the results of a recent

periclinal division in the T2 layer can also be seen. The shell zone is at an early stage of development. One of the cells of this zone is labelled "s". A later stage is illustrated for Hedycarya in PLATE 19, fig. 2. The shell zone is now more prominent and as noted by Tucker (1959) for Drimys winteri it has a greater number of layers towards the adaxial* side of the meristem. At this stage the tunica is clearly two-layered but a few periclinal divisions were apparent in the T2 layer.

In its early development the floral meristem is in a state of transition from the tunica-carpus configuration typical of vegetative apices to the mantle-core configuration of many floral apices (Gifford, 1954; Tucker, 1959). Thus as in many plants, the tunica which consists of a T1 layer of invariably anticlinally dividing cells and a T2 layer of predominantly anticlinally dividing cells and carpus - which consists of cells which divide in various planes, are replaced by a multilayered meristematic mantle of cells overlying a vacuolate and non-meristematic core. When Gregoire (1938) introduced the mantle-core concept for reproductive apices he considered that the reproductive apex had arisen de novo. It has since been amply demonstrated that the reproductive apex, when it does differ from the vegetative, has originated by a reorganization of the vegetative apex (Philipson, 1949). This reorganization occurs in a number of plants by the peripheral zone of the carpus extending down the flanks of the

* I.e. adaxial to the inflorescence axis.

apex and comprising, together with the tunica, the meristematic mantle (Gifford, 1954). As the tunica is a discrete part of the floral apices of Hedycarya and Laurelia, I shall follow some authors (e.g. Tucker) and refer to it as part of the mantle.

Although the floral apices of Hedycarya and Laurelia are organized into a mantle of relatively non-vacuolate deeply staining cells overlying a core of vacuolate cells, from the stage of tepal initiation onwards, they display an unusual feature. For, within the vacuolate core a considerable number of cell divisions were observed, even at a time when the floral apex had almost ceased its activity. Such divisions, were not of course nearly as frequent as those within the mantle.

When the inflorescence apex has completed the initiation of bract pairs in acropetal fashion, it is transformed into a floral apex which terminates the growth of the inflorescence axis. This terminal floral meristem is ahead of the subjacent pair of floral meristems in its early development. Thus, in PLATE 21, the terminal bud of a male inflorescence has a short pedicel and well developed tepal primordia (fig. 1). In the subjacent pair of floral apices of the same inflorescence, there is virtually no pedicel present as yet and the tepal primordia are just being initiated (fig. 2). A marked contrast to vegetative and inflorescence apices of both genera is found in the lack of any vertically flattened rib meristem in the floral apices.

The floral meristem in Hedycarya

The floral apex of male and female plants usually produces a pair of bracts at the base of the receptacle. Their midribs lie in the frontal plane which is perpendicular to the sagittal plane - which longitudinally bisects the subtending bract and inflorescence axis. A male floral apex with young bract primordia on its flanks is shown in fig. 1, PLATE 27. At this stage the floral apex, excepting the terminal one, is tilted towards the inflorescence axis. As seen in apical view the floral apex and bracts have an elliptical shape (fig. 1b). The short axis of this ellipse lies in the sagittal plane, as in Drimys lanceolata (Tucker and Gifford, 1966). A male bud was sectioned when the pair of bract primordia were 70μ high. At this stage the apex had a diameter along the frontal plane of 130μ and a height of 32μ . The apex was in a state of transition from the tunica-corpus to the mantle-core configuration. The centrally situated zone of corpus initials, a characteristic of the vegetative apex at maximal surface area, was still apparent. However, the lower cells of this zone were more vacuolate in the young floral apex. The peripheral zone was less well marked than in the vegetative and inflorescence apices and its lowermost cells were more vacuolate. Rib meristem was still present but less extensive and not as vertically flattened as in the inflorescence and vegetative apices. The T2 layer was well marked with vertically elongated cells, although some periclinal divisions were observed within it.

After tepal primordia have been formed, at a stage when the outermost stamen or carpel primordia are being initiated, the meristem has a mantle of 5-6 irregular layers in male buds (PLATE 21, fig. 1) and 6-8 layers in female buds (PLATE 22, fig. 1). Some periclinal divisions were observed in the T2 layer, irrespective of those divisions which initiate primordia and this layer is therefore not as discrete as it was in the vegetative apex near maximal surface area. By the time most of the stamens had been initiated the mantle had been reduced to 3-4 layers in male buds. Periclinal divisions were more infrequent in the T2 layer at this stage (PLATE 22, fig. 2). Similarly in female buds, the mantle had been reduced to 3-4 layers when the last carpel primordia were being initiated and as in the male bud at a comparable stage, the T2 layer was more discrete than earlier, with somewhat vertically elongated cells (PLATE 23, fig. 2). Throughout stamen and carpel initiation, divisions were observed in varying planes within the vacuolate core of the apex, to a depth of up to about 18 layers from the apical surface. A cell of the core is shown dividing in a male bud of Hedycarya near the end of stamen initiation in PLATE 23, fig. 1 at "V".

Soon after the ultimate stamen and carpel have been initiated, the mantle of the vestigial apex of male and female buds becomes vacuolate and some of the cells of the T1 layer become modified into trichomes, one of which can be seen at an early stage of development at "t" in PLATE 23, fig. 2. In the formation of a

trichome, the cell becomes extended upwards and protrudes above the surface of its neighbours, as in the figure. When the trichome is about two and a half times its original height, the nucleus has completely migrated to above the level of the surface of the vestigial apex, as in PLATE 24, fig. 1. Mature trichomes are unicellular and by anthesis, those on the floor of the receptacle are up to 900μ long and taper to a point. They measure up to 50μ in width and are widest near their base. Their thick lignified walls are about 10μ thick. At anthesis, their nuclei, which are approximately centrally situated, show signs of degeneration.

At the stage shown in fig. 1 of PLATE 24, the apical meristem had completed the initiation of carpels and it can be seen that quite a large vestigial apex is present. A few divisions were still occurring within the mantle and core. Divisions had ceased shortly before the stage illustrated in fig. 2. At a comparable stage in the development of stamen primordia the vestigial apex of the male bud is in general smaller, measuring about a third the width of the female one.

The floral meristem in Laurelia

After tepal initiation the floral meristem of male and carpellate flowers has a mantle of 5-6 irregular layers overlying a vacuolate core. The T1 layer was vertically elongated at this and subsequent stages. Near the end of stamen initiation in the male flower and carpel initiation in the carpellate flower, the

mantle is reduced to 4 irregular layers and the T2 layer is now somewhat elongated vertically. Some periclinal divisions were apparent within the layer and therefore disturbed its discreteness. Throughout stamen, staminode and carpel initiation, divisions in varying planes were noted within the vacuolate core to a depth of approximately 12 layers from the surface of the apex. Soon after the ultimate stamen or carpel has been initiated in the male or female buds, the cells of the mantle of the small vestigial apex become markedly vacuolate (compare figs 1 and 2 of PLATE 25). Trichomes are formed on the floor of the receptacle and on the vestigial apex in a manner similar to that described for Hedycarya. At anthesis those on the floor of the receptacle of the carpellate flower are about 500 μ long, 30 μ wide. They taper to a point but differ from those of Hedycarya in that they do not bulge outwards near their base. At this stage many of them do not have heavily thickened walls, although the approximately centrally situated nucleus of each is showing signs of degeneration. The largest trichomes in Laurelia are on mature fruits. They are unicellular, approximately 40 μ wide, with walls 10 μ thick and up to 12 mm. long (PLATE 26, fig. 1).

The initiation of tepals

Hedycarya

A male bud is shown in latero-apical view after four tepals have been initiated, in PLATE 27, fig. 2. They enclose a domed floral apex. Bracts analogous to those shown in fig. 1, have been

excised except at their bases ("B"). In figs. 2-6, the tepals of male buds have been numbered consecutively, beginning with the oldest*. It can be seen that either (a) the first tepal arises closest to the subtending bract ("S.B.") as in figs. 2, 3 and 5; or (b) the first tepals arise as a pair, closest to the pair of bracts ("B"), as in figs. 4 and 6. Following the initiation of the first tepal or pair of tepals, the other tepals arise in close succession in a variety of positions, as shown in figs. 2-6. In some cases, after the first tepal has been initiated, a pair of tepals are formed simultaneously, closest to the pair of bracts (fig. 5).

The male floral apex is a convex mound with an ad-abaxial diameter of about 220μ and height of about 60μ above the level of insertion of the subtending bract, when the first tepals are initiated (PLATE 21, fig. 2). It is therefore somewhat larger than the female inflorescence apex when it initiated the first pair of bracts (see p. 58).

Laurelia

In both male and carpellate flowers, the first sepals arise as a pair, with their midribs in the frontal plane. These tepals and the enclosed domed apex ("A.M.") become comparatively large before other tepals are initiated (PLATE 27, figs. 7, 8). The other tepals (see fig. 9) are initiated in either clockwise or anticlockwise succession. The first formed tepals of Laurelia

* This is argued on the basis that the largest tepal ("1") represents the oldest one. This appeared to be the case from an examination of many buds at different stages of tepal development.

resemble the pair of bracts commonly found in Hedycarya, which are inserted above the subtending bract, in that they are decussate to the subtending bract and inflorescence axis and are initiated some time before the tepals in Hedycarya or other tepals in Laurelia. However it seems best to regard this pair of appendages as tepals in Laurelia for they resemble the other tepals in shape, size and vasculature and are inserted only slightly below them. It is possible that these lower tepals in Laurelia have recently evolved from bracts analogous to the pair commonly found on the floral axis of Hedycarya.

The floral apex of male and carpellate flowers of Laurelia is a convex mound with an ab-adaxial diameter of about 72μ , but with its largest diameter of about 175μ at right angles to this, at the time when the first pair of tepals are initiated. It has a height of about 70μ above the level of insertion of the subtending bract. It is therefore comparable in size to the male floral apex of Hedycarya at this stage except that it is more flattened in the sagittal plane.

Discussion

The absence of bud scales in Hedycarya and Laurelia has been contrasted with their presence in Laurus and Umbellularia. It is a characteristic of many trees and shrubs of the New Zealand flora, including some occupying subalpine habitats, that during the winter, apical buds are not sheathed by special protective structures, in contrast to "most trees and shrubs of the North

Temperate Zone" (Wardle, 1963). Bud scales are also not present in the New Zealand species of Beilschmiedia of the Lauraceae (pers. comm. G.H. Roper, V.U.W. Botany Department). Perhaps the frequent absence of bud scales in members of our flora is a reflection of our comparatively oceanic climate which allows of vegetative growth throughout most of the winter, at least at lower altitudes. Absence of bud scales in many subalpine plants may be a reflection of the relatively recent derivation of these forms (Dawson, 1963; Fleming, 1963). It should be noted however that buds are frequently protected by the hairy nature of the young leaves, or by gummy exudates or the sturdy nature of the young leaves in the outermost part of the bud (pers. comm. Dawson).

No major differences were found between the apical meristems of Hedycarya on the one hand and Laurelia on the other, although minor differences were present, as outlined in the foregoing pages. Kasapligil stated that the "structure of the apical meristem of inflorescence buds, as well as that of flower buds, is similar to that of the vegetative shoot apex", in Laurus. This conclusion seems surprising in view of my own results on two members of what is considered to be a closely related family and in the light of Roper's (pers. comm.) observation that the maturing floral apex of Beilschmiedia tawa has the typical mantle-core configuration. It is however apparent from Kasapligil's description, photographs and drawings of the floral apex of Laurus, from the time of petal initiation onwards, that the mantle-core concept could be applied

to it. Kasapligil wrote that the "corpus" region of the floral apex originates from the peripheral zone of the corpus of the inflorescence apex and is therefore, I conclude, not strictly homologous to the entire corpus of the inflorescence and vegetative apices. He added that after formation of petal primordia "the zonation of the corpus is very inconspicuous" and "the apical meristem, consisting of only 2 or 3 cell layers, appears to be very superficial". It does not seem important to the writer what terminology one uses in comparing floral, inflorescence and vegetative apices provided that the descriptions are accurate. It is now well established that, as Newman (1965) aptly expresses it, "the features 'peculiar' to the 'reproductive' apex are those peculiar to an apex ceasing growth, or even to an apex with an increased tempo of growth prior to that cessation". The floral apices of Laurelia and Hedycarya do not strictly conform to the mantle-core configuration because of the unusual feature that cell divisions occur within the core region. In this respect these floral apices share qualities of the 'typical' vegetative and 'typical' floral apices. It is of interest that within a single Ranalean genus, Drimys, one species has been described as having a floral meristem with the typical mantle-core configuration (D. winteri, Tucker, 1959) and another species has been described as having a floral meristem with a tunica-corpus type of configuration (Tucker and Gifford, 1966a).

The absence of rib meristem in floral apices of Laurelia and

Hedycarya is a somewhat unusual feature. Newman (1965) stated that reproductive apices frequently have a more pronounced rib meristem than vegetative ones. He attributed this to differences in rates of extension growth. Thus in Michelia the vegetative apex has a weak rib meristem but the floral apex, which produces laterals at a much faster rate, has a prominent rib meristem. Whether the absence of rib meristem in the floral apices of Laurelia and Hedycarya indicates that floral appendages are produced at a slower rate than leaves is not known.

The fact that stratification of the T2 layer in the floral apex of Laurelia and Hedycarya is disturbed by periclinal divisions after tepal initiation, is also a feature of the floral apices of many plants, including Drinys winteri (Tucker, 1959), Pseudo-wintera (Sampson, 1963) and Laurus (Kasapligil).

Eames (1964) stated that the two-layered tunica seems to be the primitive form in angiosperms. While this type is common within members of primitive families, I would share Gifford's (1954) view that the apical meristem should be thoroughly studied in many more families before any possible trends in apical structure can be envisaged.

CHAPTER 4

STAMEN ONTOGENY AND THE DEVELOPMENT OF MICROSPORANGIA AND MALE GAMETOPHYTES

Initiation and early growth of stamens

Hedycarva

After tepal initiation the floral apex increases in diameter and convexity. When stamen initiation begins the apex is still tilted towards the inflorescence axis, with the exception of the terminal flower bud. At this stage the apex is either circular in transection or is still flattened in the sagittal plane to as little as two-thirds of the diameter along the frontal plane. It measures 290-410 μ in diameter along the frontal plane and 215-290 μ diameter along the sagittal plane and is approximately 35 μ in height. The stamens are initiated in centripetal fashion and at least the outermost ones are formed in spiral succession. The other, more internal stamens are so closely packed together that I was unable to determine the direction of the spiral or whether there were a number of intersecting spirals or even closely packed whorls of stamens.

Each stamen is initiated by localized anticlinal divisions in the T1 and T2 layers on a flank of the apical meristem. The cells of the T2 layer within this region increase their vertical elongation to produce a slight bulge before any periclinal divisions occur. The nuclei of such cells are also conspicuously vertically

elongated and therefore spheroidal rather than spherical in shape. The first periclinal divisions occur in the T2 layer and are soon followed by periclinal, anticlinal and oblique cell divisions in the subjacent two layers and the primordium becomes a hemispherical mound (PLATE 27, fig. 14) which becomes more conical as it enlarges (fig. 15). Only anticlinal divisions were observed within the protodermal layer of the primordium.

In general, the subprotodermal cells near the tip of the stamen divide in periclinal and anticlinal planes, but the subprotodermal cells on the flanks divide in an anticlinal plane with respect to the ad or abaxial surface of the primordium (i.e. in a horizontal plane). Cells in the central axis of the primordium divide mainly in a horizontal plane. The foregoing divisions result in a primordium which consists of relatively discrete vertical files of cells (PLATE 27, fig. 10). When the primordia are about 110μ high they are finger-like protuberances and procambium has extended acropetally into their base.

During the period of stamen initiation the receptacle becomes concave so that the outermost stamens are inserted at a level above the inner ones. This is shown in a median longisection through the frontal plane shown in silhouette in Plate 27, fig. 11. Note how the tepals curve downwards towards the centre of the bud. At this stage, in which stamen initiation is almost complete, the apex ("A" in the figure) is either flat or slightly convex (PLATE 23, fig. 1).

Laurelia

The floral apex of male flowers has a diameter of approximately 150μ at the beginning of stamen initiation and is a low convex mound about 12μ high. The floral apex of carpellate flowers is of a similar size, but concave at the beginning of stamen and/or staminode initiation (PLATE 26, fig. 2). During the course of stamen and staminode initiation the receptacle becomes concave, as in Hedycarya.

The initiation and early growth of stamens and staminodes is similar to that described for Hedycarya. During stamen initiation the cells and nuclei of the T1 layer are more vertically elongated than in Hedycarya. Fig. 16 of PLATE 27 illustrates a young stamen primordium in (a) lateral ad-abaxial view. Part of the apical meristem ("A.M.") is visible. In (b) and (c) the same primordium is shown in ^{adaxial}~~lateral~~ and ^{abaxial}~~lateral~~ view. An older primordium is shown in fig. 18.

Development of microsporangia

Hedycarya

Archeporial cells were present when stamens were approximately 150μ high. There were four groups of archeporial tissue, each representing a future pollen sac. Difficulty was experienced in determining the precise limits of the archeporial cells for the following reasons.

(a) Archeporial cells were not sufficiently distinct in appearance from neighbouring hypodermal cells.

