

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

Investigations of some Floral Vascular Systems
with particular reference to
Interpretations Involved in the Gonophyll Theory

A thesis presented in partial fulfilment
of the requirements for the degree of

Doctor of Philosophy

in

Botany

at

Massey University

John Peyton Skipworth

1969

PROLOGUE

Throughout the history of Plant Science, the Angiosperm flower has provided botanists with one of their most intriguing structural entities. The number of theories which have been advanced to account for the origin of the flower and for the nature of its component appendages are multitudinous and in large part unproven. In 1960 the British botanist Melville propounded a new theory, the Gonophyll theory, and this has excited considerable interest among floral morphologists. The basic tenets of Melville's interpretation were based on the course taken by vascular bundles, and in an arena still bedevilled by conflicting opinion, the lucid presentation of the Gonophyll theory carried some conviction.

The present writer was at the time pursuing an interest in the development of the patterns displayed by vascular tissue in vegetative shoots and did in fact demonstrate an instance in which there was considerable change in vascular pattern during the period of primary trace development (Skipworth 1962). In addition, Tepfer (1953) had reported an instance where some alteration in vasculature of a fertile shoot did take place during the time between anthesis and fruit maturity. From these two reports emanated the suspicion that when they first appear, the strands comprising the vascular system of flowers may not display the relationships apparent at floral maturity.

The aims of the present inquiry therefore became twofold.

1. An appraisal of some of Melville's observations and if necessary a reevaluation of his theory.
2. The testing of a hypothesis that vascular

systems of flowers are not the same as those revealed during floral ontogeny.

Clearly a critique of the Gonophyll theory might become especially pertinent if changes in vascular pattern prior to anthesis could be demonstrated.

It appeared clear that these aims could most satisfactorily be attained if the inquiry were based on the apocarpous flowers of the Ranales. This group contains the families from which Melville had procured much of his basic information, and the apparent simplicity of the flowers suggested that they might also be an appropriate group in which to investigate early stages of vascular development.

The Magnoliaceae, the family whose members possess flowers which were interpreted by Melville as providing a link with the gymnospermous Gnetum became an obvious starting point. From here the inquiry led to Gnetum itself and to the Winteraceae, an Angiosperm family usually supposed to be related to the Magnoliaceae but to be even more primitive. Magnoliaceous flowers possess a cortical vascular system, a feature not unknown elsewhere but conspicuously and very regularly developed in the vegetative stem in another family suspected of Magnoliaceous affinity, the Calycanthaceae. Floral vasculature of this family was therefore investigated.

Another of the cornerstones of the Gonophyll theory was provided by flowers of the Ranunculaceae, the two carpel types in the family, achene and follicle, being held by Melville to be of quite different origin. The ancestry of these was moreover viewed as involving sequences quite different from those envisaged by the vast majority of theorists. Because Melville used these two basic entities as building blocks for various types of syncarpous gynoecia, the more positive establishment

of their identity seemed of paramount importance in any critique of his theory.

Despite the attention that over the years has been focussed on certain of the taxa involved in the present inquiry, there are many intrinsically interesting features which have not been accounted for in the literature. Where the investigation of these did not involve a substantial digression from the main course of the project - as for example the phyllotaxis of floral phyllomes which might be expected in any case to have a bearing on final conclusions - their description has been included in the text.

ACKNOWLEDGEMENTS

The author would like to express thanks to two successive supervisors at Massey, Dr J.S. Yeates and Professor R.G. Thomas and also to Professor W.R. Philipson (University of Canterbury) who has been closely associated with the project throughout and has provided much of the inspiration.

The preserved material provided by Dr F.B. Sampson (Victoria University of Wellington) and Mr G. Brownlie (University of Canterbury) has been invaluable while advice on taxonomy of ornamentals received from Mr P.S. Yalden (Massey University) and Mr W. Sykes (Botany Division, D.S.I.R., Christchurch) has been greatly appreciated.

Thanks are also extended to Dr H. Jacks and Mr D. Spencer for assistance with translation of some German and Russian literature.

The Massey University Library staff, particularly Miss A. Claridge, has been most obliging and their assistance is also gratefully acknowledged.

TABLE OF CONTENTS

Prologue	page	11
Acknowledgements		v
Part One		1
Chapter I Introduction		1
1. Aims		2
2. Methods		3
3. Materials		6
4. Terminology		7
Part Two - The Magnoliaceous Flower		10
Chapter II Magnoliaceae		11
1. Introduction		11
2. <u>Michelia fuscata</u>		16
1. Introduction		16
ii. Anatomy of the Vegetative Stem		16
iii. General Floral Morphology		17
iv. Vasculature of the Mature Flower		18
a. Pedicel		18
b. Perianth		19
c. Androecium		19
d. Gynoecium		20
v. Vascular Development		22
vi. Carpel Phyllotaxis		24
3. <u>Magnolia stellata</u>		26
1. Introduction		26
ii. Anatomy of the Vegetative Stem		26
iii. General Floral Morphology		27
iv. Vasculature of the Mature Flower		27
a. Pedicel		27
b. Perianth		28
c. Androecium		29
d. Gynoecium		29
v. Vascular Development		30

4. Other Species of <u>Magnolia</u>	page 33
5. <u>Liriodendron tulipifera</u>	35
1. Introduction	35
ii. Anatomy of the Vegetative Stem	35
iii. General Floral Morphology	35
iv. Vasculature of the Mature Flower	36
a. Pedicel and Perianth	36
b. Androecium	37
c. Gynoecium	38
v. Vascular Development	39
6. Comparisons	42
1. Bracteole (<u>Michelia</u>) or Uppermost Leaf	42
ii. Perianth	43
iii. Androecium	44
iv. Gynoecium	45
v. Summation	45
7. Discussion	48
Chapter III <u>Gnetum</u>	53
1. Introduction	53
2. Floral Vasculature	54
3. Comparison with the <u>Magnolia</u> Flower	56
Chapter IV Winteraceae	58
1. Introduction	58
2. Floral Vasculature	60
1. General	60
ii. <u>Belliolum crassifolium</u>	61
3. Development of Floral Vasculature	63
1. <u>Drimys winteri</u> var. <u>chilensis</u>	63
ii. <u>Pseudowintera axillaris</u>	64
iii. <u>Belliolum crassifolium</u>	64
4. Comparison with Magnoliaceae and <u>Gnetum</u>	65
Chapter V Calycanthaceae	67
1. Introduction	67
2. The Flower	69

1. <u>Calycanthus occidentalis</u>	page 69
11. <u>Chimonanthus fragrans</u>	70
3. Stem Vasculature	71
4. Floral Vasculature	73
1. <u>Calycanthus occidentalis</u>	73
a. Bracts and Perianth	73
b. Androecium	74
c. Gynoecium	75
11. <u>Chimonanthus fragrans</u>	75
111. Development	76
5. Phyllotaxis of Floral Phyllomes	78
1. <u>Calycanthus occidentalis</u>	78
11. <u>Chimonanthus fragrans</u>	79
6. <u>Calycanthus floridus</u>	81
7. Summary	82
8. Comparison with Magnoliaceae	84
Part Three - Achene and Follicle	87
Chapter VI Ranunculaceae	87
1. Introduction	88
2. <u>Caltha palustris</u>	93
1. Introduction	93
11. Perianth	94
111. Androecium	94
iv. Gynoecium	95
v. Fruit	97
vi. Floral Bud	98
3. <u>Caltha novae-zelandiae</u>	101
1. Introduction	101
11. Flower	101
111. Fruit	102
iv. Floral Bud	103
v. Comparison with <u>C. palustris</u>	103
4. <u>Caltha cbtusa</u>	105
5. <u>Helleborus niger</u>	107

1. Introduction	page 107
ii. Vasculature of the Flower	107
iii. Fruit	108
iv. Floral Bud	109
v. Comparison with <u>Caltha</u>	109
6. <u>Aquilegia</u>	111
1. Introduction	111
ii. Flower	111
iii. Fruit	112
iv. Floral Bud	112
v. Comparison with <u>Caltha</u>	113
7. Folliculate Forms - Discussion	114
8. <u>Thalictrum aquilegifolium</u>	117
9. <u>Ranunculus</u>	120
10. Achene Bearing Forms - Discussion	122
11. Is the Achene a Reduced Follicle?	123
Part Four	128
Chapter VII Discussion and Summary	128
1. Discussion	129
1. Context of the Gonophyll Theory	129
ii. The Axillary Bud Question	132
iii. The Stamen Question	133
iv. The Foliar Primordia Question	135
2. Summary	136
Part Five - Illustrations	139
Part Six - References	179

TABLE OF FIGURES

		<u>facing page</u>
FIG. 2.1 a	Diagrammatic representation <u>Magnolia</u> flower	140
b	Vasculature - <u>Magnolia stellata</u> flower	140
2.2	Carpelloid stamens - <u>Michelia fuscata</u>	141
2.3	Pedicel vasculature - <u>Michelia fuscata</u>	142
2.4	Lower receptacle - <u>Michelia fuscata</u>	142
2.5	Androecial region - <u>Michelia fuscata</u>	143
2.6	Gynoecial region - <u>Michelia fuscata</u>	143
2.7	Floral vascular devt. - <u>Michelia fuscata</u>	144
2.8	T.S. gynoecium - <u>Michelia fuscata</u>	145
2.9	Relationship of cortical system stele and carpels - <u>Michelia fuscata</u>	146
2.10	Floral vascular systems - <u>Magnolia</u> spp. and <u>Liriodendron</u>	147
2.11	Stamen and perianth vasculature - <u>Magnolia stellata</u>	149
2.12	Perianth vasculature - <u>Liriodendron</u>	149
3.1	Vasculature - female inflorescence - <u>Gnetum</u>	150
4.1	Floral vasculature - <u>Belliolum</u>	151
4.2	Floral vascular devt. - <u>Drimys</u>	152
4.3	Floral vascular devt. - <u>Pseudowintera</u>	153
5.1	Floral appendages - <u>Calycanthus</u>	154
5.2	Carpel - <u>Calycanthus</u>	155
5.3	Stem vasculature - <u>Calycanthus</u>	156
5.4	Tepal vasculature - <u>Calycanthus</u>	157
5.5	Floral vasculature - <u>Calycanthus</u>	158
5.6	Perianth Phyllotaxis - <u>Calycanthus</u>	159
5.7	Perianth Phyllotaxis - <u>Chimonanthus</u>	160

	<u>facing page</u>
FIG. 6.1	Follicles - Gonophyll interpretation 161
6.2	Achene - Gonophyll interpretation 161
6.3	T.S. receptacle - <u>Caltha palustris</u> 162
6.4	Tepal venation - <u>Caltha palustris</u> 162
6.5	Floral (less gynoecial) vasculature <u>Caltha palustris</u> 162
6.6	Carpel vasculature - <u>Caltha palustris</u> 163
6.7	Carpel vasculature - <u>Caltha palustris</u> 163
6.8	Apex of floral bud - <u>Caltha palustris</u> 164
6.9 - 6.15	Photomicrographs of cleared half flowers and floral buds of <u>Caltha palustris</u> illustrating stages in development of the floral vascular system 164-167
6.16	Floral vascular devt. - <u>Caltha palustris</u> 168
6.17	L.S. flowers - <u>Caltha novae-zelandiae</u> and <u>C. palustris</u> 169
6.18	Floral vasculature - <u>Caltha novae-zelandiae</u> 169
6.19	Floral vascular devt. - <u>Caltha novae-</u> <u>zelandiae</u> 169
6.20	Comparison of floral vasculature - <u>Caltha</u> <u>novae-zelandiae</u> and <u>C. palustris</u> 170
6.21	Floral vasculature - <u>Caltha obtusa</u> 170
6.22	Floral vasculature - <u>Helleborus niger</u> 171
6.23 - 6.26	Photomicrographs of cleared half flowers and floral buds of <u>Helleborus niger</u> illustrating stages in the development of the floral vascular system 172-173
6.27	Floral vascular devt. - <u>Helleborus niger</u> 174
6.28	Floral vasculature - <u>Aquilegia vulgaris</u> 175
6.29	Floral vascular devt. - <u>Ranunculus repens</u> 176
6.30	Vasculature of follicles and achenes (after Eames) 177
6.31	Possible relationship between follicle and achene vasculature 178

PART ONE

Chapter I

INTRODUCTION

1. AIMS

Reference to the development of the objectives of the present inquiry has been made in the prologue to this thesis. The most fundamental of these may at this juncture be briefly restated as the testing of significant elements of Melville's Gonophyll theory. It is clear from Melville's writings that the most basic of the evidence pertaining to the theory is drawn from floral vasculature of various Ranalean species, especially certain among two families, the Magnoliaceae and the Ranunculaceae. Melville evidently considered flowers at about the time of anthesis although there seems no reason why deductions from vascular anatomy should be any more meaningful or reliable at this particular stage than at any other. Indeed as Sporne (1958), Corner (1963), and others have indicated, it is the fruit rather than the flower which should be considered as the mature structure. In the present investigation stress will be laid where possible on the development of the vascular system of the reproductive shoot from the time of its first appearance through to fruit maturation. It soon became evident that interrelationships between components of the vascular system can be seen with especial clarity prior to the opening of the flower, mainly because during these earlier stages there is little or no secondary development of conducting elements. Description of the development of floral vascular systems appears to be something which has rarely been attempted and it seemed reasonable to regard such description as a secondary aim in the present work.

2. METHODS

In order to appraise the Gonophyll theory it was of course essential to investigate the courses of vascular bundles and there are essentially two methods by which this may be done. The first is by examining serial sections of a suspected significant stage of development and the second by clearing flowers and observing, usually at rather lower magnifications, the whole of a floral vascular system. Both methods were used although the type of evidence required could in most cases be obtained more quickly, and was probably more reliable, if procured by the latter method. Serial transverse sections were prepared by the standard technique of paraffin embedding, sectioning and staining with safranin and fast green (Johansen 1940). Clearing of buds, flowers and fruits proved a more difficult proposition. Canright (1960) and Tucker (1961) have evidently met with success using 6% sodium hydroxide but it was considered that a method providing greater clarity was desirable in the present instances. The method used by Sporne (1948) was tried without absolute success, then finally a modification of a method suggested by Bersier and Bocquet (1960) was developed and used. The modified method consists of placing the required appendage or shoot in a solution of equal parts of lactic acid, phenolic acid and chloral hydrate and holding at 100°C. In most cases the operation was performed in a small watch glass which could be covered thereby eliminating evaporational loss of the presumably differentially volatile fluid components. Fresh, or to a lesser extent preserved tissue was usually clear within 24 hours although dried material required much longer periods and several changes of clearing fluid. Dried material was sometimes initially bleached in dilute sodium hypochlorite and while this did

induce more rapid and more complete clearing, it did greatly increase the fragility of the material. After clearing, the objects were stored, usually without removal from the watch glass, in pure lactic acid. This therefore involved a minimum of manipulation and consequent risk of damage especially as the material could be examined by stereo microscope without transferring to another vessel. A staining technique recommended by Morley (1949) and other lignin stains were initially employed but it was found that they were not usually necessary. Alteration of the angle of the microscope mirror during observation resulted in differential absorption and reflection of the transmitted light by the thickened xylem cells, and at certain mirror positions the vascular system could be seen with remarkable clarity. Prior to clearing, most of the shoots examined were slit in half longitudinally because a much clearer picture of the vascular pattern was usually visible from "inside" the shoot - presumably because if examined from the outside, a much greater density of primary tissues would be likely to partially obscure xylem elements.

Photographs of cleared flowers were taken and some of these are included among the illustrations accompanying the present account. Their taking presented difficulties. That of acquiring even lighting and particularly that of obtaining sufficient depth of field were substantial problems. However, no reports are known where such photographs of flowers have been published and even photographs of cleared appendages (e.g. carpels of Michelia by Tucker 1964) suggest that the difficulties encountered in the preparation of photographs for this thesis are very real. It might ultimately be possible to present stereo microphotographs although this would require highly sophisticated optical equipment the like of which seems not

available in New Zealand.

Several of the drawings included among the illustrations also require explanation. The preparation of those which depict whole vascular systems in flowers has presented difficulties not inherent in representations of stems where all parts of a shoot in a given region are of approximately the same diameter. The apex of the floral shoot is often conical, hemispherical or even concave and even in the first two of these cases it seems impossible to present in two dimensions an accurate picture by the slitting and opening technique, and in the third case surely only a three dimensional model could adequately illustrate proportions. The whole situation is of course further complicated in those flowers where there are in fact two essentially concentric but interrelated vascular systems. The apical projection technique provides pictures no less distorted in which horizontal levels are difficult to appreciate, and drawings of which become impracticably large in those cases where dozens of internodes need to be represented. Most of the drawings of vascular systems of whole or half flowers were finally compiled according to the slitting and opening technique the receptacle being assumed to be of the same diameter throughout its total length. These drawings may therefore be said to have involved what approximates to a Mercator's projection. Even this representation would not solve the problem presented by the concave receptacle although fortunately whole flower representations of this type were not finally deemed necessary.