(b) Transverse sections were not made at this stage of stamen development. It could not therefore be stated with exactitude whether each group of archesporials was one or more cells wide as seen in cross section. From an examination of longitudinal serial sections, it appeared that each group of archesporials was at least two cells wide in cross section.

(c) Some cells which resembled neighbouring archesporials (some of the latter were dividing into primary sporogenous and primary parietal cells) were undergoing a final anticlinal division before apparently functioning as archesporials. It is presumed therefore that some cells which appeared to be archesporial cells might in fact divide anticlinally before functioning as archesporials.

As seen in longitudinal section of a stamen, each group of archesporial cells consisted of a row of about 7-9 hypodermal cells which extended most of the length of the stamen. A longisection of part of a stamen is shown in fig. 12 of PLATE 27. The archesporial cells ('Ar') had a darker staining cytoplasm and somewhat larger nuclei than those of the contiguous epidermis ('Ep'). The cells immediately internal to the archesporials were more vacuolate. Cananga of the Annonaceae resembles Hedycarya in having archesporial tissue in longitudinal hypodermal rows (Periasamy & Swamy, 1959).

Each archesporial cell divides periclinally into an outer primary parietal cell ('Par' in fig. 13) and an inner primary

sporogenous cell ('Sp'). Above these two cells in the figure, are two tiers of two cells per tier which have resulted from the anticlinal division of a primary parietal and a primary sporogenous cell. This was deduced from the observation that the combined vertical length of these two tiers of cells was comparable to the length of a single parietal or sporogenous cell below or, to the length of the cell "Sp 2" above. It was also observed that the anticlinal walls separating these two tiers were thinner and therefore, it is presumed, more recent than the anticlinal walls of other cells in these layers, excluding the wall separating the two cells to the right of "Sp 2". These differences in wall thickness are not clearly shown in the figure. The primary sporogenous cell "Sp 2" is still undivided but the ~~primary~~^{sister} parietal cell has divided anticlinally. At this stage the stamens are approximately 170μ high.

The primary parietal cells undergo periclinal and anticlinal divisions to form the 5-6 wall layers of the mature pollen sac, excluding the epidermis. The primary sporogenous cells undergo further divisions to form a large number of sporogenous cells.

Early stages in the development of wall layers and sporogenous cells are shown in PLATE 28, fig. 1. In the oldest stamen visible (upper right) 2-3 wall layers have been formed. Pro-cambium has extended into the lower two-thirds of the stamens. The stamens are now four-lobed as seen in cross section and wedge shaped (fig. 17, PLATE 27). A later stage in the development

of the microsporangium is shown in fig. 2 of PLATE 28. A comparable stage is shown in transverse section in fig. 3. Large cells of two types are visible within the receptacle and stamen connective. One type is darkly staining and contains deposits of a tannin-like nature, as in Laurus and Umbellularia (Kasapligil, 1951). The other type has a large vacuole and peripheral protoplasm at maturity and resembles the "idioblastic secretory cells" of the Lauraceae (Kasapligil, 1951) and the "spherical secretory cells" which Money et al (1950) describe as a characteristic feature of many families of woody Ranales.

The stamen illustrated in longitudinal section in fig. 1 of PLATE 29 contains nearly mature sporogenous tissue. A few sporogenous cells were still undergoing division and some anticlinal divisions were apparent in the wall layers. Most of the cells of the sporogenous tissue are maturing into microspore mother cells. They have a denser cytoplasm and larger nuclei than those of the wall layers. The innermost wall layer, which encloses the sporogenous tissue, is now differentiated as the tapetum. Tapetal cells are less flattened tangentially than the other wall layers and they have a denser cytoplasm. The pollen sacs extend for most of the length of the stamen, which lacks a filament. The uppermost part of the stamen is sterile. Pro-cambium has now extended acropetally to near the tip of the stamen, as in Laurelia at this stage, but this cannot be seen in the figure.

Laurelia

Sections were not obtained of stamens at the archesporial cell stage. The staminal glands are initiated when the wall layers and sporogenous tissue are at an early stage of development. There are fewer pollen grains per stamen in Laurelia than in Hedycarya. This is because the stamen of Laurelia has only two pollen sacs, which are shorter and each sac in transection has fewer grains than in Hedycarya (compare figs. 1 and 2 of PLATE 39, in which pollen mother cells are at prophase I). During the development of sporogenous and wall tissue, which is similar to that described for Hedycarya, the stamen becomes somewhat spatulate (PLATE 27, fig. 19), being flattened dorso-ventrally. In later stages of development (figs. 20 and 21) the staminal glands enlarge and the central part of the stamen broadens. Mature stamens have a dorso-ventrally flattened filament which occupies up to almost half the length of the stamen (PLATE 9, figs. 1-10).

section. Their cytoplasm is denser and nuclei considerably larger than in wall layer tissue.

Microsporogenesis and the tapetum

Hedycarya

Meiosis begins in the pollen mother cells when stamens are 1135-1180 μ high, in comparison to stamens of Laurelia which are 660-1020 μ high at this stage.

Although the tapetum is predominantly one cell thick, it is two cells thick in places, in both genera, owing to the occurrence of some periclinal and oblique divisions while the tissue was maturing.

Nuclear division is asynchronous in the tapetum and begins when the pollen mother cells are at either early leptotene or the synizesis stage of prophase I, as is commonly the case in angiosperms (Iijima, 1962). By early anaphase I most of the tapetals are binucleate. As in Laurelia the tapetals are considerably vacuolate when they undergo nuclear division (PLATE 33, figs. 1 and 2) with the axis of the spindle aligned either parallel or at right angles (figs. 1 and 2) to the adjacent surface of the pollen sac; the former condition being more common. In Laurelia the two types of spindle orientation are found with equal frequency. At the end of the second meiotic division of the pollen mother cells, the tapetals had lost contact with one another and were becoming tangentially flattened and darkly staining (PLATE 34, fig. 2). They remain in situ during the maturation of the pollen

and are therefore of the secretory type. Only scattered remnants of the tapetum were visible when the pollen grains were two-celled with the generative cell lying within the cytoplasm of the vegetative cell. It appears that nuclear division is not completed in some tapetal cells. For, when the unicellular pollen grains were dividing, many stamens contained a few tapetal cells in which mitotic figures were present at stages from metaphase to telophase. These appeared to be abnormal stages with grossly flattened chromosome groups and chromosome bridges in some at late anaphase. They resemble the "sticky" type of tapetal division (Maheshwari, 1950). Despite a careful search no pre-metaphase stages were found, which suggests that the mitotic figures had been present since the time at which the pollen grains were initiated. Unfortunately no flowers were sectioned between pollen mother cell meiosis and pollen grain mitosis stages. One of the abnormal tapetal cells is shown in PLATE 33, fig. 3. I can find no mention of comparable "frozen" tapetal mitotic figures in the literature, and Maheshwari (1950) stated that when the sticky type of division occurs, an abnormal nucleus which may be distorted in shape, is reconstituted.

Pollen mother cells undergo meiosis at the same time in all the stamens of a flower. Despite the considerable length of pollen sacs, prophase I stages are synchronous within each sac, although adjacent ones may be at a slightly different stage e.g. early leptotene in one sac and synizesis in the adjacent one.

After prophase I there is some variation in stages within a single sac, but most mother cells are at the same stage. For example, one sac contained a range of stages from interkinesis to late anaphase II with most cells at metaphase II and early anaphase II.

From leptotene onwards, wall material is laid down inside the original wall of each mother cell and after synizesis the protoplasm loses its polygonal outline and becomes rounded with continuing deposition of this material, which recent research has shown to be of a callosic nature (Waterkeyn, 1962; Heslop-Harrison, 1966). Heslop-Harrison (1966) noted that deposition of the callose wall usually begins at late leptotene and therefore Hedycarya is typical in this respect. Waterkeyn (1962) found that this "paroi speciale" was not readily apparent when material is stained with nuclear stains and mounted in Canada balsam, but in both Hedycarya and Laurelia in material thus treated, the "paroi speciale" is visible as a bright glistening translucent zone between the original wall and cytoplasm, when sections are viewed under phase contrast. During deposition of the callosic material the external walls of the mother cells retain their polygonal outline and maintain contact with neighbouring mother cells but during the course of meiosis intercellular spaces develop in the corners between adjacent cells. As these spaces increase in size the external wall loses part of its polygonal outline. The original mother cell walls can be faintly seen

in PLATE 34, fig. 2, in which the mother cells are at telophase II. At this stage some of the middle wall layers are tangentially flattened and the hypodermal layer is enlarging into the endothecium. The mother cell wall disintegrates soon after the tetrads are formed. Heslop-Harrison (1966) noted that it is usual for stages in meiosis to become progressively less synchronized between adjacent microcytes from metaphase I onwards and this is true for Hedycarya. He attributed this to the breakdown of interconnecting cytoplasmic channels between mother cells.

Fig. 1 of PLATE 34 illustrates part of a pollen sac in which the mother cells are at early synizesis, which some recent authors consider to be a non-artefact stage equivalent to the bouquet stage in animals (Oskala and Therman, 1958; Rhoades, 1961). Each mother cell contains a single large nucleolus or a large nucleolus and one or two smaller nucleoli. Three pollen mother cells can be seen in the figure with what appears to be a single giant nucleolus embedded in the cytoplasm. Other cells (PLATE 35, fig. 1) have a nuclear membrane enclosing the nucleolus and the space between nucleolus and membrane filled with a cytoplasmic-like material which is devoid of a chromatin reticulum. In some cells (fig. 2) nucleolar vacuoles were present. These sterile cells were present with a frequency of up to 10% of the total pollen mother cells in most stamens of most flowers sectioned, including material from two different localities. They persist relatively unchanged up to the time of ~~anther~~^{anther} dehiscence although

their walls thicken and some become distorted in shape. The nucleolus in these cells was slightly larger in diameter than the generative cell nucleus in the pollen grain. It is possible that the apparent lack of a nuclear membrane in some sterile cells may be an artefact due to sectioning, as the nuclei of these cells might be more fragile than normal ones because of the lack of a chromatin reticulum.

Fig. 3 of PLATE 34 illustrates metaphase - early anaphase I. Cytokinesis is of the successive type in which a centrifugal cell-plate is laid down at the end of meiosis I (PLATE 35, figs. 3 and 4). During interkinesis nucleoli reappear but the formation of a typical chromatin reticulum does not occur. During meiosis II, as found also in Laurelia, the stages are synchronised in both halves of a dyad. Metaphase II is illustrated in PLATE 36 under ordinary light (fig. 1) and phase contrast (fig. 2) and in the latter figure the spindle fibres are clearer. Telophase II is shown under phase contrast in fig. 3 in which the second division cell-plates are formed. In most cases, as shown in figs. 1-3 the spindles of each half of the dyad are aligned parallel to each other, thereby explaining the general tetragonal arrangement of grains in a tetrad (PLATE 36, fig. 4). In a few cases the spindles are aligned obliquely to one another or are crossed at right angles which would explain the occasional tetrahedral and decussate tetrad types. Pollen grains are in permanent tetrads in the genus and Money et al., found that most

tetrads in Hedycarya angustifolia were tetragonal but that transitions to the tetrahedral type were "of not uncommon occurrence".

Laurelia

Tapetal behaviour during meiosis resembles that in Hedycarya in that nuclear division is asynchronous and begins when pollen mother cells are at early leptotene. Most cells undergo nuclear division when pollen mother cells are at from leptotene (PLATE 39, fig. 3) to the end of prophase I, but a few divisions were observed during metaphase and anaphase I. By interkinesis most if not all tapetals are binucleate. During meiosis the tapetals of Laurelia are comparatively more radially elongate than those of Hedycarya. Vacuolation and radial elongation increases during meiosis (compare PLATE 39, fig. 3 and PLATE 40 figs. 1-3) and before the end of Meiosis II the tapetals have lost contact with one another. They do not undergo tangential flattening at this stage, in comparison to those of Hedycarya. However at a time shortly before the uninucleate pollen grains undergo division, the tapetals are tangentially flattened, with a more finely vacuolate, coarse cytoplasm and deeply staining nuclei (PLATE 41, fig. 1). As a result of this flattening the tapetal cells are again in contact with one another. This secretory tapetum remains in situ and becomes absorbed by the time the pollen grains are mature (PLATE 41, fig. 2).

Pollen mother cell division resembles that in Hedycarya in

that:-

(a) Meiosis begins at the same time in all stamens of a flower and prophase I stages are synchronous in each sac, although adjacent sacs may be at a different stage of meiosis. An unusual feature found in one pollen sac only, was that in approximately one half of the sac, extending throughout its length, mother cells were at metaphase I and early anaphase I and in the other portion of the sac were at diplotene of prophase I.

(b) The "paroi speciale" is deposited from leptotene onwards and by diplotene (PLATE 39, fig. 1) the cytoplasm has lost much of its polygonal outline. As in Hedycarya the original (external) mother cell walls keep their polygonal outline for a time (PLATE 40, fig. 2) but intercellular spaces develop (fig. 2) and the original wall becomes more rounded (fig. 3). This wall is ruptured when the tetrads separate.

The most significant difference in microsporogenesis in the two genera is that in Laurelia quadripartitioning does not occur by the deposition of successive cell-plates. Early anaphase I is shown in PLATE 40, fig. 1 and in PLATE 42, fig. 1 a pollen mother cell can be seen at this stage under phase contrast, which shows the spindle fibres particularly clearly. At the end of telophase I (fig. 2) nucleoli reappear in the nuclei but as in Hedycarya no definite chromatin reticulum is reconstituted. At this stage it can be seen that a centripetal furrow has formed around the edges of the cytoplasm, between the two nuclei.

This peripheral furrow does not advance inwards much by the time of anaphase II which is illustrated under ordinary light (fig. 3) and phase contrast (fig. 4) in PLATE 42. Notice the structures at the left equatorial side of the cell, which have the superficial appearance of spindle fibres but in this cell are aligned parallel to the equator. These structures, which can also be seen in PLATE 40, fig. 3, appeared in all mother cells during meiosis II. In some cells they were aligned at right angles to the equatorial region of the cell as can be seen in the cell at anaphase II under ordinary light (fig. 1) and phase contrast (fig. 2) in PLATE 43. It is possible that these structures are residual parts of spindle fibres from the first meiotic division and have undergone re-alignment in some cells. This possibility is supported by the presence of apparent remnants of spindle fibres at the equatorial region of telophase I cells (PLATE 42, fig. 2)*. The centripetal furrow again becomes active and near the end of telophase II has extended to almost the centre of the cell as shown in PLATE 43, figs. 3 and 4 (phase). At this stage a cell-plate is extending centrifugally across the equator of each half of the dyad. At a later stage, shown in figs. 1 and 2 (phase) of PLATE 44, furrowing is complete and in each half of the dyad the cell-plate has completed its centrifugal growth. This type of quadripartitioning

* Professor A. Frey-Wyssling of the Swiss Federal Institute of Technology, Zurich, an authority on the fine structure of cytoplasm examined my photographs and was also of the opinion that the structures might represent degenerating spindle fibres.

in which there is a combination of furrowing and cell plate formation has apparently not hitherto been recorded for pollen mother cells. Fig. 3 illustrates a young pollen tetrad with tetragonal configuration. Some pollen tetrads were arranged tetrahedrally.

During meiosis cell divisions were observed within the wall layers of the anther and were of common occurrence throughout the filament, but by the time that the pollen grains had separated from one another the only divisions within the stamen (excluding those within the appendages and those forming vascular tissue) were near the base of the filament. During meiosis, the endothecium is not as vacuolate nor as radially enlarged in Laurelia as in Hedycarya. The endothecium is well developed at the time of pollen grain division (PLATE 39, fig. 4) and at maturity it has the radial bars of thickening (PLATE 41, fig. 2).

Some stamens were sectioned in which the tapetum had aborted and was a darkly staining zone of crushed cells around the pollen mother cells (PLATE 44, fig. 4). It is presumed that this pollen sac would not have produced viable pollen in view of the role which the tapetum plays in the development of the pollen (Heslop-Harrison, 1963, 1964). A pollen sac with sterile pollen, which may have been the result of such an abortive tapetum is shown at left in PLATE 41, fig. 2. However other stamens were sectioned in which the tapetum appeared normal but the pollen mother cells were crushed and deeply staining and this would also give rise to sterile pollen sacs.

Development of the pollen grains

Hedycarya

The first division within the microspores occurs at approximately the same time in all stamens of a flower. The stamens are 1320-1710 μ high at this stage in comparison to those of Laurelia which are 1560-1860 μ high. Although there is a variety of division figures within a single pollen sac, all four cells within a tetrad are at the same stage of division (PLATE 38, fig. 1). Maheshwari (1950) stated that this is the usual condition for plants with microspores in permanent tetrads, although in Pseudowintera the four cells of a tetrad are not usually at the same stage of division (Sampson, 1963).

Fig. 4, PLATE 36, illustrates a tetrad shortly before division begins. Some exine has been deposited on the exposed faces of this tetrad. A tetrad is shown at prophase (fig. 1) and metaphase early anaphase (fig. 2) in PLATE 37. The division into unequal-sized cells is anticipated in that the distal pole of the spindle is blunter than the proximal (internal) one and the equator of the spindle lies closer to the distal (external) surface of each microspore. In fig. 3, two cells of a tetrad are shown at anaphase and in fig. 4 division has been completed. The smaller generative cell is always cut off towards the distal face of the microspore and a "curved watchglass-shaped wall" typical of asymmetrical spindles (Steffen, 1963) separates the generative and vegetative cells.

At the time when the pollen grain is undergoing its first division, the endothecium, which as in Laurelia is confined to the exposed sub-epidermal part of the pollen sacs, has enlarged radially to near its maximum size, but the radial bands of fibrous thickening are not yet present.

The generative cell soon rounds off and the cytoplasm of the vegetative cell begins to extend around it (PLATE 38, fig. 2, microspore at upper centre) and it soon comes to lie within the cytoplasm of the vegetative cell (fig. 2, microspore at centre right) where it is distributed at random. The cytoplasm of the generative cell is more hyaline and less vacuolate than that of the vegetative cell. During the maturation of the pollen grains, the vegetative nucleus becomes less deeply staining (as can be seen in some grains in fig. 3) and this common phenomenon which also occurred in Laurelia, has been attributed to a loss in DNA content (Steffen, 1963). The endothecium now bears the characteristic bands of thickening.

Shortly before dehiscence, radially adjacent pollen sacs of a stamen become continuous by the breakdown of all but the most internal part of the separating wall. The middle layers at this stage are crushed beyond recognition. The epidermal cells are now tangentially flattened with a wavy outline, but even at the time of dehiscence they have not broken down and many have nuclei in good condition, as are those of the endothecium. This is also the case in Laurelia.

Dehiscence is longitudinal and latrorse and occurs by the separation of cells along a line of weakness at the outermost part of the wall which separated adjacent radial pollen sacs. A flower with dehiscent stamens is shown in PLATE 5, fig. 2 and in some of the stamens the innermost part of the separating wall between adjacent pollen sacs can be seen. Pollen is shed in the two celled condition.

Laurelia

Money et al., (1950) illustrated and described the mature pollen grain of Laurelia as spherical or somewhat ellipsoidal with a furrow which commonly encircles the grain. In contrast to this monocolpate type, some genera of the Atherospermoideae e.g. Atherosperma, are dicolpate. In Atherosperma the two furrows on the grain are extensive, with tapering ends which nearly meet (Money et al., 1950). In the Magnoliaceae the pollen has a relatively broad furrow on the distal face and in the related Degeneriaceae, the furrow is of distal origin too and extends around the sides of the grain towards the proximal pole. Money et al., commented, "The furrow is much constricted in the vicinity of the distal pole and broadens markedly on the lateral surfaces of the pollen. Additional constriction and elimination of the distal part of the furrow would yield a dicolpate condition Further extension of the furrow until its tapered ends meet at the proximal pole would form an alternately constricted and expanded groove which completely encircles the pollen as in

Laurelia Novae-Zelandiae According to such an interpretation, the encircling furrow would be on a meridian as in Degeneria, and fundamentally different from the encircling furrows of certain Nymphaeaceae, where, as shown by the coherent tetrads of Victoria, the grooves are zonal and oriented at right angles to the polar axis In the case of the Laurelieae(*), the orientation of the furrows in relation to the polar axis and to the distal and proximal surfaces of the pollen should be studied by someone having access to living flowering representatives." Now when pollen grains are in tetrads in Laurelia, there is as yet no sign of the furrow. It is present soon after the grains have separated (PLATE 41, fig. 1). Fortunately the separated grains do not immediately become rounded and have for a time a shape which betrays their orientation when in the tetrad stage, with the more rounded distal face and proximal edge preserved. When a tetrad is viewed externally such that only two of the four grains are apparent, it can be seen that the grains are considerably elongated and thus their distal faces have an elliptical outline. Examination of recently separated tetrads revealed that the furrow passed along the centre of the distal face of a grain, encircling its long axis and then passed along the proximal edges of the grain to the proximal pole. The two widest parts of the furrow were at right angles to the proximal-distal axis (see text-figure 15 and Plate IV, figure 42 of Money et al's paper). This observation

(*) Synonymous with Atherospermoidae.

therefore supports Money et al's interpretation.

Exine is deposited on the outside of the grain (excluding the furrow) before it is two-celled (PLATE 45, fig. 1). Before the first division occurs, the grain becomes roughly spherical and the nucleus migrates to one side of the grain, away from the furrow (fig. 2) and at this stage vacuoles are present in the cytoplasm. According to La Cour (1949) it is this vacuolation which leads to the migration of the nucleus. Sometimes part of the nucleus is flattened against the wall of the grain (fig. 3). A stage in prophase is illustrated in fig. 4, with a tapetal nucleus visible to the left of the grain. At metaphase (fig. 5) and late anaphase (Plate 46, fig. 1) it can be seen that the equator of the spindle is displaced a considerable distance from the centre of the cell and this displacement is greater than in Hedycarya. It is concluded that the generative cell is cut off against what represents a radial wall of the grain when at the tetrad stage, since the generative cell lies the maximum distance from the germinal furrow (Plate 46, figs. 2, 3 and 4). This is an unusual feature as in the cases in which the polarity of the pollen grain can be determined at this stage, the generative cell is usually cut off against the distal or proximal side of the grain (La Cour, 1949).

Soon after the two cells are formed, the cytoplasm of the vegetative cell develops many vacuoles as shown in figs. 3 and 4 (phase). This finely vacuolate stage is lost a short time after

the generative cell lies within the vegetative (PLATE 47, fig. 1). A similar vacuolate stage has been recorded in Pseudowintera (Sampson, 1963) and in Beilschmiedia tawa (Roper, pers. comm.). During maturation of the grain the cytoplasm of the generative cell becomes conspicuously more hyaline than that of the vegetative cell (PLATE 47, fig. 2). In contrast to Hedycarya the generative cell does not become spherical, but retains to some extent its original shape. Pollen is shed in either the two or the three-celled condition. When the generative cell does divide before it is shed from the anther, this division occurs within a day or two of dehiscence. A pollen grain in which the generative cell is at telophase is illustrated in PLATE 48, fig. 1. The vegetative nucleus is in a different plane of focus. Fig. 2 illustrates a three celled grain and the two male cells are shown lying above the vegetative nucleus. They resemble the vegetative cell in their spindle shape and hyaline cytoplasm.

At dehiscence, the endothecium is radially thickened and the middle wall layers are flattened and crushed (PLATE 41, fig. 2). The semi introrse-latrorse dehiscence occurs by the outward opening, beginning at the base, and upward bending of an elliptical red coloured part of the anther wall which is hinged at the top (frontispiece; PLATE 5, fig. 4). A considerable amount of pollen adher^e_s to the inside of this flap, as can be seen in the upper two carpellate flowers shown in PLATE 5, fig. 1, from whence it would be readily brushed off by visiting insects. Dehiscence

occurs by the separation of cells around the edges of the flap which form a stomium-like region. Thus in transverse section, four stomium-like regions of small unthickened cells can be seen in indehiscenced stamens (PLATE 39, fig. 4).

Discussion

Stamens

As outlined in Chapter 2, the stamens of Hedycarya and Laurelia differ markedly in appearance and structure, but the stamens of Peumus and Monimia provide a link between the Atherospermoideae and Monimioideae. The stamens of the Atherospermoideae are obviously closely related to those of the Lauraceae. There is however greater variation in stamen structure in the Lauraceae in that there may be 2 pollen sacs (e.g. Laurus), as in probably all of the Atherospermoideae or 4 pollen sacs. In the latter case the sacs are either at the same level with each pair of sacs dehiscing by a single valvular flap, as in Beilschmiedia (Roper, pers. comm.), or one pair of sacs is situated above the other pair and each sac dehisces separately, as in Umbellularia. In Cinnamomum there are transition forms between two and four chambered anthers (Kasapligil). In view of the predominantly four chambered stamens in angiosperms it seems logical to assume that the stamens with 2 pollen sacs represent a derived condition. Thus Kasapligil (1950) maintained that the stamen of Laurus with its two pollen sacs had been derived from a four celled type of anther and in support of this view mentioned the presence of

teratological stamens with an incomplete diaphragm in each sac. The stamen of Beilschmiedia with its 4 chambers which dehisce by means of only 2 valves, might well represent an intermediate stage in the derivation of the 2 chambered lauraceous stamen. I did not find any ontogenetical, morphological or teratological indication in Laurelia to suggest that the anther had once been four chambered. The second type of four chambered stamens in the Lauraceae are more difficult to interpret. Some workers have suggested that the four chambers may have been derived from a stamen such as that of Laurus by the development of a transverse median partition in each of the two sacs. Kasapligil commented on the frequent dichotomies at the tip of the median vascular strand and at the tip of lateral filament traces in Umbellularia. He suggested that such dichotomies may indicate that this genus once had four terminal microsporangia. This seems unduly speculative to the writer, at least with respect to the forking of the median strand, as many stamens have this feature irrespective of the number or the location of pollen sacs e.g. some stamens of Hedycarya. Kasapligil added that the dichotomies "could be interpreted in accordance with Wilson's (1937) theory that stamens are derived from dichotomous branch systems which had terminal sporangia". He did not however interpret dichotomies within the staminal glands in accord with the Telome theory since he considered the glands had arisen de novo. It seems likely that the primitive 'Atherospermoideae-Monimioideae' stamen had

four pollen sacs, but it is debatable whether such a stamen had a filament and staminal appendages, as apparently suggested by Money et al. (see Chapter 2). The filament-less, eglandular stamen of Hedycarya could conceivably have been directly derived from the apparently primitive leaf-like ranalean stamens.

Tapetum

Hedycarya and Laurelia resemble Cassytha (Sastri, 1962) and Beilschmiedia tawa (pers. comm. Roper) in having a secretory tapetum but differ from the other genera of Lauraceae so far studied, which have the periplasmodial type (Sastri, 1963). Sastri (1963) who made a few observations on microsporogenesis in Atherosperma found that this genus, which as I have stated, appears to be closely related to Laurelia, had the periplasmodial type of tapetum. I therefore conclude that the two types of tapetum do not have great taxonomic significance at least within the Monimiaceae and Lauraceae.

Cytokinesis

Hedycarya resembles all members of the Lauraceae so far studied in having successive cytokinesis by cell-plate formation (Sastri, 1963).

In view of the discovery of an apparently new type of cytokinesis in Laurelia, it would seem desirable that I should now summarize the types of cytokinesis which have been recorded in angiosperms. Periasamy and Swamy (1959) have pointed out that there has been some ambiguity in the use of the terms "successive"

and "simultaneous" and consider these terms should designate not merely a temporal relationship but two different cytological processes. They state that the important feature is whether or not the walls are initiated by a centrifugally spreading cell-plate or by a centripetal constriction furrow. Although centrifugal cell-plate formation usually occurs in a successive manner with the first wall being formed at the end of meiosis I and although centripetal cytoplasmic constriction usually occurs in a simultaneous manner, there are exceptions. I have criticised the choice of the terms "successive" and "simultaneous" and suggested that pollen tetrads should be described as being formed by "successive" or "simultaneous", "centrifugal cell plates" or "centripetal constriction furrows" (Sampson, 1963). The following types of cytokinesis have been recorded:-

(1) Cytokinesis by successive centrifugal cell plates deposited at the end of meiosis I and II, as in Hedycarya and many other plants (Maheshwari, 1950).

(2) a. Cytokinesis by simultaneous centripetal constriction furrows at the end of meiosis II, as in Nicotiana and many other plants (Maheshwari, 1950).

b. A minor variant of this type occurs when one of the furrows appears at the periphery of the pollen mother cell at the end of meiosis I. It does not however reach the centre of the mother cell until the second furrow (which appears at the end of meiosis II) does. Quartet formation is therefore simultaneous.

Magnolia kobus is an example of this type (Stoudt, 1960).

The above two types are by far the commonest.

(3) Cytokinesis by means of simultaneous centrifugal cell plates which develop at the end of meiosis II, as in Helleborus (Waterkeyn, 1962), Illicium, Schisandra and Kadsura (Hayashi, 1960, 1965).

(4) Cytokinesis by means of successive centripetal constriction furrows as in some of the Annonaceae (see Periasamy and Swamy, 1959).

(5) Cytokinesis by means of simultaneous constriction furrows, but a transient cell-plate or cell-plate precursor is present at the end of meiosis I. This has been recorded in Zygogynum (Swamy, 1952) and Pseudowintera (Sampson, 1963) of the Winteraceae and in Magnolia (Farr, 1918; Hayashi, 1960). In Helleborus, in which cytokinesis occurs simultaneously at the end of meiosis II by cell-plate formation, Waterkeyn (1962) found that the equator of the spindle was invaded by basophilic granules during interkinesis. These were grouped into an equatorial plate which Waterkeyn considered to be a mitochondrial plate. It is possible that Zygogynum, Pseudowintera and Magnolia might therefore have such mitochondrial plates rather than transient cell-plates or cell-plate precursors, unless of course the mitochondrial plate itself represents a cell-plate precursor.

(6) The type recorded for Laurelia in which a centripetal furrow, initiated at the end of meiosis I, reaches the centre of the mother cell at the same time (as far as can be ascertained) as centrifugal cell-plates, which are generally oriented at right angles to the

furrow. These cell-plates are initiated at the end of meiosis II.

It is possible that cytokinesis in Laurelia is merely of the "2b." type described above. For, according to Waterkeyn (1962) who studied microsporogenesis in Helleborus by means of ordinary light and fluorescence microscopy as well as by electron microscopy, cell plate formation and centripetal furrowing may not be mutually exclusive. He quoted West (1930) who found in Viola that at the end of meiosis II, "In pollen mother-cells in which furrowing has begun, delicate cell-plates are seen at the equator of the spindles These probably assist in the formation of the tetrad wall, although they appear to be merely evanescent structures." Waterkeyn found that in Helleborus the granulose cell plates which form at the end of meiosis II are transformed into callose walls which become enclosed centripetally by less dense callose deposits. It would seem possible to me that this phenomenon may occur in other plants which have been described as having cytokinesis by means of simultaneous centripetal constriction furrows when Waterkeyn's methods are used.

It is surprising that Atherosperma should have cytokinesis of the successive type (Sastri, 1963) and this demonstrates that the two basic types of cytokinesis do not have taxonomic value in the Monimiaceae.

Microspores

Hedycarya is apparently the only genus within the Monimiaceae to have pollen in permanent tetrads (Money et al., 1950). It

seems obvious that the permanent tetrad condition has evolved separately by parallel evolution in view of its presence in a number of families which are not closely related e.g. Winteraceae and some of the Droseraceae, Typhaceae, Ericaceae, Apocynaceae, Asclepiadaceae, Juncaceae and Orchidaceae (Maheshwari, 1950).

Permanently united tetrads have been recorded within the woody Ranales in Hedycarya, the 6 genera of the Winteraceae (Bailey and Nast, 1945), 11 genera of Annonaceae (Canright, 1963) and in Lactoris of the Lactoridaceae - a monotypic family which Carlquist (1964) considers is of unquestionably annonalian affinities. Although it is possible that all of these genera have inherited the permanent tetrad condition from a single ranalean group of ancestors, the Winteraceae does not appear to be closely related to the other families (Bailey and Nast, 1945; Money et al., 1950). According to Carlquist (1964) the permanently united tetrads of Hedycarya on the one hand and the Annonaceae and Lactoris on the other are "undoubtedly parallelisms" despite his view that the Monimiaceae was one of the families which had "the greatest constellation of morphological and anatomical features like those of Lactoris".

In contrast to Hedycarya, the generative cell is cut off against the proximal (internal) corner of the grain in Pseudowintera (Sampson, 1963) and Zygogynum (Swamy, 1952). This feature has not been investigated in the other ranalean genera with permanent tetrads. Hedycarya resembles Cananga of the

Annonaceae (Periasamy and Swamy, 1959), Degeneria (Swamy, 1949), Austrobaileya (Bailey and Swamy, 1949) and at least some of the Magnoliaceae (Swamy, 1952) in having the generative cell cut off against the distal side of the grain.

CHAPTER 5

ONTOGENY, STRUCTURE, FUNCTION AND MORPHOLOGICAL NATURE OF THE STAMINAL APPENDAGES OF LAURELIA

The vascularization of mature staminal appendages of Laurelia has already been described and compared with some other members of the Laurales (Chapter 2). Some theories as to the morphological nature of these appendages have been briefly mentioned.

Ontogeny, structure and function

Each gland arises laterally a short distance above the base of the stamen when it is about 230μ high. At this stage 2-3 wall layers have been formed in the anther and sporogenous cells are dividing vigorously. The gland is initiated by anticlinal elongation followed by anticlinal division of a group of surface cells simultaneously with the anticlinal elongation followed by anticlinal and periclinal division of cells in the subjacent hypodermal layer, near the base of the filament (PLATE 29, fig. 2). Some periclinal and anticlinal divisions then occur in the subhypodermal layer beneath. An anticlinally dividing cell of this layer can be seen in PLATE 30, fig. 1. The young gland is now a small mound (PLATE 27, fig. 19) which increases in size by general cell enlargement and division, predominantly in anticlinal and periclinal planes. The glands therefore originate in a manner similar to stamens and other floral appendages.