3. MATERIALS

Because critical developmental stages are often transitory it was felt desirable to procure living material at all stages in some abundance. Fortunately many of the species dealt with were found growing at Massey University and others were obtainable in or near Palmerston North. In some instances preserved or dried material had to be resorted to and in this there was sometimes a paucity of appropriate vital stages. Accordingly, evidence pertaining to a few of the species mentioned must be regarded as incomplete although it would seem that only good luck would, in the absence of abundant living material, provide the investigator with a complete picture of the development of floral vasculature.

4. TERMINOLOGY

Although it is not proposed to enter a discussion of priorities of names which should be applied to various structures and features, it does seem necessary to clarify some of the terms which will be used. Examination of published accounts reveals that in several instances which are pertinent to the present investigation, the one feature has been described by different authors under different names. In compiling the present account, an attempt has been made to choose terms which seem most suitable, and to be consistent in their use.

The term "strand" or "vascular strand" is applied to the strandlike aggregations of xylem and phloem cells which are parallel to the axis. These may well be vascular bundles although the term "bundle", which seems properly to apply to aggregations of primary xylem and phloem, would not embrace all vascular tracts in a fertile shoot. Except where it is clear that only primary tissue is involved (and only a transverse section can determine this with certainty in many cases) the term "bundle" or "vascular bundle" is avoided. The expression "trace" or "vascular trace" is applied to the continuation or branch of a strand which has clearly ceased to be parallel to the axis and is passing to an appendage of foliar nature (including stamens and carpels).

Several of the species examined have well developed cortical vascular systems. One of the early workers on such groups was Worsdell (1908) who in fact referred to "medullary" and "cortical" steles although more recent writers (Smith 1928, Canright 1960, Tucker 1961, Balfour and Philipson 1962) have written in terms of a single normal stele plus a cortical system of bundles, strands or traces and it is in this latter fashion that tracheal

elements in the cortex will be regarded in this account.

The term "tepal" is evidently most appropriately used to designate a perianth member in cases where sepals and petals are not distinct. It will be used in this sense.

Because it is debatable whether a flower can be considered to be a mature structure (or whether it represents rather a stage in maturation of the fruit) the term "floral maturity" will be avoided. "At anthesis" appears to define more precisely the stage usually implied by "floral maturity" and in fact considerable use will be made of the former term.

The terms "torus" and "receptacle" have at various times been applied to the same structure. Torus was used by some earlier morphologists (e.g. Goebel 1887) although its widespread current useage in descriptions of walls of tracheal elements has perhaps led to its partial replacement by "receptacle" in most modern literature. Receptacle will be used in this account.

The anatomical term "midvein" is preferred to the more morphological "midrib." In carpels "dorsal vein" and "ventral vein" are used instead of their presumed leaf counterparts "midvein" and "lateral vein." This is partly out of deference to the opponents of the theory of equivalence of appendages and partly because it is descriptively more precise if positions of veins are to be considered.

Importance will be placed on the vascular pattern when vascular tissue first appears in cleared preparations. It is realised that prior to this stage it might be possible to reconstruct a pattern provided for example by procambial strands although this, which could only be compiled through serial sections, would be very time consuming and there is no reason to suspect that it would

be especially rewarding. Unless positively indicated otherwise "differentiation" or "maturation" are terms used throughout this account to describe the stage at which vascular tissue becomes visible in cleared preparations.

PART TWO

THE MAGNOLIACEOUS FLOWER

Chapter II Magnoliaceae

Chapter III Gnetum

Chapter IV Winteraceae

Chapter V Calycanthaceae

II MAGNOLIACEAE

1. INTRODUCTION

Not all, but the majority of Angiosperm taxonomists regard the Magnoliaceae as a primitive family, at least one in fact (Hutchinson 1959) ranking it as the most primitive of all. Probably the largest and best known woody Ranalean group, its alleged primitiveness rests primarily on the fact that flower parts are spiralled and that there is virtually no evidence of fusion. Features such as the elongated receptacle and laminar stamens with adaxial sporangia lend the notion support, and in addition several authors (e.g. Hallier 1905, Arber and Parkin 1907, Melville 1960) have alleged resemblances with various Gymnosperm groups. Nevertheless the wood is of a comparatively advanced type (McLaughlin 1933), while the existence of both a stele and a cortical vascular system in the flower and the associated complex vasculature of floral appendages, provides characters of singular distinction. Older accounts included in the Magnoliaceae Cercidiphyllum, Euptelea, Trochodendron, Schizandra, Illicium and even the Winteraceae although now it is more usual to regard each as comprising a distinct family. The cytological findings of Whitaker (1933) and the morphological evidence presented by Bailey, Nast and Smith (1943) have, in supporting this notion, provided the suggestion that the Magnoliaceae (sensu stricto) are rather isolated from the others. Nast (1944) reached the conclusion that some other families, particularly the Winteraceae, were more primitive.

In his circumscription of the family, Dandy (1927) who supported the narrower view, delimited nine genera

and these seem to constitute a natural and in most respects uniform group although Dandy did place Liriodendron alone in a second tribe. Canright (1952, 1960), who split one of Dandy's genera and therefore treated ten, provided convincing evidence of evolutionary trends within the family and these suggest that Magnolia and Michelia are in most respects the more primitive members, while Liriodendron is relatively advanced.

Most facets of the general morphology of the Magnoliaceae have already been investigated, the series of papers by Canright (1952, 1953, 1955, 1960) supplementing earlier work and providing present day botanists with as complete an outline as for most Angiosperm families. Few accounts however relate specifically to floral vasculature. The treatise of Ozenda (1949) embraces much more than the Magnoliaceae and is lacking in some significant details although to a considerable extent Canright's more precise reports rectify deficiencies. Canright's papers on stamen and carpel vasculature refer particularly to vasculature within the appendages rather than to vasculature of the whole flower, the fashion in which bundles originate, or the relationship they bear to each other. Melville (1963) certainly has treated the floral vascular system as a whole although his descriptions and his figures are too brief to be of critical value. Moreover he too seemed concerned only with vasculature at anthesis. The reports of Holm (1909), Skvortzova (1958) and Tucker (1961) make only passing reference to vascular systems, and their accounts are in any case based only on one species. Ozenda (1947) treated several species of Magnolia from the point of view of their vascular systems although the essential features were embodied in his 1949 treatise.

Knowledge seemed especially lacking in the general area of development of floral vascular systems in the family until information pertaining to this was provided by Skipworth and Philipson (1966). Their suggestion was that when the vascular system first appears in the floral bud it is rather different from that revealed at anthesis. A generalized picture of the vascular system of the Magnoliaceous flower when that system first appears was presented and the present chapter embodies much of the ground work for that paper.

Published work makes it clear that flowers of all members of the Magnoliaceae (s.s.) have in addition to the normal stele, a well developed system of cortical strands. Evidently this cortical system does not extend below the flower into vegetative regions. Clearly branches from both systems run regularly to each carpel and probably to each perianth member although such may not be the case with stamens. Melville (1960, 1963) has interpreted this flower as a composite structure (fig. 2.1). He believed that the cortical system in the region of the lower tepals, bracts and upper leaves was derived from upward branches of each of the two lateral traces of upper foliage leaves. That is, these leaves were regarded as sterilized gonophylls which retained part of their fertile branch systems "adnate to and fused with the stem" with each branch joined to a lateral trace of a higher appendage. He believed that stamens were borne on branches which have arisen on or in the axils of upper perianth members. These branches, which are linked to the cortical system of the region of the tepals below them, comprise the cortical system in the androecial portion of the axis. Above the stamens, each carpel is regarded as receiving its midvein and ovular supplies from the stele while the cortical system in this region is believed again to con-

sist of "sterilized ovuliferous branches" linked together vertically and joined below to upper extensions of the cortical system of the androecial region. Because Melville apparently altered his interpretations between the writing of his respective papers, the summary presented here may in fact be too brief to do his theory justice. However, a more detailed appraisal can more appropriately be included in the discussion at the end of this chapter.

At all events, the Magnoliaceous flower considered in this light, is seen by Melville as a relatively primitive structure and this of course is by no means a novel idea. Whether it really strengthens Parkin's theory of the anthostrobilus (Parkin 1923) as Melville claims, or whether there has been established real similarity with Gnetum, thereby providing "at last evidence to link the Dicotyledons with the Gymnosperms through their reproductive organs" is debatable. Melville's observations, which in fact do not align absolutely with those of Ozenda or of Canright, do require substantiation and a critical appraisal of the Gonophyll theory in so far as it applies to the flowers of the Magnoliaceae became therefore an important facet of the present investigation.

None of the ten genera of the Magnoliaceae (s.s.) are native to New Zealand although cultivated species from three of them were available in Palmerston North. Several species of Magnolia (M. soulangiana, M. grandiflora, M. campbelli and M. stellata), two of Michelia (M. fuscata and M. doltzopa) and Liriodendron tulipifera were initially obtained, Magnolia stellata, Michelia fuscata and Liriodendron tulipifera finally being subjected to detailed examination. Supposedly primitive as well as advanced members of the family were therefore treated. The aspects of especial interest were the development of the floral vascular system and an appraisal of Melville's

interpretations and deductions.

2. MICHELIA FUSCATA

1. Introduction

Michelia fuscata is a small attractively flowered tree with the propensity in Palmerston North for producing flowers all the year round. Leaves are of oval outline, 4-10cm. long, glabrous, dark green and shining, and as is the case throughout the family they are simple and alternate. Associated with them are large deciduous stipules - another family characteristic. The white or pale green, pink tinged flowers when open measure 2-4cm. across. These flowers are borne singly in an axillary position.

11. Anatomy of Vegetative Stem

There are few unusual features concerning the arrangement of tissues in the stem. Prior to secondary thickening, from 30 to 40 bundles of normal type and orientation comprise the eustele. Even before the metaxylem has fully differentiated, areas of sclerenchyma appear these becoming particularly prominent as a "cap" outside each bundle. Aggregations of stone cells are at all stages prominent in parenchyma, most especially in the pith. Less than 1mm. below each node one strand departs from the others, runs through the cortex and divides several times to produce the traces of the stipules. At this same level two other strands depart separately from the stele and run almost horizontally in the cortex to provide lateral veins in the petiole. The midvein of the leaf originates fractionally higher and commonly divides into three as it passes through the

cortex. Nodes are therefore multilacunar - another family character (Sinnott 1914).

Secondary tissue appears in normal fashion. Many of the phloem cells become extensively sclerified soon after they arise and phloem always contains prominent aggregations of stone cells. Phellogen appears in the outer two or three cell layers of the cortex.

111. General Floral Morphology

At anthesis the scar of a bracteole is clearly visible about half way up the abaxial side of the pedicel which is about 2cm. in length. Before the flower bursts it is enclosed by the stipules associated with this bracteole after the fashion that stipules typically enclose all buds in this family. The bracteole itself is essentially foliar. A second very small bracteole sometimes found opposite the larger one is also enclosed by the stipule. The flower usually has six perianth members and an indefinite number of both stamens and carpels. Floral appendages are clearly spirally arranged. At maturity the gynoecium is markedly stipitate although most of the length of the gynoecial stalk (about one cm. at anthesis) is acquired during rapid elongation of the single internode between lowermost carpel and uppermost stamen after the flower has opened. In outline the tepals, each of which is from one to two cm. long, are usually ovate although the uppermost may be very narrowly so. Stamens are narrowly oblanceolate, anther lobes being borne laterally. The connective is broad and extends beyond the anther. Carpels are unilocular, bivular, free and densely packed. The stigmatic surface is apparently confined to the distal extremity of the ventral margins and at anthesis these margins are completely fused. Near the base of each carpel the ventral surface is fused with

the receptacle. Some of the upper stamens are frequently carpelloid even to the extent of their bearing ovules on the exposed adaxial surface (fig. 2.2).

iv. Vasculature of the Mature Flower

a. Pedicel

At the base of the pedicel 20-25 normally oriented vascular bundles can be seen in a transverse section. Shortly above this level five or six of the bundles begin to run obliquely out into the cortex, and immediately below the bracteole these bundles would clearly be described as cortical. Very rarely do any of the bundles in this region bifurcate and all maintain straight, approximately parallel courses. The vasculature of the bracteolar node is somewhat variable. Either one of the cortical bundles does bifurcate, or two ultimately comprise the pair of lateral traces of the bracteole. The bracteolar midvein comes from the stele, and the three traces to a bracteole are in very close association or are even temporarily fused in the cortex prior to their subsequent separation in the base of the appendage (fig. 2.3). One or sometimes two strands arise near this point and continue to ascend the pedicel as cortical strands. Of the other cortical strands below the bracteole, one passes into the stipule recalling the situation in leaves (Ozenda 1949, Canright 1955), and the remainder, usually two or three, continue as strands in the upper part of the pedicel. Sometimes the stipule trace provides a branch which continues to ascend as a cortical strand. The bud in the axil of the bracteole, which apparently never develops further, receives its vascularization directly from the stele.

Immediately above the node, some of the stelar strands divide radially and commence to run diagonally

through the cortex shortly to become recognisable as cortical strands. For the greater part of the distance between bracteole and perianth therefore, the pedicel contains 20-25 straight, parallel strands comprising its stele and five or six similar strands, its cortical vascular system. Some of these latter strands are direct continuations of cortical strands below the bracteole and others have arisen from the stele immediately above the node. In addition some are ascending branches from bracteole and stipule traces.

b. Perianth

The origin of the vasculature of the tepals is much more obscure than that of the bracteole. This is largely because shortly below the level of insertion of lower tepals the strands of the cortical system anastomose to produce a seemingly irregular reticulation. From this however three traces usually enter each of the lower three tepals and in these the lateral traces in particular bifurcate several times near the base to produce the major veins. Occasionally the midvein of one of these lower tepals may arise in the stele, the strands of which at this level also tend to anastomose. Whether a trace has come from stelar or cortical system, it could be regarded as a branch from another which continues to ascend as part of the cortical system. The three higher tepals receive their vascular supply in a comparable fashion. A pair of traces from the cortical system seem always to provide lateral veins although the midvein in most cases originates in the stelar complex. As it passes through the cortical system this latter trace produces one or perhaps two short branches which join strands of the cortical system (fig. 2.4).

c. Androecium

Above the insertion of tepals, strands of both

stelar and cortical systems resume more or less straight courses as they ascend the axis although there is some degree of reticulation in both systems. There are between five and eight strands in the cortical system and 15-20 in the stele. Almost all stamens receive one trace which originates as a branch either of a cortical or of a stelar strand, or is an entire stelar strand. In the two latter cases, as the strand passes through the cortex as a stamen trace it produces an ascending branch which becomes part of the cortical system (fig. 2.5). Throughout the androecial portion of the floral axis there is some multiplication of strands in the stelar system although evidently this only compensates for those lost to stamens and the cortical system. At the level of the upper stamens there are usually 12-15 strands in the stelar system and, because of the supplementation from the stelar system, a similar number in the cortical system. Occasionally one or two of the upper stamens receive three traces in which case the midvein comes from the stelar system and the laterals from the cortical system (fig. 2.5). As in other cases where a trace from the stelar system runs to a stamen, these potential midveins also produce one or sometimes two branches which continue to ascend as part of the cortical system.

d. Gynoecium

Canright (1960) has reported on a study of carpel vasculature in representatives of all genera in the family although Michelia fuscata is treated only very briefly. In fact, in the stipe there is as elsewhere a system of cortical strands as well as the normal stele and these are the direct continuation of the vascular tissue in the androecial region. These 12-15 strands in each system continue with some reticulation in the lower third of the gynoecial region of the axis although more termin-

ally on the shoot the number of strands particularly in the stele decreases.

Each carpel receives three traces. In all except the upper eight to twelve carpels the strand which becomes the dorsal trace departs from the stele as a branch which arises about or just below the level of the base of the carpel to whose vasculature it contributes. In the terminal carpels the dorsal trace is an entire stelar strand. In either case this trace, which is called the "stelar bundle" by Canright, ascends obliquely through the cortex and near the level of the top of the insertion of the appropriate carpel it passes between two cortical strands. At this point it bifurcates, the larger of the two branches so produced descending to provide the dorsal vein of the carpel and the smaller (the "ascending stelar bundle" of Canright) running up parallel to the axis. This latter branch itself shortly bifurcates and each of the two portions contributes to one of the two ventral veins in the carpel. Although the ventral carpellary veins are formed partly from branches whose origin has therefore been in the stele, each also receives a rather stronger component from adjacent, but at the particular level, quite independent cortical strands (fig. 2.6).

There is some variation to this general pattern. Firstly while it is usual for the two branches of the ascending stelar bundle to fuse with branches from the cortical system to make up ventral strands, these ascending stelar branches sometimes fuse directly with the cortical strands, either just above or just below the departure of the branches to carpellary ventrals. Secondly terminal carpels are occasionally vascularized entirely from the stelar system. Thirdly the supply from the cortical system to carpellary ventrals involves,

in the case of some of the higher carpels, the whole of a strand with no branch continuing up in the cortical system. And fourthly (as pointed out by Canright for the whole genus) there is considerable variation in the amount of "dip" of the dorsal trace.