The primordium enlarges as a mound of increasing diameter

(PLATE 27, figs. 20 and 21) which is blunter than a stamen primordium. Cell division is general throughout the primordium and no apical or subapical initials were observed, presumably because growth is so multi-directional. Cell division becomes most frequent around the periphery of the primordium and infrequent near the base, where the cells become vacuolate (PLATE 30, fig. 2). Eventually a stalked mushroom-shaped gland is formed. A surface cell "s" is undergoing periclinal division and pairs of cells have been formed from recent periclinal divisions of surface cells, in the figure. This unusual feature of periclinally dividing surface cells in a flower (Tucker, 1961) was encountered in one other floral part (see on). Procambium has now formed in the base of the gland but is not visible in the section illustrated, which is non median. It is visible in the transverse section of glands at this same stage of development (PLATE 31, fig. 1). At this stage the pollen mother cells are at prophase I of meiosis. When the uninucleate pollen grains are dividing in the anthers, a few cells were still dividing within the glands, in addition to those cells which were initiating vascular tissue. By this time the base of the stamen filament has elongated and glands were now inserted some distance above the base of the stamen. When the anthers contained mature pollen grains, cell division had ceased within the glands (PLATE 31, fig. 2). The epidermal and subepidermal cells of the inner face of the gland (to which the stalk is attached) are large vacuolate cells and contain

deposits of a tannin-like nature. In contrast, the epidermal cells of the outer face of the gland are smaller, less vacuolate and lack the tannin deposits. This is correlated with the fact that only the outer face of the gland secretes nectar. Each of the epidermals of the outer face contains several spherical inclusions which at this stage are up to a third of the diameter of an epidermal cell nucleus. They stain dark blue with haematoxylin. As such inclusions do not occur elsewhere in the flower it would seem that they are in some way associated with nectar secretion. Beneath this epidermis are several layers of cells which do not contain the inclusions. In contrast to the subepidermal layers beneath the inner face of the gland, these layers have a dense cytoplasm.

A stamen from an open flower was sectioned in which the gland had been secreting nectar. It was found that many of the spherical inclusions in the epidermis of the outer face were as large as the epidermal nuclei. The largest inclusions stained a light red colour with haematoxylin but some of the small inclusions stained the dark blue colour of earlier stages. As there were intermediate forms in size and colour it is presumed that there are present different stages in the development of a single type of inclusion. The subepidermal layers of the secreting face no longer have a dense cytoplasm but instead have usually a single large vacuole or in some cases several large vacuoles. The nuclei of these epidermals and subepidermals are well developed

and show no signs of degeneration, with the exception of the nuclei of some disintegrating epidermal cells (see on). I would think it likely that the vacuoles in the subepidermal layers contain the sugar solution which is secreted. At the earlier stage in which these cells had a dense cytoplasm, staining with iodine revealed that they were packed with starch grains. Epidermal cells of the outer face however, contained few if any starch grains; what few starch grains they possessed may have escaped from subepidermal cells during the preparation of the sections. Hydrolysis of the starch before secretion begins would presumably be responsible for the production of a sugar solution in the vacuoles. It is problematical just what role the smaller vacuoles and large inclusions of the epidermal cells play in the secretion of nectar. According to Esau (1953) closely packed thin walled cells beneath the epidermis and rich in cytoplasm constitute, together with the epidermis, the secreting tissue in many nectaries. However according to Eames (1961) it is only rarely that the epidermis overlying the subepidermal secretory tissue is itself secretory.

Kasapligil refuted Daumann's (1931) suggestion that secretion of nectar from the glands of Laurus occurred through the cell wall of the epidermis and thin cuticle. He found that in Umbellularia, and by implication in Laurus too, although this is not definitely stated, "the cuticle breaks down and the epidermis disintegrates around the glandular surface ... just before the opening of the

flowers. Apparently the secretion occurs through the inter-cellular spaces of the ground tissue and the breakdown of the epidermal cells facilitates the ejection of the sticky secretion to the glandular surface." He did not describe the structure of cells within the gland nor suggest from what cells nectar might be secreted. Now in Laurelia, as a concomitant of nectar secretion, the cuticle of the secreting face is ruptured in places and some of the epidermal cells are damaged, apparently by internal pressure exerted by the escaping nectar. As is general for nectaries according to Percival (1961), there is no secretion of nectar in Laurelia before the beginning of anthesis. Secretion of nectar is therefore quite similar in Laurelia and Umbellularia although it begins later in Laurelia and the epidermis is not as extensively damaged during the process of secretion.

As in Umbellularia, the mature gland of Laurelia contained spirally thickened tracheary elements. No sieve tubes and companion cells could be found within the vascular tissue which still contained many procambial cells. Kasapligil too was unable to find definite phloem elements in the glands of Umbellularia. It seems therefore that sugars enter the gland by means of relatively undifferentiated tissue, as in the ovules of many plants including Hedycarya and Laurelia (at least up to the fertilization stage).

When the flowers open, the nectar is visible as a colourless liquid which gives a glistening appearance to the outer faces of

the glands (frontispiece). Nectar runs down from the glands and accumulates at the bottom of the flower as a result of continuing secretion. Large numbers of bees and blowflies were seen to visit flowers to obtain nectar from trees at Lake Ponui as well as small flightless animals e.g. mites. It is doubtful to what extent the red colour of part of the anthers attracts the insects to the nectar, for they are not in general sensitive to the higher wave-lengths of the spectrum, which includes red. However some red coloured flowers do attract bees by virtue of the large amount of ultra-violet light which they reflect (Wigglesworth, 1964). The blowfly Calliphora visited flowers of Laurelia and this insect is sensitive to red light (Wigglesworth, 1964). In any case the insects would be attracted to some extent by the yellow colour of the glands and by the taste of the nectar itself, once they had alighted on the flower. The flowers are odourless to humans and although they may not be odourless to bees, the olfactory acuity of man and bees is said to be quite similar (Wigglesworth, 1964). The glands of any functional stamens of carpellate flowers also secrete nectar in enough quantities to attract insects to such flowers. Although therefore the functional stamens of carpellate flowers may not be of great importance in supplying much pollen to the carpels in comparison to the pollen supplied by male flowers, they are of great importance in attracting pollen-carrying insects to the carpellate flower, thereby effecting pollination. This may

explain why the few functional stamens, which are present on so many carpellate flowers, have not disappeared during evolution. It should however be borne in mind that Trimenia and Piptocalyx of the Trimeniaceae, which is closely related to the Monimiaceae, also have some flowers which are transitional from bisexual to unisexual, but these genera lack staminal appendages (Money et al.). Because of the large number of male flowers in close proximity to carpellate flowers on the same tree, self fertilization would be a much commoner occurrence than cross fertilization, unless some type of self incompatibility mechanism were operating.

The nectar had a sweet taste and tests showed that it was predominantly sucrose, with perhaps traces of raffinose (see Appendix). It would be interesting if traces of raffinose were in fact present, in view of Percival's (1964) conclusion, after studying the nectar of 889 species of angiosperms, that "a pure sucrose nectar, with the single oligosaccharide raffinose could almost be safely said to be Ranalean". She did not however examine nectar from any plants in the more primitive woody Ranales but rather 37 species within the Helleboraceae, Ranunculaceae and Berberidaceae.

Morphological nature

The following theories have been proposed to explain the morphological nature of the staminal appendages of certain members of the Laurales (sensu Hutchinson).

- (1) Kasapligil and earlier Mez (1889) considered that the

appendages had arisen de novo to serve as nectaries. Daumann (1931) suggested that this was accomplished by partial splitting of the staminal primordium into three parts of which the two lateral ones became nectaries.

(2) Both Eichler (1878) and Engler (1926) interpreted the appendages as stipular formations on the stamens and Gluck (1919) interpreted them as stipular glands.

(3) Money et al. and a number of earlier workers (cited in Kasapligil) interpreted each appendage as a staminode. Thus according to Money et al. each functional stamen of Laurelia, for example, bears two "associated staminodes". Eames (1961) considered the appendages to be staminodal in origin and stated that they had arisen by fasciculation (i.e. aggregation into groups) followed by transformation (i.e. sterilization) of part of the fascicle into nectaries. He thought that each gland might sometimes represent more than one staminode and stated "each stamen, with its associated nectaries, represents a fascicle of three stamens, probably five in those genera where the stamen base has five bundles".

Each of the above theories will now be considered in detail.

(1) De novo theory

Kasapligil put forward the following arguments in support of this theory. (a) He believed the glands could not be homologized with stamens or staminodes from an ontogenetic point of view because the stamens and staminodes are produced by the floral apex,

"whereas the staminal glands arise from 'lateral meristematic regions' of the stamens". This argument does not seem valid to the writer. As Eames (1961) pointed out, some lauraceous genera have the "attachment of nectaries on the receptacle free from the stamen". Examples of this feature in the Monimiaceae are Atherosperma and Dryadodaphne (Money et al., 1950) and in the Lauraceae Beilschmiedia tawa in which Roper (pers. comm.) found that the appendages were produced by the floral apex. It could therefore be argued that with further evolution the appendages became attached to the staminal filament, as in Laurus (PLATE 31, fig. 3) and Laurelia. Note how in the stamen illustrated (as in some stamens of Laurelia - see PLATE 9, fig. 2) the filament is broader below the glands than it is above them. This suggests the basal parts of the appendages may be fused (in the phylogenetic rather than ontogenetic sense) to the staminal filament. The reverse argument * - that the appendages have arisen on the stamen filament but during the evolution of some genera have migrated onto the receptacle - does not seem so convincing in view of the general tendency of floral evolution to be in the direction of aggregation rather than separation of parts. In Laurelia, at least, the appendages are initiated in a manner similar to that of stamens and staminodes. Although Kasapligil does not give a detailed account of the initiation of the glands in Umbellularia, from his description and illustration initiation could well be

* Not put forward by Kasapligil, who seemed unaware that some lauraceous genera have the appendages inserted on the receptacle.

similar to that in Laurelia

(b) Kasapligil's second argument was that "evidence from vascular anatomy" suggests the de novo origin of the appendages. However he did not give details of this evidence beyond stating that the gland does "not exhibit a constant pattern", giving details of the variation and commenting on the "profusely ramified vasculature of these organs". Eames (1961) attacked this theory and reasoned that the complex vascular structure within the secretory region had developed simultaneously with the nectar secreting function. He added that "the origin and course of the vascular supply is the same as that of the stamens".

Although Kasapligil's theory is an interesting one, I do not consider there is definite evidence to support it, as indicated above. A number of the Laurales have staminal glands which do not function as nectaries, including Beilschmiedia tawa (Roper, pers. comm.) and Hortonia of the Monimiaceae (Money et al.). Money et al., state that "at times" the appendages assume a glandular function but do not cite examples. If Kasapligil's theory is correct, we must assume that the considerable number of lauraceous genera, in which the appendages do not function as nectaries, once had this function which has been subsequently lost, leaving a vestigial non-functional nectary. This does not seem very likely to the writer. It has been shown in a number of cases that nectaries have been modified from an organ which has lost its original function, although the latter part of Eames's (1961)

statement that all floral nectaries are either "localized areas where nectar is secreted, or organs transformed from their original form and function", may be an overstatement.

(2) Stipular_theory

This theory has not received support in recent times, if only on account of the absence of stipules on lauraceous leaves, and does not seem to merit serious consideration. Kasapligil noted for the Lauraceae that "the nodal anatomy of the foliage leaves and of the stamens is unilacunar and the leaves are entire; therefore, the occurrence of stipules would not be expected (cf. Sinnott and Bailey, 1914)". The Monimiaceae also have unilacunar nodal anatomy (Money et al.).

(3) Staminodal_theory

This theory seems the most attractive one and I will consider it under several sub-headings.

(1) Vascularization

Eames' views that vascularization supports the staminodal origin of the appendages have already been mentioned (see above). In their morphological survey of the Monimiaceae, Money et al. concluded "the vascularization of the three associated appendages provides no cogent evidence for interpreting the two sterile members as lobes, stipule-like parts or glandular outgrowths of the fertile microsporophyll. The veins of the staminodes^(*) (regardless of the degree of concrescence of the three appendages)

(*) Money et al., are applying this term to the staminal appendages.

usually do not arise as branches of the vascular strand of the fertile stamen, but extend independently and more or less extensively downward into the torus. Although the vascular strands of the staminodes commonly arise as branches of a trifurcating toral bundle, this is not invariably the case. Not infrequently the vascular strand of a staminode arises from an independent part of the vascular system of the receptacle." There is considerable variation in the vascularization of stamens and their appendages even within a single species, as described for Laurus and Umbellularia (Kasapligil, 1951) and Laurelia (Chapter 2). However it would seem that basically the stamens and appendages have a similar vascularization, it being assumed that the dendritic pattern in the appendages is a recent development, and any fusion between staminal traces and appendages traces, is a reflection of the phylogenetic fusion of the two types of organs.

(11) Teratology

Kasapligil (1951) made mention of the discovery by some earlier workers of occasional teratological staminal glands, within some lauraceous genera, which resembled anthers in the presence of "sterile or fertile thecae which open by means of valves". Eames (1961) also mentioned this phenomenon and considered it to be evidence supporting the staminal origin of the nectaries. In my opinion it is dangerous to read too much into 'hybrid' structures which are apparently produced by occasional ontogenetic aberrations. When however more or less intermediate

forms occur between two hypothetical structures with regularity, far stronger evidence is provided for common or derived origins. For example, in the carpellate flower of Laurelia, the more externally situated staminodes* regularly bear appendages which show varying degrees of reduction in size and vasculature, compared with those of the functional stamens. This provides strong evidence that the more reduced internally situated staminodes (PLATE 9, figs. 13-15) have each been derived from a stamen and its associated appendages. If then these appendages represent staminodes, the apparently simple staminodes within the carpellate flower are "second generation" staminodes.

(iii) Morphological resemblances

There is some external resemblance between appendages and stamens in some lauraceous genera, as Eames (1961) noted when describing the filament-like stalk and "more or less" anther shaped tip of the staminal appendage of Persea. In the New Zealand Litsea calicaria (Lauraceae) too, there is a considerable resemblance between the stamens and appendages. It is of interest that Laurelia and some other lauralean genera have stamens, staminal appendages and staminodes within a single flower (PLATE 5, fig. 5). Some resemblance can be observed between the staminal gland and the uppermost portion (presumed to be the sterilized anther) of reduced staminodes. There is also similarity between the stalk

* I.e. those closest to the functional stamen(s) when the latter are present.

of the gland and the lower filament-like part of the staminode. An ontogenetic resemblance was also found between the two structures in that the upper part of the staminode has surface cells on the flattened adaxial face which undergo periclinal divisions as found elsewhere in the flower of Laurelia only in the staminal gland. A median longisection of such a staminode is illustrated in PLATE 32, fig. 1; an enlarged part of the upper portion of a somewhat younger staminode is shown in fig. 2, in which at "e" for example, two cells can be seen which have resulted from a recent periclinal division of an adaxial epidermal cell.

Conclusions

As indicated in the foregoing, I consider there is strong evidence for the staminodal origin of the appendages. Before any final conclusions are made, it is desirable that a study be made of the comparative structure and ontogeny of the staminal appendages of all members of the Laurales which possess them.

A question requiring explanation is, why are there invariably two appendages associated with each stamen? Beyond stating that the association arose by fasciculation and partial sterilization of stamens, Eames (1961) gave no explanation for this 2:1 ratio. Now in some genera e.g. Umbellularia, not all of the stamens bear appendages. In this genus the two outer whorls usually lack them, in contrast to the third whorl. In view of the not uncommon presence of transitional forms between glandular and eglandular stamens in the outer whorls of Umbellularia

(and Laurus), Kasapligil concluded logically enough, that the outer staminal whorls were at one time glandular. The 2:1 ratio of appendages: stamens would be met if an ancestral lauraceous flower had:-

either - successive whorls of stamens in which one whorl had twice as many stamens as the next and so on - and the former whorl became sterilized and associated with the latter;

or - each whorl had the same number of stamens and two whorls became sterilized and associated with every whorl which remained functional.

The second condition seems the more likely of the two alternatives, (although these are by no means the only alternatives), in view of the fact that many lauraceous genera have flowers with whorled stamens with the same number of stamens per whorl, e.g. Laurus, Umbellularia (Kasapligil, 1951). Although Laurelia has spirally arranged stamens, the closely related Doryphora has whorled stamens of three per whorl. If the whorled arrangement does represent the ancestral condition, then the spiral arrangement of stamens in Laurelia would be a derived condition, which is unusual in that the spiral arrangement of floral parts is generally regarded as a primitive condition (e.g. Thorne, 1963; Hutchinson, 1959).

Addendum

In a book by Curtis (1967) which has recently become available, it is stated that the staminal appendages function as nectaries in Atherosperma. They therefore resemble those of Laurelia in this respect.

CHAPTER 6

CARPSEL ONTOGENY AND THE DEVELOPMENT OF MEGASPORANGIA AND FEMALE GAMETOPHYTES

Carpel ontogeny

The floral apices of Laurelia and Hedycarya are slightly convex mounds of roughly 200 μ and 300 μ diameter respectively, when the first carpels are initiated in spiral centripetal succession. A carpel is initiated by localized divisions at the periphery of the meristem, in a manner similar to that described for stamens (Chapter 4). Each carpel becomes a hemispherical mound (PLATE 48, fig. 3, carpel at left) by general cell enlargement and division within the primordium.