Although there is some sub-division of strands in the stele this does not keep pace with the provision of carpellary midveins and the number of stelar strands falls, especially as the upper portion of the axis is ascended. The uppermost carpels are in fact vascularized by the three or four strands which remain in the stele immediately below them. The course taken by cortical bundles could fairly be described as undulating, adjacent strands being closest together near the departure of ventral traces to a carpel. The departure of whole cortical strands to carpellary ventrals, which frequently occurs with some of the upper carpels however, results in a reduction in number of strands in the cortical system - sometimes to non-existence at the level of the ultimate or penultimate carpel.

v. Vascular Development (fig. 2.7)

The first vascular tissue to appear above the bract is the traces in the lower tepals and the strands of the cortical system with which these are continuous. Conducting elements then appear in higher tepals and later maturing extensions of these comprise cortical strands which join with those running to lower tepals. This junction may be direct but it is more commonly to a ring of vascular tissue which characteristically arises at this stage between cortical strands near the level of insertion of lower tepals. Whether this ring is itself formed by the strands extending down from the upper tepals or whether it is an independent structure is not deter-

mined. The supplies of these upper tepals also tend to be interconnected by a ring of vascular tissue and this appears at the same time as vascular tissue is appearing in the lowermost stamens. Again it does not seem possible to decide whether or not the ring is in fact formed by the bases of the stamen traces or is an entity without these. Vascular tissue seems to first become visible at the base of each stamen and from here matures downwards to form the cortical system in this portion of the flower, and in the other direction to form the vasculature within the stamen. It will be noted that the true stele of the adult flower is not yet present although this soon begins to appear - at the same time in fact as traces in upper stamens and the cortical system with which these are associated. At first the stele consists of a few (6-12) strands only, each one of which terminates either in the midvein of a tepal or the supply to a stamen. Carpellary dorsal traces appear next and only at this stage does the stele in lower regions come to consist of the number of strands evident at maturity. Virtually simultaneous appearance of dorsal bundles in carpels and the stelar system in general prevents the establishment of a positive impression as to whether or not the stele is made up largely of an aggregation of the basipetal extensions of carpellary dorsals. After carpellary dorsals and the stele have become distinct, carpellary ventrals appear together with the cortical system with which they are associated. Vascular tissue comprising carpellary ventrals appears first in the carpels and its subsequent extension into the cortex ultimately involves fusion with a similar cortical extension of the ventral bundle of a carpel lower on the axis. The cortical strands so formed are essentially straight and parallel and only assume their undulating course as the flower further enlarges.

Of the vascular tissue concerned with the supply to appendages the last to appear is the ascending stelar bundles. Apart from the ascending stelar bundles there seem therefore to be three stages of formation of the floral vascular system. The first involves the cortical system in perianth and androecial regions, the second the stele throughout, and the third the cortical system in the gynoecial region (fig. 2.7).

vi. Carpel Phyllotaxis

Only a few comments need be made on carpel phyllotaxis in Michelia fuscata as this has been thoroughly investigated by Tucker (1961). She found that carpels were spirally arranged in several fashions. Seven, eight and ten parastichies were observed in ten flowers and dorsal traces in each parastichy were observed to arise from the same vascular sympodium. Tucker's drawings illustrating phyllotaxis pattern were evidently compiled from a large number of camera lucida drawings of serial transverse sections of mature flowers. Because it is believed that phyllotaxis can at least sometimes quite accurately be determined from examination of a single transverse section near the apex (Skipworth 1962) an attempt was made to verify Tucker's findings by this method. Even though very young floral shoots were investigated this was not found particularly satisfactory, largely because only relatively few carpels are visible in any one section (fig. 2.8). It does seem however that the vascular pattern formed by the dorsal traces and the stelar strands with which they are associated is comparable with the pattern in many vegetative shoots (Esau 1943, Girolami 1953, Snow 1955, Balfour and Philipson 1962). As several of the phyllotaxis fractions recorded by Tucker (2/7, 3/7, 3/8, and 4/10) are associated both with dext-

rorse or sinistrorse trace union and dextrorse or sinistrorse ontogony a picture more complex than most vegetative shoot apices is presented.

Some features not remarked upon by Tucker seem worthy of consideration. Not all flowers were found to be regular in their phyllotaxis although, as in most stems with spiral leaf phyllotaxis, there were usually two series of contact parastichies. In this instance dorsal trace connections run through one of these two. Tucker did not consider the supply of ventral traces in relation to phyllotaxis and, although it may rarely do so, ventral trace union does not usually follow the same series. Ventral carpellary veins of a given carpel are in fact usually linked with those of the contact series not followed by dorsal traces (fig. 2.9) although apparently with considerable irregularity.

3. MAGNOLIA STELLATA

1. Introduction

A member of the largest genus in the family, Magnolia stellata is, in New Zealand, a deciduous shrub about three metres tall which produces an abundance of showy flowers in August-September. Leaves are generally obovate, between four and eight cm. long, dark green above and paler below. The large stipules are conspicuously hairy. Flowers are solitary, terminal, and from six to ten cm. across.

ii. Anatomy of the Vegetative Stem

In most respects anatomy is very similar to Michelia fuscata. Between 40 and 60 normally oriented bundles comprise the eustele in the primary stem and once more there are prominent areas of sclerified tissue, especially in the pith and outside the phloem. Near the apex, where nodes are very short, as many as three concentric "steles" may be apparent in one cross section. The central one of these is the true stele while the outer two each comprise a ring of strands passing out to leaves and associated stipules. The suggestion is that subsequent elongation of each internode involves mainly the tissue in the upper region. A situation such as that described in Rhododendron magnificum by Philipson and Philipson (1968) where leaf traces run in the cortex parallel to the stele for a substantial part of the internode would presumably be arrived at if elongation were immediately above the node. It could be noted however that it is possible that elongation in this region may

be involved in the establishment of the cortical system in the Magnoliaceous flower. In the vegetative stem traces to leaf midveins do not in this case depart conspicuously higher than the single stipular trace and it is noticeable that several traces, usually five, each of which arises independently, separately enter each petiole.

iii. General Floral Morphology

Although there are no genuine bracts, the leaf nearest the flower is always small. All floral appendages appear to be spirally arranged. Perianth members, of which there are 12-18, are not distinguishable as sepals and petals, all being of ligulate shape and from two to five cm. long. After anthesis they become reflexed and their margins recurved. There are 20-30 stamens and a similar number of carpels. Carpels are unilocular, bi- or triovulate, but in Palmerston North at least, only one seed at most matures in each carpel. They are separate and densely packed although as in Michelia fuscata their adaxial surface is fused to the receptacle at its base.

iv. Vasculature of the Mature Flower (fig. 2.10a)

a. Pedicel

Below the flower the anatomy of the uppermost vegetative node is clearly different from the others. The traces to the leaf concerned depart from the stele further below the leaf than in other cases and therefore run a greater distance in the cortex before passing out to the appendage. Eight to ten traces are usually involved as is the case lower down. There are three major differences from ordinary leaf nodes however. First, several cross connections between traces are evident as these traces pass through the outer cortex. Second, from leaf (and stipule) traces, or from connections between them, branches

are given off and these continue to ascend the cortex. Third, fewer traces enter this leaf and its stipule. That is, two or three of the traces do not in fact enter the appendage but remain as part of the cortical system. Occasionally there occurs an upward branch from a trace to the penultimate vegetative leaf and this passes up in the cortex to unite with a trace to the uppermost leaf. All traces to the uppermost leaf originate from the stele at the same level. This is also the case with the supply of the penultimate leaf. Above the uppermost leaf there is a cortical system consisting of eight to twelve strands and a stelar one of about 40 strands and this situation obtains through the whole of the internode below the lowermost tepal. Most of the cortical strands originate as upward branches of leaf (or stipule) traces while occasionally others arise from the stelar system at the level of departure of the leaf.

b. Perianth

There is substantial development of cross connections between cortical strands these occurring regularly between the nearest two strands to the point of insertion of a tepal. Usually three traces are involved in the supply of each tepal. In most cases these are branches either from vertical strands or from connections between these strands. Usually in fact, the junction of a trace with the cortical system is at or near a point at which a cross connection joins a vertical strand. Not infrequently a trace from the stele runs across the inner cortex to join or to pass through the cortical system finally to provide a midvein. Many tepals therefore receive a pair of lateral traces from the cortical system and a midvein from the stele. Others receive all traces from the cortical system (fig. 2.11). Eight to twelve cortical strands are usually evident below the perianth while 15-20 can be

seen immediately above. The reason for the increase is not obvious at this stage.

c. Androecium

Although there is some undulation of cortical strands in the androecial region of the axis, these do tend to maintain approximately parallel courses as they ascend. Strands are occasionally linked by cross connections. The stele in this region consists of 30-40 strands. Characteristically one trace departs from the cortical system and runs to each stamen although just before entering the stamen each trace divides into three. Some stamens receive their supply solely from the stele, the trace involved in most of these cases linking as it passes through the cortex with cross connections between cortical strands. The supply from the stele to a stamen involves either a whole strand or a branch of one. Instances were observed where one or more of the upper stamens received three traces - a midvein from the stele and two others as branches from adjacent cortical strands.

Strands in both systems continue without substantial alteration into the gynoecial region of the axis.

d. Gynoecium

Throughout the gynoecial portion of the axis, strands in both the cortical system and the stele are regularly disposed with respect to each other. Each cortical strand follows an undulating course which over short distances brings it very close to, or in lower regions results in its temporary fusion with adjacent cortical strands. That is, the cortical system comprises a regular lattice consisting basically of 12-15 strands. Between androecial and gynoecial regions from 30 to 40 strands comprise the stele and throughout the latter region these also follow undulating courses involving temporary fusion with adjacent strands although with less regularity than

is evident in the cortical system. Carpels receive three traces very much after the fashion described for Michelia fuscata. The dorsal trace originates from a stelar strand and the two ventrals as branches from adjacent strands of the cortical system. At the level at which the base of the carpel departs from the axis the ascending stelar bundle departs from the prospective dorsal trace, briefly runs parallel to the axis, then bifurcates with each of the branches so produced joining one of the two ventral traces of the same carpel. These ascending stelar bundles, either before or after their bifurcations, provide branches to ovules, while the ovary wall is vascularized by branches from both these and the ventral traces. There seems no variation in this pattern, even near the apex - a difference from Michelia fuscata.

v. Vascular Development

The first vascular tissue to become visible is the strands of the cortical system in the region of the perianth together with the lateral traces of perianth members. The stele in this region appears at approximately the same time as the cortical system in the androecial region, while carpellary ventrals and the gynoecial cortical system together with the carpellary dorsals and the stele of both gynoecial and androecial regions, appear virtually simultaneously.

In the perianth, vascular tissue first appears near the base of the lowest members and evidently matures downwards as cortical strands and into the appendages as lateral traces. Cortical strands and the associated lateral traces of tepals more distal on the shoot appear a little later and join the strands already established near the point where the strand begins to run out as a trace. At first there are no cross connections between

them although these soon do appear. In many cases they seem clearly to be extensions of midveins the first sign of which is also at the base of tepals. The stele at this stage is composed only of strands which terminate as tepal midveins although the question as to whether or not these strands are formed before midveins or are in fact basal extensions of midveins could not be determined in the material examined.

Stamen traces make their appearance in a manner strongly comparable with tepal laterals. Traces first become visible near the base of the stamens and appear to mature into the cortex, then parallel with the axis, until each unites with one lower down thereby forming the cortical system in this region. The inward and downward extension of the lowermost stamen traces in most cases joins the cortical system of the perianth although some join traces of tepal midveins which have originated in the stele. This explains the higher number of cortical strands in the androecial region than in the perianth region. Cross connections between cortical strands appear later, usually but not always in association with one of the stamens possessing a supply from the stele. The lateral traces in the stamens, which join the main staminal trace near the base of each appendage, appear much later, while the undulation of cortical strands in this part of the axis also becomes evident much later - probably following the cessation of apical growth.

As is the case with stamens and perianth the vascular supply of lower carpels matures before that of upper carpels. Dorsal traces are visible in each carpel before there is any connection between them and stelar tissue, and it is again true that at any one level there are only as many stelar strands as there are carpellary dorsals connected to the stele above that level. Observations

suggest strongly that the maturation of a dorsal trace into the stele occurs contemporaneously with the apical maturation of a stelar strand, and that the two join some 5-10 plastochrons below the carpel in question. Unlike the situation in Michelia fuscata and lower in the flower in Magnolia stellata, strands appear in the cortical system before carpellary ventrals. When the latter traces do appear the undulations of cortical strands are not as marked as they are at maturity and certainly in no case are adjacent traces fused. As in Michelia fuscata the ascending stelar bundle is the last to appear apart from various traces within the carpels.

4. OTHER SPECIES OF MAGNOLIA

In the course of this study less detailed observations were also made on three other species of Magnolia, M. soulangiana, M. grandiflora and M. campbelli and some differences from the situation described in M. stellata are worthy of note.

There are different numbers of strands in both cortical and stelar systems in the four species and only in M. stellata are there more than eight tepals. Nodal anatomy of tepals in M. soulangiana, M. campbelli and M. grandiflora is in fact more similar to that of Michelia fuscata than is that of Magnolia stellata. In each of these three species examined more briefly, the stelar system contributes much more to the vasculature of stamens than it does in M. stellata. In M. soulangiana for example lower stamens are supplied solely from this system, a single strand and single trace with a pair of branches near the base of the stamen being involved in each case. In this species, higher stamens almost invariably receive three traces - a midvein from the stele and laterals from the cortical system (fig. 2.10b). Three traces are received in this latter fashion by most of the stamens of M. grandiflora.

In these three species there seems to be more constancy with respect to the gynoecial region. The most noticeable variation seems in fact to be the extent of the undulation of cortical strands at maturity. M. campbelli is very similar to M. stellata in this respect but in M. soulangiana partial fusion between adjacent strands

occurs near the apex rather than the base of the gynoecial region. In M. grandiflora there is at anthesis a complete reticulation throughout.

5. LIRIODENDRON TULIPIFERA

1. Introduction

Well known as the tulip tree, Liriodendron tulipifera is large (upwards of 25 metres high) and deciduous. Leaves are alternately arranged with a 6-18cm. long lamina and a 4-10cm. petiole. They are rather irregularly three-lobed with a somewhat truncate apex and are glabrous, simple and stipulate. Flowers are terminal and 4-8cm. across. As has already been indicated, Liriodendron, a genus of only two species, has on various grounds, cytological, anatomical and morphological, usually been regarded as an advanced member of the family and one standing rather apart from the rest.

ii. Anatomy of the Vegetative Stem

General anatomy is similar to that of Michelia fuscata and Magnolia stellata with between 30 and 50 strands comprising the stele prior to the advent of secondary thickening. Usually six traces depart from approximately equidistant points round the stele and these run almost parallel into the base of the petiole in which they provide lateral veins. Soon after their departure from the stele most of them produce a branch which enters the associated stipule.

iii. General Floral Morphology

Apart from the fact that it is slightly smaller there is no suggestion that the leaf nearest the flower is in any way unusual. In common with the situation

in other members of the family, stipules from this node enclose the flower during development. The flower has nine separate perianth members which appear to be spiralled and which are clearly distinguishable as three sepals and six petals. Each is 4-8cm. long by 2-4cm. broad and of oval or obovate outline. Sepals are readily distinguishable by their much broader base. All perianth members are pale green to pale orange-pink and all display a palmate type of venation. There are 30-45 stamens each from two to four cm. long. The filament is thin and rarely more than one cm. long while the connective is not obvious and does not extend beyond the two cm. long, laterally disposed anthers. Carpels, 25-40 in number, are also spirally arranged, free, unilocular and biovular. The adaxial surface of the ovary is evidently fused to the receptacle. At anthesis the style, which is winged and at least two cm. long, is tipped with a rather small, terminal stigma. After fertilization carpels become dry and remain on the floral shoot for a year or more during which time the aggregation conveys a strikingly strobiloid appearance.

iv. Vasculature of the Mature Flower (fig. 2.10c)

a. Pedicel and Perianth

Immediately above the uppermost vegetative node on the floral shoot, usually twelve strands depart from the stele to comprise the cortical system in the internode below the lowermost sepal. Six of these tend to be larger and to alternate with the six weaker strands. These twelve strands run straight and maintain approximately parallel courses until slightly below the level of the sepals at which a more or less horizontal strand runs between them. From this ring of vascular tissue some 25-35 traces depart independently of each other.

Six to ten of these run to each sepal and a further five or six extend up the axis as part of the cortical system.

In this region the cortical system is supplemented by a further five or six strands which pass out from the stele leaving this about the level of (or just below) the insertion of sepals. There is a tendency for these ten to twelve strands to be connected or partially so at the level of departure from the cortical system of petal traces although this is not always the case. Each petal receives from five to eight separate traces all from the cortical system and within the appendages, these traces divide rarely as they pursue slightly diverging courses. Some petals appear externally to be inserted above others although all traces to them depart from approximately the same level. Usually some of these traces are much stronger than others although this seems irregular and there is no obvious midvein. Neither is there any suggestion at this stage of regularity of relationship between perianth traces and cortical strands other than that in most instances one of the traces, which has arisen from the stele at the level of the sepals, is associated with each petal. As traces depart from the cortical system, most do so as branches of strands the larger portion of which continues to ascend as part of the cortical system above the level of the petals.

b. Androecium

In the androecial portion of the floral axis as elsewhere in the flower, cortical and stelar systems are concentric. Near the base of this region there are ten to twelve cortical strands which are upward extensions of the cortical system of the perianth region although they are present in the form of a complex and irregular reticulation which in fact obtains throughout the androecial portion of the axis. Above the lowest stamens, the

cortical system is supplemented by five to eight strands which have originated from the stele at approximately the level of insertion of petals and which run diagonally up and out through the cortex. Other strands leave the stele at irregular intervals and also join the cortical complex or perhaps pass through it as they run to stamens. Stamens all receive three traces which in most cases arise close together although the origin of the three is quite separate. The precise contribution to each stamen made by the two elements of the cortical system (i.e. the residual system extending up from lower regions and the strands originating from the stele at or above the level of the petals) cannot be determined with certainty at this stage. Since only the former component is usually present at the level of the lower stamens, these stamens must be vascularized by this component. Throughout the androecial portion of the axis, the stele consists of some 12-15 strands which are generally straight although there are occasional anastomoses and bifurcations.

c. Gynoecium

Immediately above the upper stamen, 12-15 strands emerge from the cortical complex of the androecial region and these follow undulating courses to the apex. In some instances, the undulations of adjacent strands cause them to come into close association or in contact over short distances this being especially noticeable in older flowers. Stellar strands, of which there are also 12-15, follow straighter courses although in most flowers there are several instances of dichotomies in this region. Carpels each receive three traces after a fashion strongly reminiscent of Michelia and Magnolia. The dorsal vein either originates as a branch from a strand of the stele or comprises an entire stellar strand. This latter fashion is the rule for the more terminal carpels although

it also occurs more rarely much lower in the gynoeceium. As they pass between adjacent strands of the cortical system, the potential dorsal traces each give a branch which briefly runs parallel to cortical strands (the ascending stelar bundle) then passes out to the carpel as a single strand. This provides the vascular supply to the ovules. The ascending stelar bundle is not connected to the cortical system or to carpellary branches originating in this system as it is in each of the other two genera that have been examined. The adjacent cortical strands between which the dorsal trace has passed each provide three or four separate traces which run in the carpel wall. It is doubtful whether or not the highest of these to any one carpel (which ultimately run near the ventral midline, presumably as ventral traces) are any stronger than the others.

v. Vascular Development

Above the uppermost leaf the first vascular tissue to become recognisable is portions of strands in the cortex near the base of each sepal. As they mature, these strands run down and towards the middle of the shoot and at the level of the uppermost leaf they can clearly be seen to comprise part of the stele. The traces in each sepal join these strands near their points of initial appearance although the course of sepal traces is first straight into the cortex along a shoot radius at right angles to the axis, then in most cases tangentially in the cortex in the same horizontal plane to link up with other traces of similar origin and finally with the original strands (fig. 2.12). Vertical connections in the cortex between traces to sepals and those to the uppermost leaf (or associated stipules) appear a little later. The supply to lower petals appears appreciably after that to

sepals though in a virtually identical fashion. That is, a strand from the stele near the level of sepal insertion, which extends up and out, is established. In the cortex near the base of each of these petals, this strand bifurcates each branch running tangentially in the cortex and dividing two or three times to provide petal traces. Vasculature of the upper petals arises in a less regular fashion although apparently as a result of a third burst of activity. Both the disposition of traces at anthesis and the order of initiation therefore suggest three distinct perianth whorls. Strands in the cortex between each whorl, and the connections in the cortex between supplies of adjacent perianth members, each appear after the establishment of the supply from the stele. Additional traces also appear in the sepals and petals and these ultimately join established vascular rings although there seems no direct association between these and the developing cortical system. While the vascular supply to upper petals sometimes does arise as with lower perianth members, the main strand frequently runs to the ring formed in association with lower perianth members rather than to the stele.

Traces in stamens, which again first appear near the base of each appendage, mature downwards either entirely in the cortex (where even at the time of their first appearance they follow irregular courses) or towards the stele. In the former case, which applies mainly to lower stamens, strands associated with stamens join those of the cortical system in the region of the upper petals recalling therefore the situation obtaining with higher perianth members. In the latter instance the strands join the stele at various levels. At first each stamen is furnished with only one trace, the two laterals appearing later and joining the cortical network. By the time these stamen laterals mature the originally separate though

undulating strands of the cortical system have become irregularly fused to form the lattice already described for this region of the flower.

In the gynoecial portion of the floral axis, the first vascular tissue to appear is that of the stele, followed some 10-15 plastochrons later by the cortical system. The appearance of this vascular tissue appreciably before that in the appendages is in marked contrast to other regions of the Liriodendron flower and in fact has not been observed anywhere else in the family. At the time of their first appearance vascular strands are generally straight although minutely corrugated. Subsequently traces appear in the carpels and join the stele or the cortical system, the dorsal trace becoming visible appreciably before any others and first appearing at the base of the style. This evidently matures mainly basipetally finally to become part of the stele. The ventral and ovary wall traces appear rather later and join the cortical system the strands of which have by this time assumed their broadly undulating courses. As with other species in the family that have been described, the ascending stelar bundle is the last of the major traces to appear.

6. COMPARISONS

The taxa that have been dealt with may now be compared.

1. Bracteole (*Michelia*) or Uppermost Leaf

In *Michelia fuscata* the bracteole receives its midvein directly from the stele and its two laterals from cortical strands which also originate in the stele though much lower down. The strand entering the stipule also originates at this lower level. Ascending bundles which branch from strands as they pass through the cortex, continue as part of the cortical system. The cortical system above the bracteole also comprises strands which have originated at the same level as that of the stipule and bracteole laterals but which have bypassed the bracteolar node. It also contains some strands which have originated in the stele at the level of the bracteole.

The node of the uppermost leaf of *Magnolia stellata* is very similar to that of the bracteole of *Michelia fuscata* except that all traces involved originate at the same level below the node (i.e. the midvein does not arise higher than the others) and that a larger number of traces is involved. A more or less complete ring of vascular tissue runs between strands in the cortex although there is no difference in the composition of the cortical system above the node.

In the origin of traces to the uppermost leaf, *Liriodendron tulipifera* closely resembles *Magnolia stellata* and the traces again tend to be connected by a ring of vascular tissue. The number of traces to the leaf differs

and the fact that cortical strands do not usually extend up from the ring is a further point of contrast.

11. Perianth

An anastomosis of strands and the existence of vascular rings complicate the picture in the cortex in the region of the perianth and at anthesis vasculature is more variable than it is at the uppermost vegetative node. In Michelia fuscata lower perianth members are usually vascularized entirely from the cortical system while with the upper members the midvein comes from the stele and the two laterals from the cortical system. In Magnolia stellata it can only be said that sometimes a stelar strand provides the midvein while the cortical complex provides either all traces or the laterals. Other species of Magnolia tend to resemble Michelia fuscata more closely in that lower perianth members are vascularized from the cortical system while upper members possess midveins associated with the stele. In Liriodendron it is lower perianth members (sepals) which tend to display a midvein connection to the stele, the other traces of each sepal joining a ring which apparently comprises part of the cortical system. The origin of traces to upper perianth members (petals) is sometimes similar to sepals but more frequently all traces enter from a ring connecting cortical strands.

In Michelia fuscata and Magnolia soulangiana the cortical system and the traces with which it is associated develop before the stele and its associated traces. There are suggestions that the cortical vascular rings are formed as a result of tangential connections between traces to different perianth members and that cortical strands mature down from these rings either to join a lower ring or simply as pedicel strands. Certainly these

rings are ultimately in direct continuity with cortical strands which extend above and below them. In the examined representatives of these two genera the midveins of higher perianth members appear later, join the vascular ring where one is present, and extend in to comprise part of the stele. The development of traces associated with sepals as described for Liriodendron tulipifera provides a rather clearer picture. The suspicion that vascular rings are formed by tangential connection between traces to different sepals is endorsed and in this case from portions of the ring corresponding to each sepal, one trace extends into the stele. Cortical elements parallel to the axis appear later and connect directly with the ring. Lower petal traces have similar connections although as has been suggested, the strand corresponding to that which extends from each sepal to the stele often links in this case rather with the cortical ring below it. Other cortical strands appearing later also link the two rings. The traces of upper petals seem not to be associated with a ring and evidently connect only with cortical strands.

iii. Androecium

The vasculature of stamens at anthesis is also variable in each of the three genera. The cortical system in each is an irregular network from which stamen traces arise although there is a strong suggestion that the stele provides, in varying degrees, strands which supplement the cortical system and which also provide stamen traces. Stamens in Michelia fuscata typically have a single trace; in Magnolia, Liriodendron and occasionally in Michelia fuscata (upper stamens) there are three traces to each stamen. In either event a single trace appears first in each stamen and matures downwards to become part of the cortical system or of the stele. Where they are present,

lateral stamen traces always link with the cortical system while on the other hand contributions from the stele always become a stamen midvein or a solitary stamen trace. It has been observed in Magnolia soulangiana that the ascending branch from the midvein trace which effectively becomes part of the cortical system, gives rise to stamen midveins higher on the axis (fig. 2.10b). This situation was believed by Skipworth and Philipson (1966) to be typical of three-veined stamens in the family although it was pointed out that "the vascular supply to stamens is variable and in no case easy to observe."

iv. Gynoecium

From the point of view of their vascular supply, the most constant of the floral appendages among the genera examined were the carpels. In each case the dorsal trace emanates from the stele as a single strand, while the ventral supply always involves two traces from independent cortical strands. At anthesis adjacent cortical strands may be fused over parts of their total length but in each of the cases examined they were clearly independent earlier in their development. The ascending stelar bundle is always the last to appear and whilst there is some variability in its course at anthesis, in each of the three genera it does always follow the same general direction and never extends beyond the one carpel.

v. Summation

There is little doubt that throughout the flower there are two concentric conducting systems and that the stelar system supplements the cortical in many places - less regularly in lower whorls but particularly consistently in each carpel. The situation found in the supply to each carpel where the cortical system provides

the ventral traces (laterals) and the stele the dorsal trace (midvein) is one which occurs more frequently than any other among lower appendages. This arrangement has been noted in the bracteole of Michelia fuscata and if not with absolute consistency in the supplies to the perianth and stamens in each of the flowers examined. Where it is possible to trace a strand from stele to appendage (i.e. where the identity of the strand is not lost in the cortical reticulation) it always contributes to a midvein and conversely these stelar strands never directly become lateral veins in the appendage. Lateral traces (and admittedly some midveins too) seem always to be connected to the cortical system. However, closeness of relationship between cortical and stelar systems is exemplified during development of sepal vasculature of Liriodendron. Here the ring of vascular tissue in the cortex, which is like the cortical rings so frequently observed in the family at this level, and which in this case provides all of the major traces in each perianth member, is at first connected only to the stele. It could even perhaps be argued that such rings should therefore be regarded as part of the stele. However they clearly exist in the cortex and subsequently become continuous with cortical strands extending above and below them. Although in this instance the stele does not provide only midveins, evidence from perianth trace development elsewhere in the family suggests that at least sometimes lateral appendage traces are continuous with vertical strands before the ring is developed and therefore before there is any connection with the stele. Moreover in the case of higher perianth members even in Liriodendron, the first formed strand associated with a developing appendage often joins a vascular ring associated with a lower appendage rather than the stele.

Cortical and stelar systems and the traces with which they are associated make their appearance at various and differing rates in the flowers examined. One appears earlier at lower levels and frequently the other higher on the axis. It appears that there is some tendency for traces developing basipetally to join whichever system is most extensively developed at the time of their maturation.

7. DISCUSSION

(With Particular Reference to the Cortical System)

In his account of the floral vasculature of Magnolia stellata, a species which he clearly considered to be typical of the family, Melville (1963) made several statements the validity of which can be questioned in the light of the present findings.

He described the cortical system as beginning "a little below the flower at one of the foliage leaves." He went on to say: "Here, traces pass upwards within the cortex from each of the two lateral nerves of the triple leaf trace These cortical strands link up with the lateral trace of the leaf or scale leaf next above. This in turn gives rise to a similar pair of traces . . . and so on upwards through the perianth. Often the scale leaves and lower tepals are without any direct connection to the central stele." The present account raises doubts as to the accuracy of Melville's observations with respect to Magnolia stellata, and certainly the origin of the cortical system in Michelia fuscata is different. Here cortical strands clearly originate from the stele in an internodal or even nodal position. Moreover, some of these by-pass the bracteolar node and some originate from the stele at the node, a feature also observed in Magnolia stellata. In addition, some cortical strands are upward extending branches of traces to stipules, a feature also noted in both Magnolia stellata and Liriodendron.

An important criticism of the interpretation of the bracts in terms of the Gonophyll theory rests on the fact

that in Michelia fuscata a lateral bud occurs in the axil of a bracteole which is inserted above the point of origin of the cortical system. "This being so,the cortical system of the pedicel cannot be explained in terms of fusion of branch systems associated with the axils of appendages" (Skipworth and Philipson 1966). As there is no reason to suppose that the cortical system of the pedicel is not directly continuous with, and of the same morphological nature as that of the flower, all aspects of the Gonophyll interpretation of the Magnoliaceous flower, based on fusion to the axis of sterilized branches, must be regarded with grave circumspection.

According to Melville's interpretation strands ascending in the cortex must originate as a single branch (which shortly bifurcates) from the supply to a bract or equivalent appendage. Clearly therefore two strands may be envisaged as ascending from one leaflike appendage but not more. Moreover, in Magnolia stellata as well as in Michelia fuscata and Liriodendron, traces to stipules also frequently provide ascending strands - a situation which would in itself presumably require further appendages. Solitary leaves in this family can surely not be equated with a whorl of appendages as would seem to be required by Melville's interpretation.

Melville interprets a pair of ventral carpellary traces as arising from the dorsal trace of the same carpel and therefore originating essentially from the stele. His contention is that the bifurcating ascending stelar bundle, whose branches indeed link with the appropriate carpellary ventrals in Magnolia stellata (and also in Michelia fuscata), is the base of a typical fertile branch. By such an interpretation, each carpel is a complete gonophyll, more specifically a gynophyll. In this structure the dorsal trace is the midvein of the

subtending leaf and the ascending stelar bundle and terminal portions of the ventral veins, the fertile non-foliar portion. In all known cases, including Magnolia stellata, however, the ascending stelar bundle appears markedly after distinct and separate establishment of connections between the dorsal trace and the stele and between ventral traces and the cortical system. Moreover, in Liriodendron the ascending stelar bundle supplies the ovules directly and never joins ventral traces.

According to the gonophyll interpretation, perianth members and bracts are both leafy portions of gonophylls but carpels include also the associated fertile shoots. It has already been pointed out that the findings of the present inquiry suggest that the vascular supply of bracts, perianth members and carpels are strongly comparable and that each typically has a midvein derived from the stele and laterals from the cortical system. This similarity in turn suggests morphological equivalence of at least these three classes of appendage and therefore supports the classical interpretation of the carpel as a lateral appendage of the same order as a foliage leaf.

In order to explain the continuity of the cortical system in the gynoeceal region of the axis, Melville evokes the concept of "capture" of some strands by others. "Only a few of the ovules on the fertile branches of the gonophyll could be enclosed by its blade. Unwanted sterilised branches passed on upwards between the enfolding gonophyll blades. When these sterile branches fused with the axis, they anastomosed with their neighbours above." Anastomosis of fused branches in this fashion - "a form of development unknown in the ontogeny of plants" (Skipworth and Philipson 1966) - is a needlessly complex assumption if the findings of the present work are accepted. The explanation that ventrals are supplied by

the cortical system and dorsals by the stele involves in fact the expectation that the cortical system would be continuous. Moreover, there seems no reason why the explanation clearly demonstrated for the pedicel should not also apply to the gynoeceium.

For two reasons mention of stamens has been avoided in this discussion so far. This is primarily because Melville's explanation for their vasculature evidently varied quite considerably and also because the present findings do not perhaps present as conclusive a picture of the essential nature of stamens as is provided for other floral appendages.

In his earlier paper, Melville (1960) clearly regarded stamens as being produced on fertile branches which arose in association with an upper tepal but which were fused with the main axis. Some portions of his 1963 paper are also to this effect. Melville's fig. 25:8 (1963) for example shows a tepaline androphyll with fertile branches extending throughout the androecial region, and on page 11 it is stated that cortical "traces belonging to the upper tepals give rise to a succession of short branches externally" each of which "forks twice to give rise to the triple trace of a stamen. The tepals therefore are androphylls bearing two fertile branches..." Yet on page 12 of this same paper Melville wrote: "In the androecium the microsporangia fused with their subtending gonophyll blades but retained the triple nerve system of the foliar portion." By the earlier interpretation the gonophyll blades were the tepals but according to this second interpretation each stamen had its own blade, evidence of which remains as the three nerves. In the last paragraph on page 12 it is each stamen which is in fact referred to as an androphyll. Earlier on the same page Melville stated: "Occasionally in the androecial

region a trace passes inwards and downwards to join the central stele . . . in the manner of a leaf trace. Such traces apparently represent the midvein traces of androphylls the blades of which have been suppressed." It is difficult to avoid the conclusion that Melville has answered the question as to the involvement of blades with individual stamens in three conflicting ways which could be translated as 'never' 'always' and 'occasionally.'