Hedycarya

As in the young stamen primordium, the young carpel primordium consists of relatively discrete vertical files of cells, because in general the subprotodermal cells near the tip of the primordium divide in periclinal and anticlinal planes, whereas those on the flanks and in the central axis divide mainly in horizontal planes. When the carpel is 55 μ high, there is a small adaxial protuberance near the base of the primordium. This protuberance is formed by localized anticlinal division and anticlinal elongation of a few protodermal and subprotodermal cells and marks the appearance of the adaxial lip or "Querzone" or "cross zone", typical of peltate carpels (Troll, 1933, 1939). At this stage (not illustrated)

a periclinally and anticlinally dividing subprotodermal initial had recently developed within the Querzone and had undergone its first periclinal division. Recent derivatives of this cell also divide periclinally and anticlinally and the adaxial lip increases in size (compare fig. 2, PLATE 23 and fig. 1, PLATE 24). Between this initial and the periclinally and anticlinally dividing subprotodermal cells at the apex of the carpel, arise two arcs of subsurface initials, as in Pseudowintera (Sampson, 1963) and Drimys winteri (Tucker, 1959). They form, together with anticlinally dividing surface initials directly above them, a continuous rim of meristematic tissue which forms the sides of a tilted bowl (PLATE 48, fig. 3, carpels at right and centre). When the carpel is approximately 300μ high (fig. 4) procambium of the dorsal strand has formed in the lower two-thirds of the carpel (PLATE 24, fig. 2). The aperture or cleft of the carpel soon reaches its maximum size (PLATE 48, fig. 4) as in Drimys winteri (Tucker, 1959) and Pseudowintera. It resembles these latter plants in that it remains the same size during further development (figs. 5, 6 and 7). Shortly before anthesis the carpel is closed by appression of the sides of the cleft, leaving a vertical line on the side of the carpel where once it was open (fig. 8, between x and y). Most of the locule is formed below the cleft, by intercalary growth of a cylindrical nature. In longitudinal sections (figs. 5c, 6b) it can be seen that the locule does not reach the base of the carpel and this lowermost solid stipe

portion is a result of basal growth. At the stage shown in 6b, the ovule ("ov") has been formed.

The stigmatic region in Hedycarya arises by the growth of solid tissue above the cleft. This tissue is morphologically the uppermost part of the original abaxial carpel protuberance. This is a considerable contrast to the primitive conduplicate ranalean carpels such as Degenaria (Swamy, 1949) and Drimys lanceolata (Tucker and Gifford, 1966b), which possess long clefts, and a contrast also to the more modified conduplicate carpels such as those of Pseudowintera (Sampson, 1963) and Drimys winteri (Tucker, 1959). In these plants the stigmatic region arises by the formation of receptive tissue around the outside of the cleft thereby forming the so-called "stigmatic crests" (see Bailey and Swamy, 1951). During growth of the stigmatic region in Hedycarya cell division is not confined to the protodermal and apical sub-protodermal layers, despite the fact that the subjacent tissue comprises large vacuolate cells from an early stage of development onwards (PLATE 24, fig. 2). Divisions were frequent within the vacuolate tissue e.g. the anaphase division figure in the cell "m". There is thus a resemblance to the large vacuolate cells of the lower part of the floral apex (see Chapter 3).

Transverse sections of a carpel, slightly older than the one shown in PLATE 48, fig. 6, are illustrated in PLATES 50 and 51. The sections are at successive levels beginning near the apex. Figures 1-3 of PLATE 50 illustrate sections through the stigmatic-

stylar region and it can be seen that the tissue is a solid cylinder, lacking a stylar canal. Figs. 4 and 5 of PLATE 50 and fig. 1, PLATE 51 are sections through the cleft. The cleft widens internally near its base to form the uppermost part of the locule (fig. 1, PLATE 51). Figs. 2-4 show sections through the ovular region. Note the presence of the ventral (ovule) bundle in figs. 3 and 4 and the megaspore mother cell at prophase I in fig. 4.

There is no localized terminal stigma but instead the uppermost part of the carpel consists of a knobbly mass of globose projections which serve as pollen traps. This region occupies more than half the total length of the carpel (PLATE 48, fig. 8). The projections are formed by the maturation (enlargement) of spherical secretory cells and some tannin-filled cells which are situated close to the surface (PLATE 47, fig. 3). No comparable type of stigma has been described for a ranalean genus and it is of interest that during the course of evolution of Hedycarya, the large secretory cells, so prevalent in the woody Ranales (see Money et al.), have been utilized to form what are apparently pollen traps. The stigmatic surface consists of unicellular receptive trichomes (i.e. stigmatic papillae) of a different appearance from epidermal cells investing the rest of the carpel. Similar, but longer receptive trichomes occur in Laurelia. A few weeks before pollination, the carpel of Hedycarya undergoes a considerable increase in size, after it has assumed its more

or less mature shape. This can be seen by comparing the carpels shown in fig. 4, PLATE 47.

The solid sterile carpels of Hedycarya lack the adaxial meristems and develop as solid finger-like protuberances which possess trichomes before these are present on normal carpel primordia. Each such sterile carpel is vascularized by a single strand which runs medianly through the structure and the strand branches near its tip (PLATE 10, fig. 7). The least reduced solid sterile carpels have a terminal stigmatic region which is similar to that of normal carpels, though more reduced. Morphologically each sterile solid carpel seems to represent a normal carpel, shorn of its "Querzone".

Laurelia

Early carpel growth resembles that described for Hedycarya, although the young carpel primordia of Laurelia have a more finger-like shape and the adaxial lip (cross zone) is not present until carpels are about 90 μ high. A carpel 150 μ high is shown in fig. 1, PLATE 52, with an as yet weakly developed adaxial meristem. A later stage is shown in fig. 2 in which the procambium of the dorsal strand has formed in the lower three-quarters of the abaxial side of the carpel (not clearly seen in the section illustrated). Comparison with an approximately comparable stage in Hedycarya (PLATE 24, fig. 2) reveals that the central cells of the abaxial lobe are not as vacuolate in Laurelia. Note how the cells of this lobe are in relatively discrete vertical rows. As in

Hedycarya cell division occurs throughout the carpel at this stage.

An important contrast to carpel development in Hedycarya is that the cleft continues to elongate for a considerable time after its formation (PLATE 49). Tucker and Gifford (1966b) found similar differences in carpel growth between Drimys winteri with its short cleft and D. lanceolata with its relatively long cleft. The cleft deepens by accelerated cell division at the ventral margins of a horseshoe-shaped primordium, as seen in a transection through the cleft. As in Hedycarya, the locule develops below the cleft by growth of a hollow cylindrical nature and the lowermost solid part of the carpel (see fig. 3, PLATE 49) is a result of basal growth. As in Hedycarya too, the stigmatic region arises by growth of solid tissue above the cleft. The stigma is less extensive than in Hedycarya although receptive trichomes cover all of the carpel above the cleft (fig. 5).

PLATES 53 and 54 illustrate transverse sections of a carpel at successive levels beginning at the apex. The carpel is at about the stage of development of the one illustrated in fig. 4, PLATE 49. Figs. 1 and 2 of PLATE 53 illustrate sections through the stigmatic-stylar region and figs. 3-6 illustrate sections through the cleft, fig. 3 being close to the apex of the cleft. Fig. 7 shows the tip of the adaxial lip or "cross zone" ("cz") which at a lower level is joined to the horseshoe-shaped abaxial part of the carpel to form a hollow cylinder (figs. 8 and 9, PLATE 53, figs. 1-2, PLATE 54). Figs. 2-5 of PLATE 54 show

sections through the ovular region; in fig. 4 procambium of the ventral trace can be seen within the ovule and in fig. 5 this trace ("tr") is within the carpel wall. At this stage the ovule contains a 1-nucleate embryo-sac.

During maturation of the carpel the cleft becomes closed, as the cells lining each half of the cleft become appressed together. This adhesion is weak and with little force the cleft of mature carpels can be re-opened without much tissue being damaged. Actual closure of the locule occurs when the uppermost part of the adaxial lobe bends inwards and a little downwards (compare figs. 4, 5 and 7 of PLATE 49) and becomes pressed against the upper innermost part of the locule wall. Coupled with this, the edges of the superficial part of the adaxial lobe are sealed by appression of the lowermost part of the cleft around them.

Mature carpels are shown in figs. 6 and 7 of PLATE 49, a few days after pollination which accounts for the withered stigmatic region. The external tip of the cross zone is readily apparent in side view of the carpel (fig. 6, "cz") and the ovule is a considerable distance below this zone. The outside edge of the cleft is also readily apparent (fig. 7).

Development of megasporangia and female gametophytes

Hedycarya

Carpels were not sectioned during the process of ovule initiation. The ovule arises as a protuberance on the adaxial wall of the locule directly beneath the adaxial lip, such that

the vertical plane of bisection of the lip when prolonged downwards, bisects the ovule (PLATE 55, fig. 1). The carpel in this figure is 614μ high and at this stage the epidermal cells of the stigmatic region have begun their differentiation into receptive trichomes and are slightly more elongated anticlinally than epidermal cells elsewhere. The young ovule primordium contains fairly discrete layers of cells, but some periclinal divisions occur within the subprotodermal layer and two cells which have been formed by a recent periclinal division within this layer can be seen in fig. 2.

A hypodermal primary parietal cell and subjacent megaspore mother cell are present when carpels are about 1040μ high. These cells have arisen from the periclinal division of a hypodermal archesporial cell. The ovule has begun to invert to an extent such that the young megaspore mother cell and primary parietal cell face the bottom of the locule. The inner integument has recently been initiated by anticlinal elongation and periclinal division of a ring of protodermal cells, as is usual in angiosperms (Esau, 1953). These initial divisions are soon followed by other periclinal and anticlinal divisions in the protodermal and subprotodermal cells adjacent to the initial integument cells. Soon after its formation, the primary parietal cell undergoes a periclinal division and the derivatives divide anticlinally. This is later followed by other periclinal and anticlinal divisions of these derivatives to form a number of layers of cells at the

micropylar end of the ovule. These layers are also built up by periclinal divisions within the surface layer of the ovule, as in Laurelia and Peumus (Mauritzon, 1935), and a periclinally dividing surface cell can be seen at "p" in fig. 3.

A single aberrant ovule was sectioned which contained two megaspore mother cells (at the synizesis stage of prophase I*) and is shown in fig. 4. This ovule is sectioned at right angles to the one shown in fig. 3. At this stage the outer integument has been initiated in a manner similar to the inner one although its growth is asymmetrical and as in Laurelia too, it is not even weakly developed on the side of the ovule which lies against the funicle (fig. 3). This phenomenon is common in anatropous ovules (Esau, 1953) and appears, from illustrations, to be the condition in Peumus (Mauritzon, 1935) and in some Lauraceae e.g. Litsea (Sastri, 1958) and Beilschmiedia (Roper, pers. comm.). The micropyle is formed by the inner integument alone, as in Laurelia, even in the mature ovules.

By the time the megaspore mother cell is at prophase I of meiosis, the ovule has undergone a further 90° rotation and is appressed to the adaxial lateral wall of the locule (PLATE 51, fig. 4; PLATE 55, fig. 3). At the end of meiosis a linear, or less commonly T-shaped tetrad of megaspores is formed, the innermost of which is functional. In the T-shaped tetrad in PLATE 56, fig. 1, there is a diagonal wall separating the upper pair of

* During the preparation of this section the nucleolus of the innermost mother cell has been displaced into the cytoplasm.

megaspores. The nucleus of one of these lies in a different section. According to Maheshwari (1950) this type of tetrad in which the wall separating the micropylar megaspores lies at an angle of about 45° with respect to the chalazal megaspores, is not infrequent in angiosperms. The ovule is now fully inverted. One fully inverted ovule was sectioned with well developed integuments but the megaspore mother cell within had only reached the prophase I stage (fig. 2). It is possible that such a megaspore mother cell may not undergo much further development, for a carpel in an open flower was sectioned with a somewhat similar ovule in which however the megaspore mother cell had an attenuated nucleus of distorted shape at a stage of prophase I. In other ovules of the same flower from which the ovule shown in fig. 2 was obtained, the non-functional megaspores had degenerated and the functional megaspore had undergone considerable enlargement (fig. 3). In this section only two of the three degenerated megaspores can be seen. The carpel is $1880\mu - 2250\mu$ high at this stage.

Flowers are fully open with pollen tubes extending through stylar tissue when embryo sacs are at the 2-nucleate (PLATE 56, fig. 4) and subsequent stages. As can be seen in the figure, the micropylar end of the embryo sac is blunter than the chalazal and this shape is maintained, at least during early post-fertilization stages. Some withered pollen tubes were observed within micropyles and between inner and outer integuments of

ovules at the 2 and 4-nucleate stages, including the ovule illustrated, although the tubes cannot be clearly seen in the photo. No pollen tubes were observed to have penetrated the micropylar nucellus tissue. Perhaps there is some physiological barrier preventing the growth of pollen tubes into this tissue until the embryo sacs are mature. No ovules were sectioned which contained 8-nucleate embryo sacs, despite the fact that a number of carpels were sectioned from fully opened flowers. It is obvious that an 8-nucleate embryo sac does form since young seeds contained in addition to a uni-nucleate zygote and cellular endosperm, the remains of 2 synergids and 3 antipodal cells. In view of the fact that no ovules were sectioned with embryo sacs older than the uninucleate stage until after pollination, it is possible that the pollen tube may act as a stimulus to the further development of the embryo sac. Heslop-Harrison (reported in a discussion on embryo sac physiology in Linkens, 1964) stated that in some orchids there is no completion of meiosis until pollination has taken place and no formation of an embryo sac and that, "there is certainly a very close correlation between the advent of the pollen tube and the completion of embryo sac formation". He added that a similar embryo sac development can be achieved by replacing the stimulus of pollination by a synthetic auxin like α -naphthaleneacetic acid.

Shortly after fertilisation the outer integument consists of 3-5 layers of cells and the inner comprises 4-6 layers.

Laurelia

In this genus too, carpels were not sectioned during the process of ovule initiation. The ovule arises on the adaxial wall of the locule (PLATE 57, fig. 1) in a similar position to the ovule in Hedycarya. The archesporial cell ("a.r.") is present in this young ovule which is within a carpel 650μ high. The epidermal cells of the stigmatic region have begun to differentiate into receptive trichomes and are more elongated anticlinally than the other epidermals. The archesporial cell divides periclinally into a hypodermal primary parietal cell ("p" in fig. 2) and a sub-jacent primary sporogenous cell ("s") which as in Hedycarya, enlarges into the megaspore mother cell. The functional stamens of carpellate flowers with ovules at this stage contained microspore mother cells which were undergoing meiosis. As the megaspore mother cell enlarges, the inner integument is initiated (PLATE 58, fig. 1) in a manner similar to that described for Hedycarya. The carpel is now about 670μ high. The first division of the primary parietal cell is periclinal (fig. 2) and in the ovule illustrated the outer integument has recently been initiated by the periclinal division of protodermal cells, as can be seen at "o.i." which is close to the base of the inner integument. Functional stamens in this flower contained uninucleate microspores. When the megaspore mother cell is at early prophase I the outer integument is more apparent (fig. 3). The results of a periclinal division within the surface layer of the ovule

can be seen at "s". Procambium of the ventral strand has now been differentiated in the base of the ovule. The ovule illustrated in fig. 4 (contained within a carpel 1860 μ high) has undergone rotation so that the micropylar end faces the base of the locule. The megaspore mother cell within is at the diplotene stage of prophase I. In this figure the two derivatives of the primary parietal cell have each undergone an anticlinal division. The ovule does not undergo further rotation but remains with its micropyle directed downwards. Total rotation has therefore been approximately 90° in comparison to the ovule in Hedycarya which undergoes a total rotation of approximately 270° . There is no great uniformity in ovule development within a single flower. Thus, one flower contained ovules in which megaspore mother cells were at prophase I, anaphase I and telophase I stages and other ovules contained a tetrad of megaspores. At the end of meiosis a T-shaped, or less commonly linear, tetrad of megaspores is formed. In T-shaped tetrads the wall separating the micropylar pair of megaspores may be longitudinal (PLATE 59, fig. 1) or diagonal. In the photo the innermost functional megaspore is not in clear focus. On two occasions it was observed that the megaspore directly above the functional one was the first to degenerate as shown in the figure. As the innermost megaspore enlarges into the uni-nucleate embryo sac (fig. 2) pollen grains become bi-cellular in functional stamens. Fig. 3 illustrates an ovule in which the embryo sac nucleus is at prophase and the carpel

at this stage is 2700μ high. At the end of this division the two nuclei move towards opposite ends of the sac (PLATE 60, fig. 1). As in Hedycarya the chalazal end of the sac is more pointed than the micropylar. Division of these two nuclei is not always synchronous as an embryo sac was sectioned containing a micropylar nucleus at prophase and two smaller chalazal nuclei. A 4-nucleate embryo sac is shown in fig. 2, within a carpel 3500μ high. Fig. 3 illustrates an 8-nucleate embryo sac before there has been wall formation or migration of polar nuclei. Figs. 1-3 are drawn to the same scale and it can be seen that there has been a progressive reduction in the size of nuclei as more are formed. A mature embryo sac consisting of three antipodal cells, central fusion nucleus (the polar nuclei fuse before fertilization) and egg apparatus is shown in fig. 4. At this stage the outer integument is 2-3 cells thick and the inner integument is 2-4 cells thick. The cells of the inner integument lining the micropyle are considerably enlarged (fig. 4). The embryo sac is separated by approximately 7-9 layers of cells from the micropylar surface of the nucellus.