It can only be said that the results of the present inquiry do suggest that where stamen supply comes from three distinct points (as it does in Magnolia stellata) each stamen is fundamentally equivalent to a leaf. Species characterized by a single stamen trace offer no evidence pertaining directly to the argument although it could fairly be said that if the lateral supply were removed from all stamens in Magnolia stellata, a situation very similar to that found in Michelia fuscata would be arrived at. Furthermore in Michelia fuscata, while most stamens possess a single trace, the occasional higher stamens with three traces do receive these in the fashion characteristic for three trace stamens and for other appendages, i.e. a median trace from the stele and two laterals from the cortical system.

Based on the initial appearance of traces, it is submitted that with respect to the Magnoliaceous flower, this inquiry supports the classical interpretation whereby all floral appendages are of leaf rank. The basic assumptions of the Gonophyll theory are shown not to be supported by evidence of developmental anatomy.

III GNETUM

1. INTRODUCTION

Long regarded as Gymnosperms with some Angiosperm features, the Gnetales comprise a small taxonomically isolated and rather diverse group. Many investigators have attempted to assess their phylogenetic position although Melville (1960) seems the first to have placed especial reliance on the course of vascular bundles in reproductive structures. His conclusion was in fact that vascular anatomy in Gnetum is very similar to that in the Magnoliaceae and that "there is at last evidence to link the Dicotyledons with the Gymnosperms through their reproductive organs." In their monograph on Gnetum Maheshwari and Vasil (1961) did include reference to floral vasculature and for the purpose of comparison with Magnoliaceous floral anatomy, their description seems to require a little amplification but mainly confirmation.

Gnetum is dioecious although strobili generally display evidence of both male and female parts with one or the other being abortive. The whorls of flowers⁺ which are borne along the axes of strobili, are subtended by collars of bracts.

Preserved material of Gnetum gnemon was available for the present investigation.

⁺The term flower is used with respect to Gnetum because the structure has been directly compared by Melville with an Angiosperm flower. This usage although convenient here is not found extensively in modern literature.

2. FLORAL VASCULATURE

(Fig. 3.1)

From six to ten strands ascend the axis of the strobilus. They maintain approximately parallel courses although there is some anastomosis between them at nodes. At these nodes, traces to bracts and flowers depart from the stele. One conspicuous trace runs to each bract although this divides several times within the bract itself. In megasporangiate strobili the vascular supply to each flower sometimes arises as an upward branch from the bract trace but more frequently it comes from the axil of the trace or from the stele slightly above this point. Maheshwari and Vasil (1961 fig. 39E) have illustrated a case of dual origin from both the bract trace and the stele although such instances were not observed in the present inquiry. In the cases seen, the single trace sometimes produced small branches to abortive flowers, then distally divided in a variety of fashions to produce the usually two traces which enter the perianth, and the one to the ovule.

Thoday (1911) produced figures which illustrate that the vascular supply to female flowers and associated bracts is of considerable variety in the genus and these suggest that G. gnemon may represent one of the simpler types of floral vasculature. Three species are figured by Thoday and in these additional traces, evidently of inverse orientation, arise from the bract trace and run to the ovule. These same species evidently also display direct vascular connections to the stele.

Vascular supply to flowers in the microsporangiate strobilus is similar. In G. gnemon each bract receives an independent trace while a second trace, which leaves the stele slightly higher, divides several times to provide the vascular supply of male (and abortive female) flowers associated with the bract. Maheshwari and Vasil (1961) figure G. ula, a species where the trace to each flower departs from the bract trace rather than from a stelar strand while Pearson (1912) has illustrated an inversely oriented trace linking the stele directly with each ovular trace in G. buchholzianum.

3. COMPARISON WITH THE MAGNOLIA FLOWER

It is clear that Melville's interpretation was based on the simple case such as Gnetum gnemon where the supply to flowers originates on the bract trace. His postulation did not utilize the various additional traces to which reference has been made in this account.

Serious fault can not be found with Melville's representation of part of an "androgynous inflorescence" (1963) although there are several standpoints from which his derivation of the Magnoliaceous flower can be criticized.

Melville's representation of Gnetum is in fact an inflorescence while his drawing of Magnolia is of a flower. It is clear that Melville envisages each male flower of Gnetum as being equivalent to a Magnolia stamen and each female flower equivalent to a carpel. However, too much stress should perhaps not be laid on these interpretations as the difficulty involved may be purely one of semantics.

The cortical system of the Magnoliaceous flower comes into being by the divergence of parts of leaf traces from the central cylinder at points well below bracts instead of at the node as in the foliage shoot. Once the cortical system is in being, some of the traces of higher appendages are inserted on this system. In Gnetum, the cortical system does not arise by the premature outward course of the leaf (or collar) traces, nor is a continuous cortical system built up in successive internodes. Melville recognised the second of these differences and

to overcome it drew attention to a peg of vascular tissue in Gnetum. He did not indicate whether this peg was to be regarded as nascent or vestigial from an evolutionary point of view. His suggestion was that the vascular loops between the ovule and the main stele that have been described in some species of Gnetum may represent the fragmentation of a cortical gallery although even if this is so it is unlike anything present in Magnolia.

Melville's interpretation of Gnetum is not inconsistent with the facts although whether Gnetum bears real similarity to the Glossopteridales, a group of which Melville admitted that "very little is yet known of . . . fructifications," is debatable and outside the scope of the present inquiry. For the reasons discussed however, the interpretation placed by Melville on Gnetum, does not seem applicable to the flowers of the Magnoliaceae.

IV WINTERACEAE

1. INTRODUCTION

Because of the possession of simple, entire, alternate leaves and flowers in which there appears to be a double whorl of petals, usually numerous hypogenous stamens and simple, distinct, unilocular carpels, the Winteraceae, a small family of woody plants, are usually associated with the Magnoliaceae. Leaves however are exstipulate, wood lacks vessels, and stamens lack a protruding connective, and these features, together with the tendency for carpels to be stipitate, conduplicate and not differentiated into ovary, style and stigma, have resulted in the common current practice of designating Winteraceae as a distinct family. Hutchinson (1921) appears to have been the first to establish the entity of the family and the work of Whitaker (1933) and of Bailey and Nast (1945) lends the distinction support. Hutchinson (1959) recognized eight genera although evidence presented by Bailey and Smith (1942) and Swamy (1949) suggests strongly that one of these, Degeneria, should be regarded as constituting a separate family.

The conclusion of Bailey and Nast (1945) that the Winteraceae is the most primitive living angiosperm family has received support from some taxonomists (e.g. Benson 1957) while Eames (1961) has stated that its members "are outstanding among angiosperm families because they show early stages in the history of many of the characteristic features of angiosperm morphology."

Tucker (1959) and Sampson (1963) have each reported on various aspects of floral morphology in certain species

and the reports of Leinfellner (1965, 1966a, 1966b) are detailed accounts of the development of carpels. The only known accounts which pertain specifically to floral vasculature are those of Bailey and Nast (1943a, 1943b) and Nast (1944) although these are by no means exhaustive and make no reference to development of vascular tissue.

The family is a south west Pacific one, five of the genera in fact occurring in New Caledonia, although one (Drimys) does extend to the Americas. Available for examination were the three species of Pseudowintera native to New Zealand (P. axillaris, P. colerata, and P. traversii), Drimys lanceolata and D. winteri var. chilensis, Belliolum crassifolium and Bubbia howeana. In the description which follows emphasis will be placed on P. axillaris and D. winteri var. chilensis, mainly because fresh flowers and buds could be obtained in almost unlimited supply. In addition, Belliolum crassifolium, which, because of the presence of a cortical vascular system in the flower, appears to stand apart from the rest of the family, will be emphasized separately.

2. FLORAL VASCULATURE

1. General

The conducting tissue of the primary stem comprises a stele of between 20 and 50 normally oriented bundles. Just below each node, three bundles depart independently though at the same level, to provide the traces of a trilacunar node - a feature which seems to be quite constant throughout the family.

Flowers are borne in inflorescences which in most cases are axillary although in Bubbia (and also in Belliolium) they should perhaps be regarded as terminal on short axillary shoots. Bracts which subtend flowers or portions of inflorescences in most cases receive their vasculature in a fashion identical with vegetative leaves, although gaps are not necessarily found in association with each trace. Smaller bracts and bracteoles may only have a single trace. In several species, stem branching appears to be more frequent than subdivision of vascular strands and as a result the number of strands finally entering a pedicel is variable and may be very small. In D. winteri var. chilensis (fig. 4.2f) there are usually between three and six, while in other species examined the number was found usually to be two or three. There is often some dichotomy of these, especially nearer the level of insertion of the perianth so that at the level at which traces are provided to the lower floral phyllomes the number of stelar strands is usually between three and eight.

The calyx throughout the family is entire or lobed

and the traces which enter it do so as branches from stelar strands. One trace is evidently associated with each sepal or calyx lobe although this trace may divide several times as it passes through the cortex. Nast (1944) reported considerable variability in sepal vasculature in all the species that he investigated in the family.

In D. winteri var. chilensis (fig. 4.2f) the most common number of traces departing from the stele and running to each petal is two although petals supplied by three or even a single trace were noted. In P. axillaris (fig. 4.3b) the midvein supply is of dual origin.

Each stamen receives a single trace although again in P. axillaris (fig. 4.3b) this can often be seen to have a dual origin. Not infrequently, a strand departing from the stele divides several times in the cortex and produces traces to several stamens.

In D. winteri var. chilensis one trace, crescent shaped in cross section, enters the base of each carpel although the precise nature of its origin from the stele cannot be determined in the flower. In each carpel, the trace divides into three, a dorsal and two ventrals. Flowers of P. axillaris provide the suggestion of three traces originating separately in the stele and running to each carpel although detail of their origin can better be determined in the bud. In D. lanceolata one, and in Bubbia howeana three traces appear to enter the carpel while three traces enter the single carpel of P. traversii. In the flowers that he examined Nast (1944) reported instances of two, four and five traces entering some carpels. As Nast indicated, most species display a small amount of residual vascular tissue above the carpels.

ii. Belliolum crassifolium (fig. 4.1)

Although anatomy of vegetative nodes is as

for the rest of the family, the genus Belliolum appears to be unusual because of the existence of elements of a cortical vascular system in addition to the normal stele.

The cortical system extends up from traces which run diagonally out to provide the vasculature of the calyx. Most of these calyx traces (from 8 to 15 in total and more than one to each calyx lobe) originate separately in the stele and only after they have left the receptacle do they divide further to produce the complex vasculature of the usually three lobed calyx. From five to nine of the traces each produce an ascending branch and all such branches anastomose extensively. At the level of the insertion of petals the cortical system is joined by traces which originate in the stele. There are the same number of these traces as there are petals and each occurs on the same radius as a petal. From the cortical complex, three traces pass out to each petal. An irregular and weakly developed anastomosis of strands continues in the cortex above the level of petals. Some branches of this end blindly, some provide solitary traces to lower stamens and others fuse with traces from the stele to provide staminal traces. All stamens receive one trace although this may be of dual origin.

There is no evidence of a cortical system above the stamens.

Nast reported briefly on floral vasculature in two species of Belliolum (B. haploopsis and B. burttianum) and indicated the presence of cortical vascular systems similar to, though probably not identical with that of B. crassifolium. He made no mention of cortical system above the petals.

3. DEVELOPMENT OF FLORAL VASCULATURE

This was observed only in D. winteri var. chilensis, P. axillaris and Belliolum crassifolium.

1. Drimys winteri var. chilensis (fig. 4.2)

The first vascular tissue to appear in the floral bud in this species is the supply of the calyx. Whether this matures acropetally or basipetally has not been determined, (fig. 4.2a). Single traces then appear at the base of each petal and differentiate in both directions. Each of these remains quite distinct in the pedicel which therefore might contain at this stage between eight and 20 strands (fig. 4.2b,c). Isolated lengths of vascular tissue then appear in the base of each stamen (fig. 4.2c), mature basipetally, join with other staminal traces and finally as stelar strands, become continuous with the supply to petals (fig. 4.2d). Carpellary traces then make their appearance as three distinct traces entering each carpel and their basipetal maturation results in their joining strands associated with upper stamens (fig. 4.2e). By anthesis, general increase in the amount of conducting tissue, which has been continually occurring lower on the floral axis during earlier stages, has obscured the separate identity of ventral and dorsal traces to each carpel (fig. 4.2f). After anthesis additional traces, each of which may link independently with the stele, often appear in both sepals and petals.

11. Pseudowintera axillaris

There is no evidence to suggest that the sequence of appearance of traces to various whorls in this species is different from D. winteri var. chilensis, although frequently all vascular tissue appears almost simultaneously. At early stages (fig. 4.3a) two distinct traces of quite independent origin, can be seen to comprise the midvein of each petal and many of the stamens clearly also possess two distinct traces. As with D. winteri var. chilensis a larger number of strands can be found in the pedicel at early stages because strands providing traces to petals tend at first to be separate from those associated with the calyx, and once again the three traces to each carpel become fused in the carpel base just before anthesis. There is a tendency for petal laterals to originate as branches from the midvein supply of an adjacent petal. By anthesis there is a substantial development of minor traces running quite randomly between those established earlier (fig. 4.3b).

111. Belliolum crassifolium

Paucity of available material rendered a complete examination of development impossible although a little information has been gathered.

Traces to perianth members and stelar strands with which these are associated become visible first. Traces then appear in carpels and at the same time most or all of the stele above the level of the perianth. Lastly, conducting elements appear in the cortex and in the stamens. Most if not all the cortical system evidently appears simultaneously.

4. COMPARISON WITH MAGNOLIACEAE AND GNETUM

The cortical vascular system present in Belliolum crassifolium immediately suggests flowers of the Magnoliaceae. However, the cortical system in Belliolum appears to originate from points on traces to sepals and does not extend below this level. This therefore presents a situation which circumvents one of the arguments advanced against the Magnoliaceae being derived from Gnetum-like ancestors - the argument that because the cortical system in Magnoliaceae arises below the lower floral phyllomes it can not be regarded as axillary to those phyllomes. However, if the calyx in Belliolum were to be equated with the strobilus bracts (collars), from five to nine members would be required to produce the appropriate number of ascending cortical strands. There is no reason to suspect as many calycine components as this and it would still be necessary to equate stamens with male flowers. Lateral connections between cortical strands are not reported in Gnetum although they are clear in Belliolum where the cortical system is in fact present as a lattice as of course is the tendency in the Magnoliaceae. Petal midveins from the stele and laterals from the cortical system also suggest Magnoliaceae while the origin of stamen traces in some cases directly from the stele and in others purely from the cortical system carries the same innuendo. There is evidence too that in Belliolum the cortical system is supplemented from the stele at various points as it is in Magnolia. The dual origin of some of the stamen traces and the origin

of the vasculature of certain petals from both the stele and the cortical network are situations very difficult to reconcile with the Gnetum interpretation yet are features which again recall the Magnoliaceae. In fact the cortical system of Belliolum conveys every impression of being of the same nature as that of Magnolia but of being relatively weakly developed.

Apart from the absence of a cortical system in members of the family other than Belliolum the general floral vascular system shows similarity throughout. The dual origin of petal and some stamen traces in P. axillaris is perhaps suggestive of some Belliolum floral appendages while the small number of strands in the pedicel is evidently peculiar to all Winteraceae.

In fairness to Melville, it may be restated that he did not cite the Winteraceae in his work. It was chosen here because in accordance with reliable opinion it may well be more primitive than the Magnoliaceae. It is therefore conceivable that it might have bridged the gap between the Magnoliaceae and Gnetum. Only with respect to one feature has this been found a possibility and the other critical objections against close alignment of Gnetum and Angiosperms of the Magnolia type still remain. In fact the paucity of a cortical system in a family supposedly more primitive than the Magnoliaceae could be interpreted as widening rather than narrowing the gap between Gnetum and Magnolia.

V CALYCANTHACEAE

1. INTRODUCTION

The Calycanthaceae contains two shrubby genera, Calycanthus from North America and Chimonanthus from eastern Asia. Calycanthus occidentalis and more especially Chimonanthus fragrans are well known in New Zealand as ornamentals. Members of both genera tend to be aromatic with shortly petiolate, exstipulate, entire, decussately arranged leaves. Flowers are bisexual and solitary, and consist of numerous perianth parts which tend to be spirally arranged, five (Chimonanthus) or approximately twenty (Calycanthus) stamens which are inserted near a receptacle rim, and 15-20 distinct, unilocular, uni- or bi-ovulate carpels borne in a fleshy cup shaped receptacle. The fruit is an aggregation of achenes largely enclosed in the receptacle.

The Calycanthaceae resembles the Magnoliaceae in the possession of spiralled perianth parts in which distinction into sepals and petals is not obvious, and large numbers of carpels and in Calycanthus of stamens. There is disagreement as to whether or not stamens and carpels are spiralled although if they are so, this criterion would also suggest Magnoliaceae. The cup shaped receptacle, the absence of endosperm in the seed, and the consistently opposite leaf arrangement are among the criteria which have however led some authors (e.g. Pollard 1908, Hutchinson 1959) to suggest that the family might more appropriately be considered among the Rosales.

The family possesses an unusual type of vascular anatomy in which four inverted cortical strands originate

in the seedling and persist throughout the length of the vegetative shoot (Fahn and Bailey 1957, Balfour and Philipson 1962). These supply a pair of traces to each leaf, the node of which might indeed be of a primitive type (Marsden and Bailey 1955).

The Calycanthaceae was chosen for investigation firstly because of the suggested phylogenetic association with primitive groups especially the Magnoliaceae and secondly because the relationship of the vascular system in the vegetative stem with that of floral parts seems imperfectly understood. In addition the cortical system does recall the Magnoliaceous flower and it was felt that the one might be more readily understood in terms of the other. The choice of Chimonanthus fragrans and Calycanthus occidentalis for detailed examination was based on the fact that both could be obtained fresh near the University and that these two apparently did provide, to a considerable extent, the range of form in the family. Especial emphasis was placed on the latter species as it appears to be the more imperfectly known.

There is little published work on flowers in the family. Eames (1961) reiterates the findings and interpretations of Smith (1928) who apart from Worsdell (1908) seems to have been the only author to have concerned himself with examination of the whole flower. Schaeppi (1953) paid considerable attention to carpels but his inquiry was apparently aimed at obtaining evidence in support of the theory of the peltate carpel rather than an objective or detailed appraisal of carpel structure.

2. THE FLOWER

(1) Calycanthus occidentalis

There is no marked distinction between leaves and tepals, tepals and stamens, stamens and carpels (fig. 5.1). The question of which should be regarded as lowermost tepals and which as vegetative leaves is largely an academic one although for present purposes the uppermost appendages which are distinctly petiolate are regarded as the uppermost leaves. Above them there is found in most cases a pair of smaller oppositely arranged appendages which are herein designated as bracts. They are of similar shape to the tepals immediately above them although successively higher tepals become at first larger and then again shorter nearer the androecium. What would be generally regarded, again on the grounds of shape, as the two or three uppermost (innermost) tepals have in fact small marginal pollen sacs. Usually about 15 appendages can be regarded as functional stamens in that normal pollen is produced. Inside these there are perhaps a further 15 appendages the general shape of which is that of stamens although without pollen sacs. The innermost of these have a more swollen base and it becomes questionable whether or not these should be regarded as non-functional carpels. Herein, a carpel is regarded as an appendage which contains a cavity (locule) whether or not there are ovules. In fact the outermost eight of the approximately 20 carpels lack ovules and only the remainder appear to be functional.

A single carpel is depicted in fig. 5.2. The style

is two or three times as long as the ovary and while its base is round or oval in cross section the terminal portion is very narrowly oval or concavo-convex in cross sectional outline and almost ligulate in shape. Epidermal papillae comprising the stigmatic surface occur towards the distal end of the carpel on the ventral surface. The extent of this stigma seems variable although usually about half way down the style the ventral concavity becomes deeper and finally closes over. The top of the locule is somewhat extended into the base of the style although there is usually a conspicuous styler canal. Two ovules which arise one above the other are attached to either side of the ventral midline. They are clearly anatropous although only one of them (apparently always the lower) is fertilized to give rise to the single seeded fruit.

(ii) Chimonanthus fragrans

Again there is no clear distinction between leaves and perianth members although the innermost six to eight differ in shape from the rest being spatulate with a distinct stalk while the outer members, those which are more leaflike, lack a stalk and are of oblanceolate-subulate shape. Although the receptacle is of the same general form as that of Calycanthus there is a distinct gap between the tepals and the five stamens. Between these and the 10-15 carpels there is another much longer internode. All carpels as well as all stamens appear to be functional.

3. STEM VASCULATURE

(Fig. 5.3)

The basic vascular structure of the vegetative stem in various members of the family, especially in Chimonanthus fragrans, is quite well documented. Prior to the advent of secondary thickening the stele consists of some 10-14 normally oriented bundles. (The number varies depending on the level at which a section is cut.) At nodes two bundles depart from the stele and these become midveins of opposite leaves. As Balfour and Philipson (1962) indicate, these are each composed of two fused strands the separate identity of which only becomes obvious further down the axis and in early ontogeny. The distance over which they are fused is about one internode - sometimes more in Calycanthus occidentalis and less in Chimonanthus fragrans. Each trace continues down, usually through a further internode, before fusing with another stelar strand.

In the cortex there are four additional bundles which are inverted and found in all but the three or four internodes nearest the stem apex. This cortical system has been shown by Balfour and Philipson to be completely independent of the stele from the time of its first appearance in the seedling. It does not reach close to the apical meristem and cortical strands appear in leaf primordia much later than stelar ones. Shortly below each node on opposite sides of the axis, pairs of cortical strands are linked by more or less horizontal connections. In Calycanthus these appear from six to eight internodes

from the apex while in Chimonanthus they differentiate later, are less pronounced and are sometimes even absent.

The lateral veins of leaves arise as branches of the cortical strands. Two adjacent strands each supply one of the lateral leaf traces, the cortical strands involved in a given leaf being a pair which have not been connected by horizontal traces immediately below the node. Proceeding up the stem it is the pair involved in a single leaf supply which are connected prior to their providing independent lateral traces of opposite leaves. In the decussate arrangement therefore the supply of all leaves in any one vertical sector is of the same origin. Balfour and Philipson regard the stele of Chimonanthus as composed of four sympodial systems each of which supplies half the midvein of one leaf at each node. The cortical system can be similarly envisaged in both of the species examined in the present investigation i.e. at each node, each cortical strand supplies one lateral trace.

The vasculature of axillary shoots bears a consistent relationship to that of the main stem. The cortical strands which have provided the lateral veins of a leaf divide again almost immediately above this to produce a second pair of traces which initially follow a course parallel to the leaf laterals. Each of these divides again thereby producing the four cortical strands of the axillary shoot. The stelar strands of an axillary shoot appear to be derived by subdivision of branches from originally two stelar strands of the parent shoot.

4. FLORAL VASCULATURE

(1) Calycanthus occidentalis

a. Bracts and Perianth

Immediately above the uppermost leaf node the four cortical strands tend to divide radially and at the level of emergence of the bracts there are usually six or seven cortical strands. Radial division of the stelar strands at this level results in a similarly large number of these. The origin of the vasculature of the bracts is similar to that of leaves i.e. traces from the stele pass out through the cortex to comprise midveins while branches from the cortical system comprise the laterals. Usually the midvein can be seen to be a dual structure originating from two adjacent stelar strands although often the connection with one of the strands is very much more prominent and develops appreciably before the other. The two cortical strands contributing lateral traces to a bract are independently linked to adjacent cortical strands immediately below the organ by more or less horizontal cross connections. Except in the appendages intermediate between tepals and stamens, all tepals receive three traces one of which is in the position of a midvein and the other two of laterals. The midvein is always connected to a stelar strand and the laterals always to independent cortical strands. As can be seen in fig. 5.4 the cortical strands involved are always adjacent although each may have arisen from a bifurcation a short distance below. As is the case lower down the axis, cortical strands which supply lateral

traces are connected to other cortical strands by cross connections. These appear appreciably after the differentiation of the ascending strands of the cortical system (some four or five internodes later) and occur at the points of departure from the cortical strands of the lateral traces of appendages. In this respect therefore the situation is slightly different from that obtaining lower down the axis where cross connections are often close to but always distinctly below the departure of laterals. The branches from the stele passing through the cortex are close to these cross connections. In the case of the higher tepals although they are at first separate they become fused to the cross connections as the floral bud matures. Those inner tepals which tend to show evidence of marginal pollen sacs usually receive only one trace and that from the stele (figs 5.4, 5.5a, 5.5b).

b. Androecium

In most stamens a double trace, the two components of which originate quite independently from adjacent stelar strands, can be seen in cleared preparations. Whether these points of origin of stamen traces should in fact be regarded as the level at which the stelar traces begin to descend, as they do in those many cases of an inferior ovary where the stele is recurrent (Douglas 1944), is very doubtful. When they first appear after maturing basipetally, stamen traces are usually joined to those of the stele almost at right angles and it appears to be as a result of subsequent stretching of stelar vascular tissue during growth that stamen traces assume their final position in which they appear to be downward branches of stelar strands. At these points at which stamen traces depart from the stelar strands several traces may originate. Usually two

on each side of a strand run to stamens and one or two more to carpels (fig. 5.5c). These three or four traces do not always have an exactly common origin; sometimes traces to carpels or inner stamens can be seen to arise as branches of the traces to the upper (outer) stamens.

c. Gynoecium

As has been stated there are several appendages intermediate in appearance between ovule bearing carpels and fertile stamens. These are vascularized as are the stamens, that is they contain two vascular strands (completely fused at maturity) which originate from adjacent stelar strands. Some of the carpels nearest the stamens are also vascularized in this fashion although most of them receive only one trace. Carpellary traces again mature basipetally but usually join the stelar strands, apparently randomly, appreciably below the level at which stamen traces depart (fig. 5.5c). About the level of the base of each carpel the single carpellary trace (which may or may not have a double origin) bifurcates, one branch becoming the dorsal and the other the ventral trace (fig. 5.2). The division of the latter to provide the two ventral traces occurs about half way up the locule. The dorsal trace continues round the ovary and finally becomes so small as to be unrecognizable in the style. The two ventrals run very close to each other near the ventral midline until they also become indistinct in the style, perhaps a little above the apparent upper limit of the dorsal trace.

(ii) Chimonanthus fragrans

The four cortical strands of the vegetative portion of the stem usually continue through the perianth to the receptacle rim. Occasionally they bifurcate. They provide the lateral veins of tepals and are linked

by cross connections as they are in vegetative regions. The strands of the stele also remain unbranched until the level of the innermost tepals and they provide median traces just as they do lower in the stem. Even the innermost tepals receive three traces.

Traces to stamens originate from a ring of vascular tissue which links stelar strands shortly below the level at which median traces to the uppermost (innermost) perianth members depart. Investigation of younger flowers indicates that stamen traces are in fact double and that each trace is at first connected to a single stelar strand. The development of extra lignified tissue adjacent to these stamen traces gives rise to the ring on which they appear to arise at anthesis.

Whilst in most significant respects the carpels are vascularized in similar fashion to those of Calycanthus, the supply to each carpel is more conspicuously a double trace this being particularly evident in younger flowers. Each component departs either from a stelar trace or from the base of a stamen trace although a reticulation of vascular tissue which develops secondarily between primary elements obscures the picture long before anthesis. Within each carpel the two ventral traces become distinct very near to the departure from the dorsal trace of the common ventral trace.

(iii) Development

In each species the first vascular tissue to appear in the floral bud is the midveins of the tepals and the stelar strands with which these are associated. Fractionally later lateral traces of tepals and with them the cortical system become recognizable although cross connections between cortical strands do not appear until much later. The stelar and cortical systems and their

branches to appendages are well developed before stamen traces make their appearance. Evidence from cleared buds indicates that there is another marked pause before carpel traces appear.

TABLE 5.1

Appendage Number (Fig. 5.6)	Angle Between Appendages	Appendage Number (Fig. 5.6)	Angle Between Appendages
1	86	16	153
2	89	17	153
3	93	18	150
4	112	19	150
5	110	20	169
6	107	21	155
7	120	22	173
8	140	23	149
9	128	24	158
10	137	25	159
11	134	26	144
12	127	27	177
13	165	28	137
14	136	29	198
15	149	30	120
16		31	

5. PHYLLOTAXIS OF FLORAL PHYLLOMES

(1) Calycanthus occidentalis (fig. 5.6)

Leaves and bracts are decussately arranged and a bijugate arrangement is evident in the lower part of the perianth. Above this the arrangement appears at first sight to be somewhat random although the angle between successive appendages tends to increase as the axis is ascended (table 5.1). Thus the angle between appendages 3 and 4 is 93° , between 7 and 8 - 120° , between 11 and 12 - 134° , between 15 and 16 - 149° , between 19 and 20 - 150° , between 23 and 24 - 149° , and between 27 and 28 - 177° . It seems reasonable to assume that a genetic spiral does run through the perianth although the existence of a Fibonacci series or meaningful Fibonacci angles (Richards 1948) seem extremely doubtful. The classical way of determining phyllotaxis is by expressing the number of turns in the genetic spiral over the number of internodes between two vertically superimposed leaves and in fig. 5.6 it might be assessed that various pairs of leaves are superimposed (e.g. 16 and 5, 17 and 3, 19 and 6). But neither the number of internodes between these nor the number of turns in the genetic spiral is constant. In fact in these instances the fractions would be $4/11$, $6/14$ and $5/13$, and among them only the latter is a member of the Fibonacci series.

Referring to fig. 5.4 it can be seen that vascular anatomy is here of little if any value in determining phyllotaxis. If the superimposed tepals are to be regarded as those whose lateral traces originate from

the same cortical bundles the figure would imply for example that tepals 7, 15 and 22 were theoretically superimposed. In fact (fig. 5.6) they are not remote from each other but two different denominators would be required for the phyllotaxis fraction. Moreover if tepals 4, 10, 20, and 29, also with laterals of the same origin are considered, the range of denominators would be further extended. In addition, if parastichies do exist, they are certainly not "vascular parastichies" (Tucker 1961).

Although similar in appearance to the leaves below it, the perianth of Calycanthus appears quite irregular from the point of view of a phyllotaxis fraction and it can be said that tepals are arranged on a genetic spiral the steepness of which varies. A critical examination of the phyllotaxis of the androecium and gynoecium was not found possible but the strong suspicion remains that appendages in these whorls are arranged on the same spiral.

(ii) Chimonanthus fragrans (fig. 5.7)

Flowers here are axillary and whether the appendages arising on a floral shoot are tepals or leaves need not be debated in this context. The lowermost appendages are definitely decussate as are the vegetative leaves although as the floral axis is ascended a bijugate pattern becomes evident. With the innermost 12-18 tepals even the bijugate appearance is lost as in fact the genetic spiral becomes more gently sloping. Even so serial sections reveal that even the uppermost appendages of the perianth are bijugately arranged (fig. 5.7). The vascular system of the floral axis behaves regularly while the phyllotaxis is decussate but its relationship with the higher appendages reveals no suggestion of regularity. There is a long internode between tepals

and stamens and although both stamens and carpels may be spiralled there is no anatomical evidence to support this.

6. CALYCANTHUS FLORIDUS

In his report, Smith (1928) confined his investigation to this species and although attempts were made to obtain material for the present inquiry in order to verify Smith's findings, suitable buds had not been procured at the time of writing.

Smith's description indicates that lower tepals each receive three or four traces and continues rather too briefly, "Thus the cortical system disappears." Eames (1961) in a description of floral vasculature in the genus reports ". . . the cortical bundles divide and all enter the lowest tepals . . ." Smith recorded that each upper tepal receives three or four branches from the stele which at this level is present as a mesh. Solitary veins to each carpel were found to depart from the stele near the rim while three veins to each carpel were described as originating from the vascular cylinder as this descends round the inner face of the cup. Smith also maintained that cortical strands in the receptacle were not inverted.

7. SUMMARY

This is confined to the two species on which observations have been made although it must be noted that in some features Calycanthus floridus may differ.

With the exception of the uppermost three or four tepals of Calycanthus occidentalis (which in fact might just as properly be described as sterile stamens) all perianth members in both species receive their vasculature in a fashion virtually identical with vegetative leaves. That is, the midvein originates from the stele and two laterals from the cortical system. There is a tendency moreover in both species for adjacent cortical strands to be joined by transverse connections in both perianth and vegetative regions. The potential midvein as it passes through the cortex is frequently linked to cross connections between cortical strands although this junction is not invariable nor is it in evidence when traces first appear. Again in both species each of the four cortical bundles of the stem tend to bifurcate as they enter the receptacle (more so in Calycanthus occidentalis) while stelar strands divide only rarely.

In both species the cortical system, which evidently terminates as lateral strands to upper tepals, does not extend beyond the receptacle rim. It is not joined at this upper level to the stele, the system which provides the entire vasculature of stamens and carpels.

Another feature common to both species is that stamens and carpels are frequently vascularized by a pair of traces which originate independently from adjacent stelar

strands. Although it is not possible to describe nodal anatomy in the same fashion as for vegetative appendages, this feature could be interpreted as suggesting a supposedly primitive bilacunar condition (Marsden and Bailey 1955) or at least bearing some resemblance to the situation in vegetative nodes. In a later chapter of this thesis a very similar type of vasculature will be described for certain floral appendages among the Ranunculaceae. An unusual feature is that carpel traces, which develop last, depart from stelar strands lower on the axis than the traces to stamens and upper tepals. Where two traces contribute to carpel vasculature they become completely fused. There is no suggestion that one of them provides dorsal and the other ventral bundles.