Discussion

Carpel ontogeny

In their classic paper on the conduplicate carpel of the Ranales and its initial trends of specialization, Bailey and Swamy (1951) described how they considered the phylogenetic development of a style had occurred in many families. They stated that the

upper sterile part of the carpel develops a "slender, more or less tapered extension. During earlier phylogenetic stages of the development of this upward projection or style, it is conspicuously conduplicate, has two extensive independent stigmatic crests, and commonly is vascularized by both the dorsal and ventral veins

During subsequent stages of its phylogenetic specialization, the "decurrent" stigmatic crests become less and less extensive and are confined to the apex of the style The ventral surfaces of the primitive conduplicate style may fuse forming a hollow tube that is jacketed by glandular cells or they may become concrescent forming a solid style with a core of "conducting" or "transmitting" tissue."

In contrast to the above, in Hedycarya and Laurelia and in at least five members of the Lauraceae - Umbellularia (Kasapligil, 1951), Beilschmiedia (Roper, pers. comm.), Cinnamomum, Litsea (Sastri, 1958) and Cassytha (Sastri, 1962) a "terminal meristem" (Kasapligil, 1951) forms a solid cylindrical growth which is covered by the receptive stigmatic trichomes. In Beilschmiedia (Roper, pers. comm.), Litsea and Cinnamomum (Sastri, 1958) a small basal part of the stigmatic-stylar region has a canal which is derived from the uppermost portion of the cleft. This type of lauralean stigma is not then analagous to certain other ranalean genera e.g. Liriodendron (Canright, 1960) which has an elongate style and a localized terminal stigma which consists of two short stigmatic crests between which is the cleft of the carpel. It

must remain an open question as to whether (a) the stigma in Laurelia, Hedycarya etc., is a new structure, in no way homologous with the type in Liriodendron, and which arose by the evolution of a terminal meristem above the tip of the carpel cleft or whether (b) the stigma in Laurelia, Hedycarya etc., arose from the type in Liriodendron by the fusion during evolution of the paired stigmatic crests and uppermost part of the carpel cleft into a solid cylinder without leaving any vestiges of the cleft and crests. Certainly the former possibility seems more attractive to the writer.

As I have stated, all but the top of the locule in Hedycarya and Laurelia is formed by cylindrical growth which occurs below the cleft. On the other hand Kasapligil stated that in Umbellularia the ovary portion of the carpel was formed by the fusion of the margins of a horseshoe-shaped primordium (i.e. by closure of the basal part of the cleft) at a very early stage in ontogeny and that "the union is very complete and hence the fusion line is not detectable in the mature ovary wall". I do not consider this likely and Kasapligil does not substantiate his statement. He may have been influenced by Bailey and Smith's (1943) paper on the carpels of the Winteraceae which he cited elsewhere in which it is claimed on the basis of the structure of mature carpels alone that there was basal ontogenetic closure of the carpel in such a way as to leave no external evidence of the closure in this region. This statement has been disproved for two members

of the Winteraceae by Tucker (1959) and Sampson (1963) who in studying the ontogenetic development of carpels found that the lower part of the locule arose by cylindrical growth. The carpel of Umbellularia bears a considerable resemblance in external shape and vascularization to those of Hedycarya and Laurelia. It does not seem likely that ontogenetic fusion could be so complete as to leave no trace of the line of fusion and it should be borne in mind that the line of fusion would pass through the centre of the ventral (ovular) vascular trace which is present in the form of procambium at an early stage in the development of the carpels of Hedycarya and Laurelia. It is of course likely, in view of the nature of the apparently primitive conduplicate ranalean carpels that there has been during evolution phylogenetic closure of the lower part of lauraceous carpels. It would seem that such closure has occurred when a horseshoe-shaped primordium later becomes ring-shaped i.e. an intercalary meristem arises below the cleft of the carpel. Eames (1961) has emphasised that the "carpels of many taxa are closed in part ontogenetically and in part congenitally; in early ontogeny, the primordium is crescent-shaped; later, it becomes ring-shaped".

Kasapligil (1951) stated that "Thus far" he had been unable to observe an adaxial meristem in the carpel of Umbellularia. Such a meristem is present in Umbellularia, as in Laurelia and Hedycarya but Kasapligil mistakenly labelled it as an ovule (in plate 28b of his paper).

The ontogeny of the carpels of Hedycarya and Laurelia seems basically similar to that described for some achenes in other families e.g. Thalictrum (Ranunculaceae) which is illustrated in figure 1184 of McLean and Ivimey-Cook (1956).

Megasporangia and female gametophytes

The ovules of Hedycarya and Laurelia resemble those of other woody Ranales including members of the Magnoliaceae, Illiciaceae, Winteraceae, Schisandraceae (see Hayashi, 1965), Cercidiphyllaceae (Swamy and Bailey, 1949), Degeneriaceae (Swamy, 1949) and Lauraceae (Sastri, 1963) in being bitegmatic, crassinucellate and anatropous with a monosporic 8-nucleate embryo sac of the Polygonum type. It is not surprising that the Polygonum type of embryo sac is universal* within those woody Ranales so far studied in view of the general opinion among embryologists that there "is hardly any doubt that the Polygonum type of the embryo sac is the most primitive" (Johri, 1963) from which the other types have been evolved.

Heilborn (1931) stated that Siparuna (subfamily Siparunoideae) of the Monimiaceae was unitegmatic. The only figure (4a) in his paper in which the integument is illustrated, does not include cell detail. It is shown to be considerably larger on one side of the ovule and I consider it possible that the ovule may be bitegmatic with the outer (incomplete) integument closely appressed

* Mauritson (1935) suggested that in Peumus (Monimiaceae) embryo sac development was probably of the bisporic (Allium) type, but could not draw a definite conclusion nor rule out the possibility that the embryo sac was monosporic because of the difficulty experienced in sectioning material at this stage.

to the inner, as is common in Hedycarya and Laurelia during later stages of development. Two members of the Lauraceae (Laurus nobilis and Cassytha filiformis) have been described as unitegmie but it has subsequently been shown that they are in fact bitegmie (Sastri, 1963). Maheshwari (1950) has noted that the number of integuments is constant in most families and only in rare cases do unitegmie and bitegmie ovules occur in the same family.

The structure and development of the ovules of Peumus (Mauritzon, 1935), Hedycarya, Laurelia and most members of the Lauraceae (Sastri, 1963) are very similar to one another, except that in Laurelia the micropyle points downwards. An unusual feature in Peumus is that the antipodal cells redivide after fertilization to form up to 20 cells which are thickened to form a weakly developed hypostase. Such behaviour of antipodal cells was not found within post fertilization stages in the seed of Hedycarya which is classified within the same subfamily as Peumus. A hypostase does form in Hedycarya but from cells outside the chalazal part of the embryo sac. According to Bambacioni-Mezzetti (1935) the antipodals may redivide in Laurus nobilis. Some members of the Lauraceae, including Beilschmiedia (Roper, pers. comm.), Sassafras (Coy, 1928), Persea (Schroeder, 1952), Cassytha (Sastri, 1962) and a species of Cinnamomum (Sastri, 1958) have considerably elongated embryo sacs. Other members of this family including a species of Cinnamomum and Litsea (Sastri, 1958) have an embryo sac of comparable shape to the three genera of the

Monimiaceae. Siparuna eggersii, the other member of the Monimiaceae which has been studied embryologically, has an aberrant and unique type of embryo sac development (Heilborn, 1931). It has a multiple archesporium in which frequently more than one uninucleate embryo sac develops but one gains ascendancy and the growth of the others is suppressed. Heilborn found that the growth of the largest embryo sac was hindered by the early formation of a hypostase beneath the chalazal region of the sac. The embryo sac becomes coiled and finally bursts. It is not until this stage that the single nucleus divides to form up to 5 nuclei although no egg apparatus is formed. Heilborn claimed that sporophytic buds "being probably the initial of a nucellar embryo" form, but do not mature. He found no traces of embryo or endosperm within well developed fruits. It is to be hoped in view of these surprising results that a more critical study can be made of the development of the ovule in S. eggersii and in other species of the genus. S. eggersii resembles Cassytha in that the latter has a multicellular archesporium. In Cassytha up to six embryo sacs reach maturity but only one is fertilized.

CHAPTER 7

POLLINATION, FERTILIZATION AND POST FERTILIZATION STAGES

Hedyocarya

The flowers are greenish and lack nectar. No insects were observed visiting flowers. It is presumed therefore that the bulk of pollen transference from male to female trees is effected by wind. Male flowers are formed in abundance each season at the tips of branches (PLATE 4, fig. 1) and it was noticed that even slight winds caused a considerable amount of pollen to be shed from the trees. The flowers of female trees within a few hundred yards of male trees were found to have plenty of pollen adherent to the stigmas and seed set is high.

There does not appear to be specialized transmitting tissue within the style. Pollen tubes pass apparently indiscriminately between cells of the style, avoiding the central vascular tissue and on reaching the ovule enter it via the micropyle. As in Laurelia, in at least some instances, only one synergid is destroyed by the entry of the pollen tube into the embryo sac. Antipodal cells persist for some time after fertilization, as in Litsea sebifera, but in contrast to most of the Lauraceae so far studied, in which they degenerate early (Sastri, 1963).

The endosperm is cellular from an early stage in which only a few endosperm cells were present. Material was not sectioned immediately following fertilization and it is therefore not known

if the endosperm is cellular after the first division of the primary endosperm nucleus. It seems most probable that it is however since in the related genus Peumus the endosperm is cellular from its inception (Mauritzon, 1935). As in Peumus a considerable amount of endosperm is formed before the zygote divides. Soon after fertilization a hypostase of thick walled cells with tannin-like contents develops in chalazal nucellus tissue (PLATE 59, fig. 4, "h"). In the illustration most of the endosperm cells have been destroyed during sectioning. By this time, the epidermal cells covering the ovule contain heavy deposits of a tannin-like nature as can be seen in the figure.

Embryo development was not studied in either genus. At maturity the embryo of Hedycarya has two cotyledons which possess serrate margins and the embryo occupies slightly less than half of the length of the seed, as illustrated in figure 3H of Perkins and Gilg (1901). Mature seeds of Hedycarya and Laurelia are of the albuminous type, since they contain some endosperm. Immature (green) and mature (orange) drupes of Hedycarya are shown in colour, approximately two-thirds actual size in plate 267 of Salmon (1963). Fruits are eaten by the native pigeon Hemiphaga novaeseelandiae (Falla et al., 1966). The endocarp of the fruit is hard and stony and it seems likely therefore that the seeds pass intact through the digestive tract of the pigeon, which therefore acts as a dispersal agent, as is the case with the similar fruits of Beilschmiedia tawa (Beveridge, 1964).

Laurelia

Pollination has been discussed in Chapter 5. In the related genera Doryphora and Atherosperma the flowers at anthesis have stigmas which are splayed out from one another to form a stellate stigmatic cluster in the centre of the flowers (PLATE 13, figs. 2 and 3). This would provide a large surface area for pollen to adhere to. Only one out of hundreds of carpellate flowers of Laurelia examined had a similar stellate "compound" stigma. In general some of the stigmatic papillae of adjacent carpels were interlocked with one another in such a way that the stigmas could be separated from one another only with difficulty. It is possible that Laurelia or its immediate ancestor once had the type of stellate stigmatic cluster found in Doryphora, Atherosperma and possibly other members of the Atherospermoideae, but that this feature has been lost because the stigmatic papillae of Laurelia evolved in such a way that they became easily tangled with those of neighbouring carpels.

I was unable to trace the course of pollen tubes through stylar tissue. The pollen tube enters the apex of the locule and passes down the side of the locule to the base and then enters the micropyle.

Money et al. have noted as a general character for the sub-family Atherospermoideae that the more or less deeply concave receptacle becomes cupuliform or urceolate "particularly subsequent to anthesis". The receptacle of carpellate Laurelia flowers

undergoes considerable enlargement after anthesis to form a pseudocarp which encloses and conceals the fruits even when the latter are mature (PLATE 6, fig. 1). The fully enlarged pseudocarp is at first green (see plate 181 of Salmon, (1963) in which the pseudocarps are labelled as fruits) and of a somewhat fleshy fibrous nature. Within a few months the pseudocarp becomes brownish-grey and woody and splits in half longitudinally (PLATE 61, fig. 1) to release the plumed fruits (PLATE 26, fig. 1 and plate 182 of Salmon (1963) in which the fruits are incorrectly described as seeds). Such plumose achenes would be readily dispersed by the wind and Gilbert (1959) has noted that the plumose fruits* of Atherosperma, which from illustrations appear very similar to those of Laurelia and other members of the sub-family, "float like thistle down".

In the mature fruit the embryo occupies approximately the same proportion within the seed as does that of Hedycarya. In contrast to Hedycarya the cotyledons of Laurelia do not have serrate margins. It was frequently found that what appeared to be mature fruits, when dissected contained unenlarged ovules which had therefore either not been fertilized, or, if they had been fertilized, had undergone little subsequent development.

Discussion

As the foregoing has shown, the plumose, wind distributed fruits of Laurelia and other members of the Atherospermoideae,

* He too called them "seeds".

which are enclosed in pseudocarps, are very different from the drupes of Hedycarya. As far as I can ascertain from the drawings and descriptions in Perkins and Gilg (1901) and Perkins (1911) all genera of the Monimiaceae have drupaceous fruits except for the subfamily Atherospermoideae. This is evidence for the view that this latter subfamily has long been distinct from the other members of the Monimiaceae. The Lauraceae too have drupaceous (and baccate) fruits but are without endosperm at maturity (Hutchinson, 1959) in contrast to Hedycarya and Peumus (Mauritzon, 1935).

CHAPTER 8

CONCLUSIONS

Various conclusions have been stated throughout this thesis, especially in the discussion section at the end of each chapter. These conclusions will not all be repeated in this chapter. In this chapter some of the more important similarities and differences between Hedycarya and Laurelia will be considered to permit me to make some conclusions as to their relationship, one to the other. I will then briefly consider the relationships which the Monimiaceae bears to other families.

Comparison of Hedycarya and Laurelia

(a) Chromosome number

Hedycarya arborea has $n = 57$ chromosomes and Laurelia novae-zelandiae has $n = 22$ chromosomes (Hair and Beuzenberg, 1959). There is therefore no simple numerical relationship between the chromosome numbers of the two genera and this suggests that they are not closely related. I have been unable to find chromosome counts of other members of the family in the literature. In the Lauraceae chromosome counts have been made of 6 genera (18 species). Results were $n = 12, 18$ or 24 (Darlington and Wylie, 1955). One worker obtained a haploid count of 21 for Laurus nobilis but another worker obtained a count of 24 for this species. Most species had $n = 12$ chromosomes and Darlington and Wylie considered that 12 was probably the basic number for the 6 genera.

There is then no simple numerical relationship between chromosome numbers in the Lauraceae and those of Hedycarya and Laurelia. Nor does the chromosome number of Laurelia coincide with that of any other member of the woody Ranales listed in Darlington and Wylie (1955). However a number of species of Magnolia resemble Hedycarya arborea in having $n = 57$ chromosomes.

(b) Pollen morphology

Hedycarya and other Monimioidae have acolpate pollen in contrast to the monocolpate pollen of Laurelia and monocolpate or dicolpate pollen of other Atherospermoideae (Money et al.). Erdtman (1963) commented that the pollen of the Monimiaceae is in need of further study but that pollen morphology corroborates the division of the family into the four subfamilies of Money et al. Money et al., considered that monocolpate pollen is the most primitive type in the woody Ranales and that dicolpate and acolpate pollen is derived from phylogenetic modification of the former type. If this is true, then Laurelia has a more primitive pollen type than Hedycarya.

(c) Wood anatomy

From the descriptions in Money et al.'s. paper, Hedycarya and Laurelia have a similar type of wood with vessels of a primitive form in which there are thin-walled angular vessel members with extensively overlapping ends and numerous scalariform perforations.

(d) Nodal anatomy and vasculature of the leaf

Money et al. found uniformly unilacunar nodal anatomy in the

family. Hedycarya, Laurelia and other members of their sub-families have a leaf vasculature which is derived from two systems of vascular strands that are separate and independent at lower levels in the stem (Money et al.).

(e) Apical meristems

No major differences were found between the apical meristems of Hedycarya and Laurelia and the meristems resembled those of a number of other woody Ranales (see Chapter 3).

(f) Flowers

Hedycarya and other Monimioidae have unisexual flowers. Laurelia has unisexual flowers in which the female flower bears staminodes, and transitional bisexual flowers with carpels, staminodes and one or a few functional stamens. Other genera in the Atherospermoideae have bisexual, unisexual or transitional flowers. It seems clear that the most primitive type of flower in the family is bisexual, as in Doryphora (Atherospermoideae). Laurelia is more primitive than Hedycarya in having some transitional bisexual flowers and in having female flowers with staminodes, whereas the male and female flowers of Hedycarya each lack vestiges of the other sex. However there is a link between the two sub-families in that Peumus of the Monimioidae has female flowers which bear staminodes (Money et al.).

(g) Stamens

As stated earlier in this study, the stamen of Laurelia with its filament bearing the paired appendages, two pollen sacs

and valvular dehiscence is a marked contrast to the stamen of Hedycarya which lacks a pronounced filament and the appendages and has four pollen sacs which dehisce by longitudinal slits. As stated too, Peumus and Monimia provide a link between the two subfamilies in having stamens with associated appendages. It does not seem clear which type of stamen has given rise to the other type (see Chapters 2, 4 and 5) and I can therefore not reach a conclusion as to whether Hedycarya or Laurelia has the more primitive stamen type.