Phyllotaxis of floral phyllomes is in each case similar, arrangement changing from decussate to bijugate to spiral. In Calycanthus occidentalis there is an abrupt change near the base of the receptacle as the genetic spiral becomes less steep. The spiral probably continues at least into the staminal region. With Chimonanthus fragrans the change in the bracts and perianth is more gradual and can be followed with reasonable clarity. There appear to be long plastochrons between perianth and stamens and again between stamens and carpels and there is no evidence of continuity of the genetic spiral.

8. COMPARISON WITH MAGNOLIACEAE

Several similarities with members of the Magnoliaceae are evident. Vasculature of perianth members is strongly comparable in the two families. The midvein in each arises from the stele while the laterals originate from the cortical system. Adjacent cortical strands tend in both families to be connected near the level of departure of traces and to this connection the potential midvein is frequently joined. The uppermost vegetative nodes in the Magnoliaceae also resemble those in the Calycanthaceae in that again, frequently the midvein comes directly from the stele and the laterals from the cortical system.

There is little real evidence of dual origin of midveins in the Magnoliaceae and the cortical system does not extend beyond the perianth region in the Calycanthaceae. These substantial differences provide anatomical evidence which probably mitigates against close alignment of the two families and to them may be added the perhaps more fundamental one of inverted orientation of cortical bundles in the Calycanthaceae and the independence of these throughout the length of the shoot. As Balfour and Philipson (1962) record, ". . . the two systems of bundles in the mature shoot arise independently of each other from the cotyledonary traces." Although not recorded in the present investigation, if normal orientation of these bundles does occur in any species or variety in the family (and this was reported by Smith) support would of course be lent to any theories propounding closer relat-

ionship between the families. Apart from this possibility, the vasculature in the perianth region might be thought strikingly similar enough in itself to warrant closer approximation of the Magnoliaceae and Calycanthaceae than is accorded by some evolutionary taxonomists, although this study of vasculature could not be said to contribute anything to the Magnolia - Gnetum question.

From an objective appraisal of floral vasculature in the Calycanthaceae one is forced to the opinion that perianth members are of the same nature as foliage leaves although the reproductive appendages may not be. Nevertheless, the origin from two sources of the trace of many stamens and carpels of Calycanthus occidentalis does suggest some similarity with foliar appendages while in the same species the morphological continuum on which all floral appendages can readily be placed might also be cited in support of a hypothesis maintaining basic similarity of leaves, bracts, tepals, stamens and carpels.

Footnote

After this section had been completed the existence of a report on "Vascular anatomy of the flower of certain species of the Calycanthaceae" (Tiagi 1963) was discovered and finally procured. Tiagi's investigation was confined to two species of Calycanthus (C. fertilis and C. floridus), species which in fact were not available for the present inquiry. Vascular development was not considered.

Two of the doubts that have been expressed about the work of Smith (1928) are clarified. Tiagi states that Smith's description of normally (rather than inversely) oriented cortical bundles in the perianth of Calycanthus floridus is "obviously incorrect" while Smith's

statement concerning cortical bundles being used up in the lower perianth is also deemed fallacious. They are in fact arranged after the fashion in which they have been described for Calycanthus occidentalis.

The generalities of Tiagi's work are in concurrence with those of the present investigation except perhaps on one point. Both stamens and carpels are described as receiving one trace in Calycanthus fertilis and C. floridus yet as has been stated, a dual supply to these organs is in evidence in both Calycanthus occidentalis and Chimonanthus fragrans.

PART THREE

ACHENE AND FOLLICLE

Chapter VI Ranunculaceae

VI RANUNCULACEAE

1. INTRODUCTION

Of all Ranalean families, the Ranunculaceae is probably the one which has been subjected to the most extensive and intensive investigation and the one in which the answers to several questions are still being sought. The family has provided abundant material for proponents of the peltate carpel theory, for those supporting involute folding of carpel margins and for the polyaxial theorists. It has also provided those who oppose these views or offer alternative theories with much of their material. Most workers have, however, confined their investigations to detailed studies in small areas and as a result, precise knowledge of anatomy and morphology is by no means complete. In the field of floral anatomy alone, for example, Fraser (1937) reported on a careful study of carpel vasculature in follicles of the Helleboroideae yet the questions posed by the development and origin of these traces and their relationship to stelar traces remain unanswered. Melville was concerned only with the frequency of the junction of carpellary ventrals from adjacent carpels in flowers at anthesis in four species from three genera. His study went no further. In a careful study of the vascular system of flowers and fruits of both Aquilegia formosa var. truncata and Ranunculus repens, Tepfer (1953) did not pay attention to earlier stages of trace development. Hiepko (1965) was concerned with vascular traces within the perianth members of several species and in Rohweder's investigation of developmental morphology (1967), little

account has been taken of vascular tissue. At present the sphere in which information seems to be conspicuously lacking is indeed the development of vascular systems, no reports of the initial appearance and subsequent development of traces prior to anthesis having been discovered. Present investigations have accordingly been concentrated in this particular sphere, especially as it appears a fruitful standpoint from which to appraise the Gonophyll theory.

At least since the theory of morphological equivalence was expounded by Goethe (1790), the gynoecial appendages achene and follicle seem almost invariably to have been regarded as of common origin. Even those expressing opinions contrary to that of morphological equivalence of leaves, sepals, petals, stamens and carpels (e.g. Neumayer 1924, Zimmerman 1930, Hagerup 1934, Grégoire 1935, Wilson 1942, Meeuse 1965) do not appear to have contested the issue as far as achene and follicle are concerned. In 1930 in fact, Chute stated "The majority of botanists have long since agreed that the achene has been derived from the follicle by reduction." The same view has been more recently expressed by Eames (1961) who writes "The follicle is the classical carpel, the form long since accepted as the primitive type, the type from which have been derived various specialized types such as the achene." The literature in fact indicates that among supporters of the classical theory, only Bessey (1898), who believed that follicles were derived from achenes, opposed this view. In the face of this uniformity of opinion the Gonophyll theory of Melville (1960, 1962) does present a different and rather striking view. According to this theory the achene is regarded not as derived by involute or convolute folding of a leaflike organ bearing marginal

or submarginal placentae, but by folding of a sterile leaflike organ, a "tegophyll," round an originally independent axillary, bifurcating, sporangial structure. In the modern scheme the fusion of the two parts is always complete and the only evidence of the primitive dichotomy is provided by the ventral carpellary veins (fig. 6.2). On the other hand, while certain follicles and legumes can apparently also be considered to have this origin, others (e.g. those of Caltha) are in Melville's opinion best explained as originating by fusion of a whorl of sterile appendages (tegophylls) and an alternating whorl of afoliate dichotomous "ovuliferous branches." The dorsal vein of the follicle is, according to the theory, the only remaining vein of the ancestral tegophyll while the ventrals are bifurcations from independent ovuliferous branches (fig. 6.1).

In developing his theory of the origin of the Caltha type of follicle, Melville recounted in some detail the results of his investigations on C. palustris. His initial observation was that the attachments of the ovuliferous branches were "somewhat variable." In the follicles that he examined, all were found to have a simple dorsal bundle which "bifurcates two or three times a little below the stigma." He also noted that each follicle has "a pair of ovuliferous or placental bundles running parallel one on each side of the ventral suture." "Usually," he stated, "the placental bundles are not attached to the same main branch of the stelar system of the flower as the dorsal bundles. The most frequently occurring arrangement is for a pair to arise together from a main branch of the stelar mesh and to supply adjacent halves of different follicles." The applicability of the Gonophyll interpretation of the follicle clearly rests on this observation - that the

most commonly occurring situation in Caltha palustris is that a left carpellary ventral for example is fused at some lower level to the right ventral of the adjacent carpel.

It seemed clear that if Melville's hypothesis were to be tested, the flower of Caltha palustris would first have to be examined. In addition it could be anticipated that other species of Caltha might offer more evidence pertaining to the same view and it might further be hoped that a clearer overall picture would be presented by examining flower and fruit at all stages of their ontogeny. The other species of Caltha that were examined were the two native to New Zealand, C. obtusa and C. novae-zelandiae. They were chosen firstly because both species have many fewer stamens than found elsewhere in the genus and accordingly the vascular system could be expected to be less complex, and secondly because neither is known from the point of view of its floral anatomy. Unfortunately the only genus referred to by Melville as providing an example paralleling the situation in Caltha palustris is Helleborus although it is implied that all of the Helleboroideae would fit the same pattern. Accordingly, this study attempts to investigate the floral vascular system of Caltha palustris especially from the point of view of its development and to supplement the information by similarly investigating two other species of Caltha and one each of Helleborus and Aquilegia. The latter genus in fact was chosen because the work of Tepfer (1953) clearly indicates that at anthesis ventral strands from adjacent carpels are regularly connected. Although not cited by Melville, this flower would surely lend his theory some support, particularly as it is a member of the Helleboroideae.

Melville's theory for the origin of the achene is

quite different though no less unusual. According to the theory this type of carpel, which in this case is a gonophyll, is envisaged as originating by complete fusion of two separate elements, a leaflike tegophyll and an axillary ovuliferous branch (fig. 6.2). At least at maturity in all instances cited by Melville, the fusion is absolute. Thalictrum aquilegifolium provides the flower with whose carpel Melville was especially concerned, although Ranunculus and Anemone are mentioned as illustrating the same phenomenon. As for the follicle, the present investigation was based on a reexamination of the species used by Melville and an extension of his observations particularly to earlier stages of vascular trace development.

2. CALTHA PALUSTRIS

1. Introduction

Caltha palustris, the Marsh Marigold, is introduced to New Zealand and found in cultivation and occasionally as a weed in moist situations in various parts of the country. It is a glabrous herb with a perennial, stout, creeping rhizome from which annual stems arise. Leaves are mostly radical with petioles up to 25cm. long and with an orbicular or reniform lamina with a crenate margin and cordate base. Nodes are trilacunar with three traces. Axillary buds give rise to aerial shoots on which two or three smaller leaves are borne, then terminally a 2-8 flowered cyme. Flowering in New Zealand takes place in September-October. Each flower consists of five or occasionally six perianth members (herein referred to as tepals), 50-100 stamens and 15-40 carpels. Floral appendages appear to be spirally arranged. Carpels mature into typical follicles and in each, virtually all of the 10-20 ovules (borne in two rows, one each side of the ventral mid-line) are effectively fertilized.

Five or six longitudinal ridges and a corresponding number of furrows provide the corrugated outline to the hollow flowering stem. The stele consists of the same number of vascular strands as there are ridges on the surface with each strand situated beneath a ridge, together with smaller strands parallel to the ridge strands one of which runs beneath each furrow.

ii. Perianth

At the base of the receptacle, traces to the tepals depart from the stele and the fashion in which they do this is very variable (figs. 6.3, 6.5). The stelar ridge and furrow strands are in effect united by an irregular ring of vascular tissue, the low points of which are joined to the ridge traces and the high points to the furrow traces. Of the vascular supply to the tepals, the midveins originate at the points at which ridge traces join the ring. Tepals (fig. 6.4) also receive a lateral supply, sometimes from the same point as the midvein, more frequently from a point on the ring close to but distinct from the point of origin of the midvein. That is, each ridge trace terminates in a trifurcation, the middle branch passing out through the receptacular cortex to become a tepal midvein, and the other two diverging to become part of the ring. In most cases these latter traces produce tepal laterals almost immediately and also branches which continue to ascend the floral axis (fig. 6.5). In fig. 6.3 the origin of the vascular supply to a total of ten tepals is depicted and in no two is the supply identical.

After they enter the base of the tepals the veins tend to fan out slightly and although branching of the major veins is not profuse, several small veins communicate between the larger ones. In many cases the most lateral of the major veins has no connection with the others (fig. 6.4).

iii. Androecium

From the vascular ring in the lower part of the receptacle the stele extends upwards as 20-25 strands which maintain approximately parallel courses. In fact, these originate from the ring as six to eight strands

each of which usually bifurcates, some more than once, almost immediately. While the points at which stelar strands depart are quite variable, it would be fair to state that they usually depart near the point at which the furrow strands join the ring (fig. 6.5). At irregular intervals each of these strands gives off three, four, or five separate branches, each of which runs to a stamen. There are also many small strands which provide a reticulation between the main components of the stele in this region. Sometimes stelar strands terminate in a stamen but more frequently they continue up to provide the supply of gynoecial components. Stamen traces therefore arise singly and no branches are produced other than a multiplicity which occur irregularly in the region of the anthers. It might be anticipated that in association with the external spiral arrangement of stamens, the vascular system in this region would display some regularity but this appears not to be so.

iv. Gynoecium

Reference has already been made to the studies on carpel vasculature in this species by Fraser (1937) and by Melville (1962). Unfortunately Fraser does not appear to have been especially concerned with junctions between strands unless these occurred immediately below the insertion of the carpel, and Melville considered a total of only eight carpels. It is strongly suspected that in Fraser's investigation only serial transverse sections were examined, while it seems certain that Melville used only cleared flowers.

All of the 20 to 25 carpels are not at the same horizontal level. In fact although the arrangement is not obviously spiral, there are usually at least two tiers of them (fig. 6.7). In their accounts, Fraser

and Melville have apparently only considered the lowermost ones - those whose vascular supply is not influenced by the position of other carpels. To obtain an assessment from the same standpoint as these previous workers, basal carpels alone were initially considered in this investigation.

The vascular supply of 22 carpels was examined. In six instances all traces to a single carpel arose from a single stelar strand although at lower levels this strand was usually connected to others. In four of these six cases the strand branched twice, firstly to produce a dorsal and then at a slightly higher level to give the two ventrals (type a fig. 6.6). In the other two instances (type b fig. 6.6) all three arose at the same point.

In ten carpels a dorsal and one ventral had a common origin although again the stelar trace involved joined another lower down. The remaining ventral trace was in five of these a separate stelar strand (type c fig. 6.6), in three it was connected at a lower level to another which supplied a higher carpel (type d fig. 6.6), and in two instances it was associated with an adjacent ventral of another carpel (type e fig. 6.6).

In two cases the ventrals of a given carpel were of common origin, (type f fig. 6.6), while there were four instances in which all three traces came from separate stelar strands (type g fig. 6.6).

Fraser, Melville, and Tucker (1966) have performed analyses similar to this although in tabulating results of the three inquiries Tucker refers to only four types. Table 6.1 is essentially a duplication of Tucker's but with the results of the present inquiry added.

In the carpel the dorsal trace, which departs from the stele appreciably below the ventrals, runs straight and produces only a very few small branches. It runs

right to the stigma, its end sometimes producing a minor anastomosis of small traces. Ventral traces also end blindly, but in the base of the style. The vasculature of the wall of the ovary arises as branches from the ventral traces as does that of the ovules. Xylem is adaxial in position throughout the length of the dorsal trace while in the ventral trace it is in the usual abaxial position except near the base of the carpel and below. Near the base of the carpel ventral traces often run very close to each other and over a short distance xylem of the two traces is almost confluent, it being disposed 90° from its position more distally in the appendage. As ventral traces enter the receptacle, they twist through another 90° so that the xylem comes to lie on the adaxial face of the trace.

Three general points concerning carpel morphology could also be made at this juncture. The ventral slit, although extending about half way down the ovary, does not run to the base - an indication that the carpel base is tubular and may in fact arise from a circular meristem. It appears possible that there is a slight degree of true fusion of the ventral surface of the carpel with the axis, and although evidently denied by Rohweder (1967) there is a residual apex in the flowering shoot (fig. 6.8).

v. Fruit

Vasculature of the pedicel remains essentially unchanged although individual strands, especially those under the ridges, become larger with the development of some secondary vascular elements. The supply to tepals also remains essentially unaltered. The stelar strands above this level become thicker to differing extents. They also frequently become more undulating,

and numerous secondary connections, some of which finally become quite prominent, develop between them. These features combine to produce an irregular lattice of vascular strands (fig. 6.15). Stamen abscission follows the shedding of pollen and their supply is never more than a single trace. Carpels enlarge substantially as seeds develop and ventral traces, together with those with which they are connected in the stele, become the most prominent of all floral traces. The ventrals of a given carpel, which in flowers are closely opposed over a short distance near the base of the carpel, frequently appear to be fused in this region. This, plus secondary connections and increased undulations of all strands brings about closer association or apparent fusion of adjacent strands.