(h) Carpels

The carpels of Hedycarya and Laurelia are similar to those of the Lauraceae in that the terminal stigmatic part of the carpel has been formed by a terminal solid meristem and this stigmatic region is therefore not homologous to the stigmatic region of many other woody Ranales, including the Magnoliaceae (see Chapter 6). If we assume that the carpels of the Monimiaceae have arisen by phylogenetic modification of the conduplicate type (see Bailey and Swamy, 1951), then the carpel of Laurelia is more primitive than that of Hedycarya in possessing a longer cleft (see Chapter 6). On the other hand Hedycarya may have a more primitive carpel vascularization because it has supraovular traces which may represent vestigial traces to formerly existent ovules in ancestors of the group (see Chapter 2). As I have noted, Atherosperma of the Atherospermoideae provides a link between the two subfamilies in that it has some carpels with the supraovular traces. An

additional difference between the carpels of Hedycarya and Laurelia is that the former has the upper part of the carpel, which is covered by the stigmatic surface, vascularized. I can reach no conclusion as to which carpel is the more primitive in this respect. The knobbly stigmatic region of the carpel of Hedycarya contrasts with the slender cylindrical stigmatic region in Laurelia (see Chapters 2 and 6). In this case it would appear that the stigmas of the two genera have evolved in different directions and that one type is therefore not necessarily more primitive than the other. The carpels of Hedycarya resemble those of the Lauraceae in that the micropyle of the ovule points upwards whereas in Laurelia it points downwards. It does not seem possible to determine which of these two types of micropyle orientation is the more primitive.

To sum up, it would appear that the carpels of Hedycarya and Laurelia are basically similar but that during the course of evolution each has retained some primitive features not found in the other and each has developed independent features.

(1) Fruits

The drupes of Hedycarya and other members of the Monimioideae are a considerable contrast to the pseudocarps which enclose plumose achenes in Laurelia and other Atherospermoideae. Here too it may not be a case of one type of fruit giving rise to the other but rather a case of evolution taking place in two different directions from a basic type. Thus, the receptacles of female

flowers are cupuliform or urceolate in both the Monimioideae and Atherospermoideae, but in the latter subfamily this feature has become exaggerated, especially after anthesis, to form the pseudo-carp.

(j) Embryology

There are no basic differences in the development of the megasporangia and female gametophytes of Laurelia and Hedycarya and the development of these stages resembles that found in most other woody Ranales (see Chapter 6).

The development of microsporangia is basically similar in the two genera. However Laurelia differs from Hedycarya and members of the Lauraceae so far studied in not having the successive type of cytokinesis in the meiotic division of the pollen mother cells. This difference is not however a diagnostic feature of the Atherospermoideae as Atherosperma has cytokinesis of the successive type (see Chapter 4).

Overall conclusions

I would conclude that Hedycarya and Laurelia and other members of the two subfamilies, insofar as they have been investigated, share a core of basic features which warrants the retention of the subfamilies within a single family. However there are a number of quite basic differences in the two subfamilies which suggests that they have been separated from each other for a long time and have undergone considerable evolution in different directions.

Relationships of the Monimiaceae

As I have indicated throughout this work, Hedycarya and Laurelia and other genera of the Monimiaceae which have been studied, seem most closely related to the Lauraceae. The two families can be conveniently separated in that all members of the Lauraceae have a single carpel per flower whereas the Monimiaceae have more than one carpel per flower with the exception of Xymalos of the Monimioidae which has a unicarpellate female flower (Money et al.). According to Bailey and Swamy (1948) larger mucilage cells serve also as a criterion for differentiating the Monimiaceae (in which they are absent) from the Lauraceae (in which they are present). The Lauraceae show far less variation in most of their features than do members of the Monimiaceae. That is to say, the Lauraceae is a comparatively tightly knit family in which the members show little variation in, for example, flower, fruit and wood structure (see Hutchinson, 1964) in comparison to the Monimiaceae in which it could be argued with some justification that the four subfamilies should be raised to the status of separate, but closely related families. The Monimiaceae also seem to retain some primitive features not found in the Lauraceae, especially in their perianth parts. There is therefore merit in Eames (1961) suggestion that the "Monimiaceae perhaps form a link between the Ranales and Laurales". With the exception of the Monimiaceae and Lauraceae, the other families in the Laurales (sensu Hutchinson, 1964) have not been studied in sufficient detail

to enable detailed comparisons to be made with them. The Monimiaceae and Lauraceae and other Laurales, as well as some other families which I will not discuss, seem clearly to occupy a place within the fringes of the woody Ranales (sensu lato). Compared to many families in the woody Ranales they are considerably advanced in a number of features. For example the Lauraceae and Monimiaceae possess vessels in comparison to the primitively vesselless members of the order e.g. Winteraceae. However the former families have a comparatively primitive type of vessel and one vesselless genus, Amborella, is considered by Money et al., to be closely related to the Monimiaceae and Hutchinson (1964) even includes it within this family. The stamens and carpels of the two families seem considerably advanced in their structure from the apparently primitive stamens and carpels in the Degeneriaceae, Winteraceae, Magnoliaceae and Himantandraceae for example, but they do appear to have been derived by phylogenetic modification of these more primitive types.

It seems beyond the scope of this work for me to discuss each woody ranalean family in turn and compare it with the Monimiaceae. Suffice to say that my results reinforce the conclusions of Bailey, Swamy and co-workers. They considered that the ranalean families possessing monocolpate pollen and phylogenetically derived dicolpate, polyporate and acolpate pollen and having "ethereal oil cells" fall into two groups which are not closely related to each other. Their groups were:-

Group A: nodes unilacunar

Austrobaileyaceae	Lauraceae
Trimeniaceae	Hernandiaceae
Amborellaceae	Chloranthaceae
Monimiaceae	Calycanthaceae
Gomortegaceae	Lactoridaceae

Group B: nodes trilacunar or multilacunar

Winteraceae	Myristicaceae
Degeneriaceae	Eupomatiaceae
Himantandraceae	Canellaceae
Magnoliaceae	Piperaceae
Annonaceae	Saururaceae

Money et al., concluded that seven families of group A "are more or less closely related, and therefore form a natural grouping". These seven families are the Austrobaileyaceae, Trimeniaceae, Amborellaceae, Monimiaceae, Gomortegaceae, Lauraceae and Hernandiaceae. What new results I have obtained in this study, especially those relating to embryology, support these conclusions and indicate that the Monimiaceae is not closely related to the Winteraceae, Magnoliaceae, Degeneriaceae and other members of Group B, insofar as they have been studied, but that the family is closely related to the Lauraceae although less closely related to the members of other families in Group A which have so far been studied in detail e.g. Astrobaileya (Bailey and Swamy, 1949) and Lactoris (Carlquist, 1964).

APPENDIX

ANALYSIS OF EXUDATE FROM STAMINAL APPENDAGES OF LAURELIA

Flowers were collected from several trees on the west side of Lake Ponui in late October and early November 1966. They were viewed under the binocular microscope and exudate was removed from the surface of the appendages by means of a sterilized platinum loop. Care was taken to ensure that the exudate collected was not contaminated with pollen grains.

Mr. H.W. Johnston and Miss M.J. Priday, V.U.W. Botany Department then tested the exudate which had been spotted on thin layer plates coated with a cellulose-silica gel adsorbent, prepared by the method of Turner and Redgwell (1966). Plates were run in a n-butanol - acetic acid - water solvent (12:3:5 being the respective proportions by volume) and sprayed with aniline hydrogen phthalate, then heated in an oven. Comparison with runs of standard sugars revealed that the nectar contained large amounts of sucrose. Mr. Johnston considered that there may have been a trace of another sugar, possibly raffinose, present too, but results were inconclusive.

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STUDIES ON THE MORPHOLOGY, ONTOGENY AND EMBRYOLOGY
OF THE FLOWERS OF HEDYCARYA ARBOREA J.R. et G.Forst.
(SUBFAMILY MONIMIOIDEAE) AND LAURELIA NOVAE-ZELANDIAE
A.Cunn. (SUBFAMILY ATHEROSPERMOIDEAE) OF THE FAMILY
MONIMIACEAE.

Volume 2 - PLATES

Thesis submitted in partial satisfaction of the
requirements for the degree of Doctor of Philosophy
in Botany , at Victoria University of Wellington,

PLATE 1

Figure 1 Foliage of Laurelia novae-zelandiae with male inflorescences a short time before flowering. In the axil of the large leaf at upper left, is a bud which is either a dormant vegetative one or an inflorescence bud which will not develop into a mature inflorescence until the following year. Photo taken at Lake Ponui on 30-10-66. Approximately natural size.

Figure 2 Mixed inflorescence of Laurelia novae-zelandiae approaching anthesis. All but the lowermost (sterile) bract pairs have abscised. Note the vegetative bud in the leaf axil at right. Further details in text. Linear magnification X 3.5'

1

2

PLATE 2

Figure 1 Compound mixed inflorescence of Laurelia n.z. near anthesis. There are three pairs of female flower buds , situated below the terminal male flower bud. Photo M.D.King. X 3

Figure 2 Compound male inflorescence of Hedycarya arborea near anthesis. The lowermost flower bud and its pedicel (facing camera) have been excised. Photo M.D.King. X 2.5

Figure 3 Foliage and inflorescences of Laurelia n.z. Approximately natural size.

1

2

3

PLATE 3

Diagrams of inflorescences of Laurelia n.z. For simplicity the flowers are depicted as being in one plane whereas they are actually decussately arranged. Not drawn to any scale.

m or M = male flower

c or C = carpellate flower

br = the position of a sterile
bract in figure 4

PLATE 3

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

PLATE 4

Figure 1 Male flowers of Hedycarya arborea. Approximately
natural size.

Figure 2 Female inflorescence of Hedycarya arborea. x 3

1

2

PLATE 5

- Figure 1 Male (lower) and carpellate flowers of Laurelia novae-zelandiae. Male flower bud at left.
Photo Prof. J.T.Salmon . x 3
- Figure 2 Male flower of Hedycarya arborea (preserved in
f.a.a.). Photo M.D.King. x 5
- Figure 3 Partly-open male flower of Hedycarya arborea. x 7
p = reduced tepal
- Figure 4 Male flower of Laurelia n.z. (preserved in
f.a.a.). Photo M.D.King. x 7
- Figure 5 Carpellate flower of Laurelia n.z. (preserved in
f.a.a.). Photo M.D.King. x 8

1

2

4

3

5

PLATE 6

Figure 1 Mature pseudocarps on Laurelia n.z. x 1.5

t = tepal

Figure 2 Mature fruits of Hedycarya arborea (somewhat
abnormally shrivelled). x 1.5

t = tepal

1

2

PLATE 7

Cleared bracts and tepals, as seen in adaxial face view,
to show their vascularization.

Figures 1 - 8 Tepals from carpellate flowers of Laurelia n.z.

Figures 9 - 10 Bracts of Laurelia n.z.

Figures 11 - 18 Tepals from female Hedycarya arborea flowers.

Figures 19 - 21 Bracts from inflorescences of Hedycarya arborea.

Laurelia tepals

Laurelia bracts

Hedycarya tepals

Hedycarya bracts

PLATE 8

Figure 1 Photomicrograph of portion of a cleared tepal of Laurelia novae-zelandiae . A lateral vascular trace can be seen at left and an isolated trace at right centre. This photo represents the area enclosed by the dotted line in the tepal illustrated in fig. 1, PLATE 7. x 135

Figure 2 A more magnified view of the isolated trace in figure 1. This photo has been mounted upside down in comparison to figure 1 of this plate. x 470

1

2

PLATE 9

Cleared stamens and staminodes of Laurelia novae-zelandiae
showing their vascularization. Further details in text.

PLATE 9

Laurelia stamens & staminodes

PLATE 10

Figures 1-6 Cleared carpels of Hedycarya arborea , showing their vascularization. In figures 1 and 3 , the broken line indicates the position of the ovule. Dotted lines in the other figures show the position of locules and ovules.

Figure 7 Cleared sterile carpel of Hedycarya arborea.

Figures 8-9 Cleared carpels of Laurelia n.z. , showing vascularization. Dotted lines indicate the extent of the ovule and locule.

s-t = level above which stigmatic surface begins

o = ovular trace

d = branch of dorsal trace

PLATE 10

0 1mm.

CARPELS

Hedycarya

Laurelia

PLATE 11

Cleared male flower of Hedycarya arborea in which the stamens have been removed. Dotted and broken lines indicate the position of insertion of stamens on the receptacle. For simplicity, traces are only shown entering the bases of those stamens which are indicated by dotted lines. Further details in text.

Hedycarya – male flower

0 4mm.

PLATE 12

Figure 1 L.s. stamen of Hedycarya arborea at a stage at which
sporogenous tissue is present. x 105

Figure 2 Longitudinally bisected carpellate flower bud
of Laurelia novae-zelandiae , shortly before
anthesis. An ovule has been exposed in the carpel
at left. Photo M.D.King. x 15

Figure 3 Apical view of female flower of Hedycarya arborea.
Photo M.D.King . x 11
 c = sterile carpel

1

2

3

PLATE 13

Figure 1 Male flowers of Atherosperma moschata. x 3

Figure 2 Carpellate flowers and flower buds (above) of
Atherosperma moschata. x 3

br = a pair of bracts

Figure 3 Flower of Doryphora sassafras. x 3

1

3

2

PLATE 14

Figure 1 Median l.s. of a terminal bud of the shoot of a female
Hedycarya arborea plant. x 40

Figure 2 Median l.s. of a terminal bud of the shoot of Laurelia
n.z. x 40

1

2

PLATE 15

Figure 1

A more magnified view of the apical meristem of Hedycarya, shown in fig. 1, PLATE 14. x 240

Figure 2

L.s. of the vegetative shoot apex of Hedycarya arborea (female plant) at a stage somewhat beyond minimal surface area. x 250

1

2

PLATE 16

Figure 1 T.s. of part of a terminal shoot bud of Hedycarya
arborea (female plant) , with the apical meristem
at centre enclosed by two pairs of leaf primordia. x 250

Figure 2 A more magnified view of the apical meristem of
Laurelia , shown in fig. 2, PLATE 14. x 250

Figure 3 Median l.s. of the vegetative shoot apex of Laurelia
n.z. soon after the period of minimal surface area. x 250

1

2

3

PLATE 17

Figure 1

L.s. of the vegetative shoot apex of Laurelia n.z.

x 250

Figure 2

A more magnified view of the putative inflorescence
apex of Hedycarya arborea, shown in fig.1, PLATE 14.

x 250

1

2

PLATE 18

Figure 1

A more magnified view of the putative young inflorescence bud of Laurelia , shown in fig. 2, PLATE 14. x 250

Figure 2

Median l.s. of a young female inflorescence apex of Hedycarya arborea. x 200

1

2

PLATE 19

Figure 1 Median l.s. of an inflorescence apex of Laurelia n.z.
x 300

Figure 2 L.s. of part of a female inflorescence bud of Hedycarya
arborea with the inflorescence meristem at left and a
floral apex at lower right. x 115

1

2

PLATE 20

Figure 1 Median l.s. of a young female inflorescence apex
of Hedycarya arborea . x 212

Figure 2 Median l.s. of a young floral apex of Laurelia n.z.
The inflorescence axis is on the right side of the
photo. x 460

s = a cell of the "shell zone".

1

2

PLATE 21

Figure 1

Median l.s. of a young male flower bud of Hedycarya
arborea, with tepal primordia. x 280

Figure 2

Median l.s. of a young male floral apex of Hedycarya
arborea. x 310

1

2

PLATE 22

Figure 1

L.s. of a female flower bud of Hedycarya arborea
in which the outermost carpels are being initiated.

x 210

Figure 2

Median l.s. of the floral apex of a male flower of
Hedycarya arborea near the end of stamen initiation.
Three stamen primordia are visible. x 200

1

2

PLATE 23

Figure 1

Median l.s. of the floral apex of a male flower bud
of Hedycarya arborea, near the end of stamen initiation.

x 385

v = vacuolate cell undergoing division

Figure 2

Median ls. of the floral apex of a female flower bud
of Hedycarya arborea, near the end of carpel initiation.

x 130

t = young trichome

1

2

PLATE 24

Figure 1

Median l.s. of part of a female flower bud of Hedycarya arborea. A large vestigial floral apex is present and is flanked by carpel primordia. x 125

Figure 2

Median l.s. of part of a female flower bud of Hedycarya arborea. A vestigial floral apex is flanked by carpel primordia which are older than those shown in figure 1.

x 140

m = a vacuolate cell undergoing anticlinal division

1

2

PLATE 25

Figure 1

L.s. of part of a carpellate flower bud of Laurelia
n.z. in which the floral apex is flanked by carpel
primordia. x 210

Figure 2

L.s. of part of a carpellate flower bud of Laurelia
n.z. in which a vestigial floral apex is present.

x 210

1

2

PLATE 26

Figure 1

Mature fruit of Laurelia n.z. (left) and mature drupe of Hedycarya arborea from which the epicarp and mesocarp have been removed to expose the endocarp. Photo M.D.King . x 2.7

Figure 2

Median l.s. of a carpellate flower bud of Laurelia n.z. at a stage in which the outermost stamens and / or staminodes are being initiated. x 160

1

2

PLATE 27

- Figure 1 Young male floral apex of Hedycarya arborea in lateral and apical (b) view. The apical meristem is flanked by two bract primordia.
- Figure 2 Latero-apical view of a young male flower bud of Hedycarya arborea showing the apical meristem flanked by four tepal primordia. The bracts have been excised at their bases (B).
- Figures 3-6 Apical views of young male flower buds of Hedycarya arborea showing the apical meristem flanked by tepal primordia which are numbered in the apparent order in which they were initiated.
- S.B. = position of a subtending bract
B. = position of a bract above the subtending one
A.M. = apical meristem
- Figures 7-8 Lateral views of young flower buds of Laurelia n.z. with the floral apex of each being flanked by two tepals. A.M. = apical meristem
- Figure 9 Young flower bud of Laurelia n.z. in lateral abaxial (a) and adaxial (b) view. The tepal primordia are numbered in the apparent order in which they were initiated.
- Figure 10 Median l.s. of a young stamen primordium of Hedycarya arborea.
- Figure 11 Median l.s. of male flower bud of Hedycarya arborea.
A = floral apex
- Figure 12 L.s. part of a stamen of Hedycarya arborea with a row of archesporial cells (Ar) adjacent to the epidermis (Ep).
- Figure 13 L.s. part of a stamen of Hedycarya arborea showing primary parietal (Par) and primary sporogenous cells (Sp).
- Figures 14,15 & 17
Stages in the development of stamens of Hedycarya arborea as seen in lateral view.
- Figures 16, 18-21
Stages in the development of stamens of Laurelia n.z.
A.M. = apical meristem
Further details in text.

PLATE 27

a

b

1

2

3

0 1mm.
Figs. 3, 5 & 6

4

5

Hedycarya

6

7

8

a

b

0 1mm.

Laurelia

0 100μ

11

Hedycarya

12

13

0 50μ

14

15

17

a

b

c

16

Hedycarya

18

Laurelia

19

20

21

0 1mm.

PLATE 28

Figure 1 L.s. of part of a male flower bud of Hedycarya arborea showing 3 stamen primordia in which sporogenous tissue is developing. x 140

Figure 2 Median l.s. of a stamen of Hedycarya arborea in which divisions are taking place in sporogenous and wall tissue. x 140

Figure 3 T.s. of stamens of Hedycarya arborea at a stage of development similar to that shown in figure 2. x 140

1

2

3

PLATE 29

Figure 1 L.s. of a stamen of Hedycarya arborea near the end
of the development of sporogenous tissue. x 130

Figure 2 L.s. of part of a stamen of Laurelia n.z.
showing an early stage in the development
of staminal glands. x 544

1

2

PLATE 30

Figure 1

L.s. of part of a stamen of Laurelia n.z.
showing an early stage in the development of
a staminal gland at lower right.

Figure 2

L.s. of part of a stamen of Laurelia n.z.
showing an older staminal gland, in non-median
section.

s = periclinally dividing surface
cell

Both figures x 544

PLATE 31

Figure 1 T.s. of stamens of Laurelia n.z. through the
staminal glands. x 140

Figure 2 Median l.s. of two nearly mature staminal glands of
adjacent stamens of Laurelia n.z. x 130

Figure 3 Adaxial lateral view of a mature stamen of Laurus
nobilis. x 30

1

2

3

PLATE 31

- Figure 1 T.s. of stamens of Laurelia n.z. through the
staminal glands. x 140
- Figure 2 Median l.s. of two nearly mature staminal glands of
adjacent stamens of Laurelia n.z. x 130
- Figure 3 Adaxial lateral view of a mature stamen of Laurus
nobilis. x 30

PLATE 32

Figure 1

L.s. of a staminode (at left) from a carpellate
flower bud of Laurelia n.z. x 120

Figure 2

L.s. of a median part of a staminode from a somewhat
younger carpellate flower bud of Laurelia n.z.

e = epidermal cell on the adaxial
surface which has been formed
by a recent periclinal division
of a surface cell

x 480

1

2

PLATE 33

Figure 1

L.s. of part of a pollen sac of Hedycarya arborea showing a tapetal cell at anaphase (left of centre). A microspore mother cell (out of focus) is at centre right and is at prophase I. x 1400

Figure 2

L.s. of part of a pollen sac of Hedycarya arborea with a tapetal cell at metaphase (lower right) and binucleate tapetal cells at left and centre.

x 1400

Figure 3

L.s. of part of a pollen sac of Hedycarya arborea to show a tapetal cell with "sticky" chromosomes , at a stage when the pollen grains are becoming bicellular.

x 1480

1

2

3

PLATE 34

Figure 1

T.s. of part of a pollen sac of Hedycarya arborea with microspore mother cells at the early synizesis stage of prophase I. Some of the microspore mother cells are sterile (see text). x 540

Figure 2

T.s. of part of a pollen sac of Hedycarya arborea with microspore mother cells at telophase II.

x 540

Figure 3

Pollen mother cell of Hedycarya arborea (at right) at metaphase-early anaphase I. x 2000

1

2

3

PLATE 35

- Figure 1 Pollen mother cells of Hedycarya arborea undergoing microsporogenesis and with a sterile pollen mother cell at top centre. x 800
- Figure 2 A sterile pollen mother cell of Hedycarya arborea is shown , with nucleolar vacuoles, at right centre.
x 560
- Figure 3 A pollen mother cell of Hedycarya arborea at telophase I (left centre). Photo under phase contrast.
x 1500
- Figure 4 A pollen mother cell of Hedycarya arborea at telophase I. x1050

1

2

3

4

PLATE 36

Figures 1-3 show stages in microsporogenesis in Hedycarya arborea.

Figure 1 Metaphase II x 1350

Figure 2 Metaphase II (phase contrast)
x 1600

Figure 3 Telophase II (phase contrast)
x 1600

Figure 4 Tetrad of microspores of Hedycarya arborea
x 1800

1

2

3

4

PLATE 37

Stages in the first division within the pollen grains
of Hedycarya arborea.

Figure 1 Pollen tetrad at prophase. x 1600

Figure 2 Pollen tetrad at metaphase - early anaphase.
x 1750

Figure 3 Two microspores at anaphase.
x 1750

Figure 4 Pollen tetrad at the end of the division.
x 1750

1

2

3

4

PLATE 38

Figure 1

Pollen tetrads of Hedycarya arborea at various stages of division into vegetative and generative cells. x 700

Figure 2

Sections of two pollen tetrads of Hedycarya arborea showing (upper centre) a microspore in which the cytoplasm of the vegetative cell is extending around the generative cell and at lower right there is a microspore in which the generative cell lies completely within the cytoplasm of the vegetative cell. Photo taken under phase contrast .

x 1800

Figure 3

Section of part of a pollen sac of Hedycarya arborea showing wall layers and maturing pollen tetrads.

x 550

1

2

3

PLATE 39

Figure 1 T.s. stamen of Laurelia n.z. with pollen mother cells
at prophase I. x 132

Figure 2 T.s. stamen of Hedycarya arborea with pollen mother
cells at prophase I.
 x 132

Figure 3 T.s. of part of a pollen sac of Laurelia n.z.
with pollen mother cells at leptotene of prophase I.
Some tapetal nuclei are dividing.
 x 480

Figure 4 T.s. stamen of Laurelia n.z. at a time when the
first division is taking place within the pollen grains.
 x 108

1

2

3

4

PLATE 40

Figure 1 T.s. of part of a stamen of Laurelia n.z. with
pollen mother cells at metaphase-early anaphase I.
x 550

Figure 2 T.s. of part of a stamen of Laurelia n.z. with
pollen mother cells at telophase I.
x 660

Figure 3 T.s. of part of a stamen of Laurelia n.z. with
pollen mother cells at anaphase II.
x 660

1

2

3

PLATE 41

Figure 1

L.s. of part of a pollen sac of Laurelia n.z.
with unicellular pollen grains.

x 660

Figure 2

L.s. of part of a nearly mature stamen of
Laurelia n.z. in which the pollen sac at
left contains only sterile pollen.

x 70

1

2

PLATE 42

Sections illustrating stages in microsporogenesis
in Laurelia n.z.

Figure 1 Pollen mother cell at early anaphase I (lower centre)
under phase contrast. The upper part of the photo
shows tapetal cells and flattened cells of wall layers.

Figure 2 Pollen mother cell (centre) at telophase I.

Figure 3 Pollen mother cell at early anaphase II (centre).

Figure 4 The same as figure 3 but under phase contrast.

All figs. x 1500

1

2

3

4

PLATE 43

Sections illustrating stages in microsporogenesis
in Laurelia n.z.

Figure 1 Pollen mother cell at anaphase II.

Figure 2 The same as figure 1 but under phase contrast.

Figure 3 Pollen mother cell at telophase II.

Figure 4 The same as figure 3 but under phase contrast.

All figs. x 1500

1

2

3

4

PLATE 44

Figure 1

Pollen mother cell of Laurelia n.z. at late telophase II.

x 1500

Figure 2

The same as figure 1 but under phase contrast.

x 1500

Figure 3

Tetrad of young pollen grains of Laurelia n.z.

x 1500

Figure 4

T.s. of a pollen sac of Laurelia n.z. to show an aborted tapetal layer (stained black) enclosing pollen mother cells at early prophase I.

x 580

1

2

3

4

PLATE 45

Figure 1 Uninucleate pollen grain of Laurelia n.z. (phase contrast).

Figure 2 Uninucleate pollen grain of Laurelia n.z. (phase contrast)
with large vacuoles in the cytoplasm.

Figure 3 Uninucleate pollen grain of Laurelia n.z. (phase contrast)
in which the nucleus is appressed against the wall
of the grain. Photo taken under phase contrast.

Figure 4 Pollen grain of Laurelia n.z. with its nucleus at
prophase as seen under phase contrast.

Figure 5 Pollen grain of Laurelia n.z. at metaphase of the first
division (phase contrast).

All figs. x 1370

1

2

3

4

5

PLATE 46

Figure 1 Pollen grain of Laurelia n.z. at anaphase (phase contrast)

Figure 2 Young two celled pollen grain of Laurelia n.z. as
seen under phase contrast.

Figure 3 Young two celled pollen grain of Laurelia n.z.
showing vacuoles in the cytoplasm of the
vegetative cell.

Figure 4 The same as figure 3 but under phase contrast.

All figs. x 1370

1

2

3

4

PLATE 47

- Figure 1 Mature two celled pollen grain of Laurelia n.z.
x 1370
- Figure 2 The same as figure 1 but under phase contrast.
- Figure 3 Median l.s. of part of the upper portion of a carpel
of Hedycarya arborea. Further details in text.
x 130
- Figure 4 Immature (left) and mature carpels of Hedycarya
arborea as seen in lateral ad-abaxial view.
x 28

1

2

3

4

PLATE 48

- Figure 1 Section of a pollen grain of Laurelia n.z. showing the generative cell dividing (telophase). The nucleus of the vegetative cell lies in a different plane of focus and is not shown.
- Figure 2 Section of a three celled pollen grain of Laurelia n.z. The two male cells are situated above the nucleus of the vegetative cell.
- Figures 3-7 Stages in the ontogenetic development of carpels of Hedycarya arborea as seen in lateral view. The opening of each carpel faces the centre of the flower.
- ov = ovule
- Figure 8 Mature carpel of Hedycarya arborea. The cleft of the carpel lies between x - y.

1

2

3

a

b

4

a

b

5

c

a

b

6

7

8

PLATE 49

Figures 1-5

Stages in the ontogenetic development of carpels of Laurelia n.z. as seen in lateral view. The opening of each carpel faces the centre of the flower.

ov = ovule

Figures 6-7

Mature carpels of Laurelia n.z. in lateral ad-abaxial view (figure 6) and lateral introrse view (figure 7). The dotted line in each carpel indicates the position of the ovule.

cz = cross zone

1

2

3

4

5

6

7

PLATE 50

Figures 1-5

Progressive transverse sections of a carpel of Hedycarya arborea in which the ovule is at the megaspore mother cell stage. Sections begin near the distal tip (stigma) of the carpel (figure 1) and are concluded in PLATE 51.

All figs. x 132

1

2

3

4

5

PLATE 51

Figures 1-4 Progressive transverse sections of a carpel of Hedycarya arborea , continued from PLATE 50. In figure 4, which is a section near the base of the carpel, a megaspore mother cell (at prophase I) lies within the ovule. Further details in text.

All figs. x 132

1

2

3

4

PLATE 52

Figure 1

L.s. of a carpel primordium of Laurelia n.z. The adaxial side of the carpel is on the right. To the right of the carpel is part of the vestigial floral apex.

x 490

Figure 2

L.s. of a carpel primordium of Laurelia n.z. which is older than the one shown in figure 1. The adaxial side of the carpel is on the left. To the left of the carpel is part of the vestigial floral apex.

x 200

1

2

PLATE 53

Figures 1-9

Progressive transverse sections of a carpel of Laurelia n.z. in which the ovule is at the uninucleate embryo sac stage. Sections begin near the distal tip (stigma) of the carpel (figure 1) and are concluded in PLATE 54.

All figs. x 132

1

2

3

4

5

6

7

8

9

PLATE 54

Figures 1-5

Progressive transverse sections of a carpel of Laurelia n.z. , continued from PLATE 53. In figure 5, which is a section near the base of the carpel, is an ovule containing a uninucleate embryo sac.

tr = ventral trace

All figs. x 132

1

2

3

4

5

PLATE 55

- Figure 1 Median l.s. of a carpel of Hedycarya arborea. The
adaxial side is at left. Further details in text.
x 140
- Figure 2 Median l.s. of a young ovule of Hedycarya arborea.
At the right and at the base of the photo can be seen
part of the carpel wall.
x 456
- Figure 3 L.s. of part of a carpel of Hedycarya arborea
to show a semi-inverted ovule which contains a
megaspore mother cell at prophase I.
p = a periclinally dividing surface
cell
x 168
- Figure 4 T.s. of an aberrant ovule of Hedycarya arborea
which contains two megaspore mother cells.
Each megaspore mother cell is at the synizesis
stage of prophase I. Further details in text.
o.i. = outer integument
x 528

1

2

3

4

PLATE 56

Figure 1 L.s. of a fully inverted ovule of Hedycarya arborea.
A T-shaped tetrad of megaspores is present (centre).
x 520

Figure 2 L.s. of a fully inverted ovule within the locule of
a carpel of Hedycarya arborea. In this abnormal ovule
the megaspore mother cell is at prophase I. Further
details in text.
x 204

Figure 3 L.s. of an ovule of Hedycarya arborea which contains
a uninucleate embryo sac.
x 204

Figure 4 L.s. of an ovule of Hedycarya arborea which contains
a binucleate embryo sac.
x 168

1

2

3

4

PLATE 57

Figure 1 L.s. of a young ovule of Laurelia n.z. (centre left).
a.r. = archesporial cell
x 550

Figure 2 L.s. of a young ovule of Laurelia n.z. (centre).
p = primary parietal cell
s = primary sporogenous cell
x 500

1

2

PLATE 58

Figure 1 L.s. of a young ovule of Laurelia n.z. (centre)
with an enlarging megaspore mother cell.

Figure 2 L.s. of a young ovule of Laurelia n.z. (centre)
with a megaspore mother cell.

o.i. = position at which the outer
integument has recently been
initiated

Figure 3 L.s. of a semi-inverted ovule of Laurelia n.z.
in which the megaspore mother cell is at an
early stage of prophase I.

Figure 4 L.s. of part of an inverted ovule of Laurelia n.z.
(upper half of photo) which contains a megaspore
mother cell at diplotene of prophase I.

All figs. x 550

1

2

3

4

PLATE 59

Figure 1 L.s. of part of an ovule of Laurelia n.z. showing a T-shaped tetrad of megaspores in which the megaspore adjacent to the innermost (functional) one, has begun to degenerate.

x 550

Figure 2 L.s. of part of an ovule of Laurelia n.z. in which there is a uninucleate embryo sac.

x 560

Figure 3 L.s. of part of an ovule of Laurelia n.z. in which the nucleus of the embryo sac is at prophase.

x 560

Figure 4 L.s. of a young seed of Hedycarya arborea.

h = hypostase

x 112

1

2

3

4

PLATE 60

Figure 1 2-nucleate embryo sac of Laurelia n.z.

Figure 2 4-nucleate embryo sac of Laurelia n.z.

Figure 3 Young 8-nucleate embryo sac of Laurelia n.z.

Figure 4 L.s. of part of the carpel of Laurelia n.z.
containing a mature embryo sac prior to
fertilization.

Stippled areas at left and right represent
the ventral (left) and dorsal vascular
tissue.

In all figures the chalazal end of the embryo sac
faces the top of the page.

1

2

3

4

PLATE 61

Figure 1 Foliage of Laurelia n.z. bearing a dehiscent pseudocarp.

Approximately natural size.

1

PLATE 62

Photo of herbarium sheet containing two specimens
of the foliage of Laurelia serrata Phil.

Nº 154147 A BOTANY DIVISION, D.S.I.R.,
CHRISTCHURCH, NEW ZEALAND

ROYAL SOCIETY EXPEDITION TO SOUTHERN CHILE 1958/59

No. 299c. *Laurelia philippiana* Looscr.

Loc. Chapu, Chilo.

Hab. On bank of river Chapu.

Coll. E.T. Godley.

Date: 22. 10. 58.

Det. E.T. Godley.

Date: 30. 12. 64.

Remarks:

L. serrata Phil.

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FEB 1966

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