The supply to each ovule, which remains as a single branch from a carpellary ventral, also increases in size while the vasculature of the fruit wall, still originating almost entirely from ventral traces, becomes much richer as a reticulation ultimately develops.

vi. Floral Bud (figs 6.9 - 6.11)

In the pedicel the ridge strands appear before those of the furrows, the latter only becoming visible after considerable development of the vascular system has taken place. In each tepal the midveins appear first and mature basipetally to join the pedicel strands immediately beneath them. The prominent lateral traces of each tepal also differentiate basipetally but do so much later. They finally join the midvein trace appreciably below the level of insertion of the tepal where the vascular tissue could fairly be termed stele. At the time at which these traces are becoming visible the vascular tissue associated with the more distal floral appendages

is appearing. Conducting elements of stamen traces are clearly defined before the traces involved become connected basally and before any connection is established to strands associated with tepals or pedicel although it remains uncertain whether procambium also differentiates in this sequence. Stamen traces, together with the traces of carpel midveins which appear only slightly later, become connected virtually simultaneously to form irregular parastichies reminiscent of those which have been described in certain vegetative shoots (e.g. Girolami 1953, Skipworth 1962). At the same time, connection is established either with the lateral tepal traces or the pedicel strands. This is a case where it appears clear that the stele is composed entirely of the traces of appendages (fig. 6.16). There is nothing at this stage to distinguish carpellary dorsals from stamen traces. A most noticeable feature is that the vascular ring at the base of the receptacle is incomplete (fig. 6.9) i.e. stamens are in five groups each of which corresponds to a single tepal and each of which is associated with only one pedicel strand. The usually short distances between branches from adjacent pedicel strands are soon bridged by vascular tissue and at about this time carpellary ventrals also make their appearance. These differentiate basipetally and usually join the basal portion of a trace to one of the higher stamens. At this stage the stele above the tepals consists of straight, approximately parallel, unconnected strands. In the lower part of their course, these provide the vasculature of four or five stamens and while some terminate as carpel midveins, and some as carpel ventrals, a few do not extend above the highest stamens. The furrow traces in the pedicel do not appear until this stage.

The evidently random development of secondary

connections between stelar traces, and the development of undulations in them near the carpels, are the main changes as the bud further increases in size and opens.

Photographs of subsequent vascular development are shown in figs 6.12 - 6.15.

3. CALTHA NOVAE-ZELANDIAE

1. Introduction

Caltha novae-zelandiae is one of two endemic species of Caltha found in New Zealand. It is the more widespread and perhaps the better known, being not uncommon in moist montane and subalpine grassland and herb field in all three islands. It is a much smaller plant than C. palustris though essentially of the same growth form. Leaves, which are all radical, are of ovate order with a distinctly cordate, often membranous base and an emarginate apex. Flowering stalks are devoid of vegetative leaves and at maturity are about 10cm. long. Each bears a solitary flower. There are most commonly six tepals each of which is conspicuously three-nerved, of linear-lanceolate shape and about 1cm. in length. There are 10-15 stamens and 5-10 carpels each with 6-8 ovules, 1-4 of which finally appear as seeds in the follicle. The receptacle is flatly dome-shaped and the vertical distance between the tepals and lower carpels is usually less than 100 μ .

1i. Flower (fig. 6.17)

The pedicel is not ridged and neither pedicel nor receptacle is hollow. There are the same number of strands in the pedicel as there are tepals. There is a ring of vascular tissue at the base of the receptacle beyond which pedicel strands do not extend and from which tepal traces arise at or very near the points of junction of pedicel strands and ring. The three traces to each

tepal seem all to arise at this one point.

The stelar tissue above this level also originates from the ring but most frequently near the midpoint between two tepals. Several traces depart from here and the details of their interrelationship are not always easy to determine. It appears however that one, two, or three of the traces departing from near this point run to stamens. A few of these bifurcate and supply two stamens. Stamens are vascularized by a solitary trace. Other traces originating from near this same point run to carpels and most of the possible variations of trace arrangement apparently occur. Perhaps most commonly a carpel receives all of its vascular supply (two ventral traces and a dorsal) from a single trace which leaves the ring independently, bifurcates once at the base of the carpel to produce a dorsal trace and a common ventral, this latter shortly bifurcating again to produce the two ventrals. In some instances the single trace to a carpel gives a branch which runs to a stamen and in others a branch or branches to a second carpel. On the other hand carpellary traces may join the ring independently or be independently connected to stamen traces or to those of another carpel. Some of the types which have been observed in the current investigation are represented in fig. 6.18.

iii. Fruit

As the fruit matures the pedicel strands, the ring, and the traces to carpels become thicker although there is no development of secondary strands. At this stage it becomes clear that only the ventral traces contribute to the vasculature of the fruit wall and the supply to the seeds.

iv. Floral Bud

The first vascular tissue to appear is that in the pedicel and tepals. At these sites differentiation is simultaneous and the tepal laterals are not appreciably later than the midvein. Isolated elements of vascular tissue then appear at the base of the stamens and these increase in longitudinal dimension to become what are clearly stamen traces. Some of them fuse and all become connected by basipetal maturation to a pedicel strand near the point at which tepal traces depart. The dorsal trace then appears in each carpel and this matures downwards and either fuses with the base of a stamen trace or joins the ring independently. Carpellary ventrals appear last of all major traces in the flower. Their basal fusion and/or their frequent fusion with the dorsal trace evidently occurs as the traces become thicker with increasing age (fig. 6.19).

v. Comparison with *C. palustris*

1. Instead of the hollow, externally ridged pedicel and the dome shaped receptacle of *C. palustris*, the pedicel of *C. novae-zelandiae* is solid and round in outline, while the receptacle is much flatter.

2. There are the same number of pedicel strands as there are tepals with each strand corresponding in position to a tepal in *C. novae-zelandiae*. The connections between these found in *C. palustris* are absent.

3. The undulating ring of vascular tissue which can be regarded as connecting vertical strands at the base of the receptacle is strongly comparable in the two species.

4. In *C. novae-zelandiae* tepals always have three conspicuous traces of common origin while in *C. palustris* there are a larger number of traces of more irregular

origin.

5. Although there are many fewer stamens in C. novae-zelandiae, in both species they are vascularized by a single trace and there is some similarity both in the junction of these traces with other stamen traces and their ultimate connection with the vascular ring (figs 6.16 and 6.18). There is moreover, similarity in the general development of conducting tissue above the ring although the many fewer appendages render the vascular system in this region far less extensive in C. novae-zelandiae.

6. Carpel traces at anthesis are strikingly different in that the three traces to a carpel usually have their origins as a virtual trifurcation in C. novae-zelandiae while in the other species the three display this arrangement much less frequently. At earlier stages the carpel traces in C. palustris are separate for some distance below the carpel (through many stamen internodes). A given strand to a series of stamens which terminates as one of the three to a carpel may originate from the ring as a single strand or more commonly be a product of a bifurcation a short distance above the ring. If this extensive axial vascular system of the androecial region of C. palustris were telescoped almost to non-existence (this would be consistent with a flattening of the receptacle) the condition arrived at would be essentially that found in C. novae-zelandiae, (fig. 6.20).

4. CALTHA OBTUSA

This species appears imperfectly known, flowers being described only briefly and mature follicles recorded as "not seen" by Allan (1961). For the purposes of the present investigation three plants were collected and grown under glasshouse conditions. Unfortunately only one flower appeared but this was gathered just prior to anthesis and cleared in the usual fashion.

Caltha obtusa is in fact very similar to C. novae-zelandiae in almost every respect although in most of its vegetative features and in the size of the plant generally it is slightly smaller. Leaves are perhaps broader and are markedly crenate in outline. Sepals, green or yellow-green in C. novae-zelandiae are in C. obtusa white and rather broader. There are probably three or four fewer stamens. There seems no reason to assume that mature follicles would be different in the two species.

In the flower examined there were five strands in a solid pedicel and five tepals on the same radii as these strands. The origin of tepal veins did not seem to be as regular as in C. novae-zelandiae and the number of veins in each varied. Again there was an apparent ring of vascular tissue at the base of the receptacle although the stamen and carpel traces which arose from this approximately midway between the tepals seemed to display greater regularity than in the other species. One carpel arose between each pair of tepals in addition to two or three stamens. In each case the three veins of a carpel arose at the same point on the ring - the

point at which stamen traces also arose. The vascular system of the flower is depicted in fig. 6.21.

It was unfortunate that more flowers together with floral buds were not available for examination although the information that has been gleaned indicates that the two New Zealand species of Caltha very closely resemble each other.

5. HELLEBORUS NIGER

1. Introduction

Well known as the winter rose, this species is introduced to New Zealand and grows readily in cultivation. Flowers are usually bisexual and consist of five outer perianth members, herein termed sepals, an indefinite number of pouch-like nectaries, an indefinite number of stamens and usually five free folliculate carpels. Hutchinson (1948) includes both Caltha and Helleborus in the Helleboroideae and they generally seem to be regarded as closely related genera.

11. Vasculature of the Flower

Five normally oriented vascular traces run in the pedicel and these give rise directly to the vasculature of each sepal. In the sepal there is usually a prominent midvein (the continuation of a pedicel bundle) together with several lateral veins most of which arise from the midvein although there is considerable variability (fig. 6.22). Shortly below the point at which pedicel traces turn out through the receptacular cortex, each pedicel strand produces a pair of branches. These diverge to either side of the pedicel trace, follow a diagonal course through the base of the receptacle, and then frequently fuse with a similar strand originating as a branch of the adjacent pedicel strand. This fusion may or may not be absolute in the flower but at all events, after a vertical distance of about 200 μ these two traces again separate and follow diagonal courses

back towards the radius at which they originated from the pedicel strand, but now above the level of insertion of the sepals. Sometimes in fact they come close to, and even fuse with, the strand which originally departed from the same pedicel strand below the sepal. Above each sepal the strands again turn and continue their course through the upper region of the receptacle. Particularly in the lower part of their course, they often bifurcate and they also give small branches which run independently up the stele for shorter distances. These latter branches in fact provide the vascular supply of nectaries and some lower stamens. The course of the larger strands is an undulating one, adjacent strands frequently giving the impression of being fused over short distances. These points of fusion seem also to be points at which stamen traces (and lower down some nectary traces) join the stele. Both stamens and nectaries receive a single trace.

The origin of the vascular supply to the five carpels is highly variable although all carpels receive three traces. By following the strands involved down through the androecial portion of the floral axis, it is usually possible to identify each of them with one of the undulating strands although the frequent fusion or approximation of these strands, especially just below the carpels, tends to obscure this.

iii. Fruit

Pedicel strands and the traces of the sepals become much thicker although there is no change in their position. Most of the ascending strands above this level also become thicker and fusions with those adjacent to them become more striking. The few ascending strands which supply only nectaries and stamens remain unchanged

even after the abscission of the organs they supply. Secondary connections between stelar strands above the nectaries appear randomly.

iv. Floral Bud (fig. 6.27)

Strands of the pedicel, which appear only a little before sepal traces, comprise the first vascular tissue to appear in the floral bud. This is followed by that of the nectaries which differentiates basipetally. Stamen traces, then carpellary dorsals follow (fig. 6.23) and the bases of these fuse to form the stelar system of the upper portion of the flower (fig. 6.24). When it first appears, the vascular system comprising the stele in this region consists of approximately straight parallel strands. Their occasional basal fusion and their connections to the pedicel strands appear at about the time at which dorsal carpellary traces appear. The stelar strands, approximately parallel at the time of their establishment, become more and more undulating (fig. 6.25) until at the time the bud bursts, some have approached each other so closely at certain points that they should at this stage be regarded as partially fused (fig. 6.26). These fusions become more abundant and more obvious as the flower and fruit mature.

v. Comparison with Caltha

There are obvious external differences. For example in Caltha the prominent nectaries are absent and in C. palustris and indeed in most other species of the genus (Hill 1918) there are many more than five carpels.

There seems no essential difference between the two genera in vasculature of the pedicel or the perianth members. There is further similarity in the origin of vasculature of the upper part of the flower which in each

case arises from the pairs of strands departing from below the outer perianth whorl. Also in each case, branches originating from adjacent pedicel strands approach each other and even fuse to contribute to the formation of a vascular ring. This is particularly prominent in Caltha but because of the steeper path taken by the strands, not quite as striking in Helleborus. From this point in Helleborus there is a tendency for the strands to run back to the region above each sepal although both in Helleborus and in Caltha palustris it is from this point that the stele of the upper part of the flower originates.

The ascending strands become undulating to produce a more or less regular reticulation in Helleborus while in Caltha palustris it is secondary connections between strands which contribute particularly to the mature, more irregular pattern of stelar tissue. At anthesis the irregular fusion of carpellary ventrals below the carpels is strongly comparable in the two genera.

There is marked similarity in the sequence of maturation of vascular tissue in the floral appendages and when that tissue first appears the patterns are almost indistinguishable.

6. AQUILEGIA

1. Introduction

The species chosen was Aquilegia vulgaris. Eames (1931) and Tepfer (1953) have each paid considerable attention to A. formosa var. truncata and although the current inquiry intends to place more emphasis on earlier stages of vascular development, it was felt that a species on which very little information appears to be documented, might, as well as providing the required information, provide at least some insight into variation within the genus.

11. Flower (fig. 6.28a)

In the pedicel there are five strands, one below each of the five sepals. Sepals each receive three traces which arise at the one point - the upper extremity of each pedicel strand. Each pedicel strand splits in fact into five, the middle three of which pass out through the receptacular cortex to the sepals, while the two outer branches diverge widely and pursue diagonal courses through the receptacle. Each of these joins a strand diverging from an adjacent pedicel strand, and the single strand so produced immediately passes outwards as a petal trace. Each strand diverging from the pedicel also produces an ascending strand prior to this junction. Ten approximately parallel strands therefore comprise the stele from which all floral appendages other than sepals are vascularized. There is moreover a vertical row, an orthostichy (sensu Snow 1955), of floral append-

ages on the same radius as each of the five sepals and another on each of the five radii in between these. In the rows directly above each sepal the lowermost appendage is a petal and the upper four or five are stamens, while on the rows in between the lowermost two are petals the remaining three or four being stamens. Petals and stamens each receive two traces one from each of two stelar strands and except in the case of those petals above the sepals where traces remain distinct, the contributing traces are completely fused in the appendage. The five folliculate carpels are alternately arranged with respect to the sepals and the dorsal vein receives two branches in the same way as does the stamen immediately below it. The carpellary ventrals depart at a slightly higher level each appearing to be a continuation of one of the stelar strands. All such strands terminate in a carpellary ventral, there being no branching in their production and no vascular tissue extending above the carpels.

iii. Fruit

In most cases, ventral traces from adjacent carpels become linked as the fruit matures and additional strands may appear in the pedicel. The only other change involves the pronounced development of sclerenchymatous tissue particularly to the outside of each strand. At dehiscence this tissue may in fact form a complete ring round the stele.

iv. Floral Bud (fig. 6.28b)

The first strands to make their appearance are those of the pedicel and sepals. The next phase involves the almost simultaneous appearance of all the stelar tissue involved in the supply of petals, stamens

and carpels with the exception of carpellary ventrals. There is however a strong impression that a single trace in each petal and stamen appears first, and matures basipetally, while the second that supplies the appendage at maturity differentiates slightly later. Carpellary dorsals appear slightly later than stamen traces but again one of the basal connections appears before the other. Carpellary ventrals are the last traces to appear.

v. Comparison with Caltha

There are substantial differences in external morphology and corresponding anatomical differences internally. Unlike Caltha for example, Aquilegia vulgaris displays two distinct types of appendage in the perianth.

The regularity of the arrangement of conducting tissue is in marked contrast to Caltha and also to Helleborus. Moreover, at no stage in development is the vascular system closely comparable with that of the other genera. Certainly there is similarity in the pedicel, the outer floral whorl, and the fashion in which strands leave each pedicel strand to become closely associated with one from an adjacent strand. It is also true that above this level strands tend to be roughly parallel at least when the flower is young and that there is one trace in each stamen and three in each carpel. In fact these rather broad similarities together with the similarity of sequence of differentiation of vascular tissue are perhaps of greater significance than such obvious differences as the double origin of stamen and carpellary dorsal traces.

7. FOLLICULATE FORMS - DISCUSSION

The floral vascular system of the species cited by Melville has been subjected to examination in some detail, and two more species in the same genus together with a species from each of two related genera have also been investigated. Even this provides a broader picture than does Melville's work although clearly the total range of variation of vascular systems in the sub-family would almost certainly be much greater than encountered so far. However the following features which occur in all species do emerge.

1. Except in the case of Caltha palustris where small strands appear between pedicel strands at a comparatively late stage, there are always the same number of pedicel strands as there are outer perianth members.

2. At its upper extremity each pedicel strand trifurcates. The two outer branches run diagonally across the receptacle and the middle one provides all or most of the vasculature of the appendage. If any trace appears before others it is the midvein and all traces mature basipetally.

3. The strands which run diagonally join, or especially early in their development come close to, those from adjacent pedicel strands. This provides the "ring" in Caltha and although essentially the same in the other genera the greater angle between its components and the pedicel strands from which these arise, presents a slightly different picture. Moreover, although not obvious in Aquilegia, these traces shortly move apart

again and tend to return towards the same radius as the perianth member with which they were at first associated. This conveys the impression of a leaf gap associated with the appendage although because only primary strands are involved the gap is not of the classical appearance.

4. The stelar tissue which ascends beyond the outer perianth, in all cases originates at or near a point midway between outer perianth members. The strands comprising it may bifurcate almost immediately but at least when they first appear they tend to maintain an approximately parallel course into the carpels.

5. All follicles observed, essentially receive three traces although these may become partly fused by anthesis.

6. Stamens, and in Helleborus nectaries, and in Aquilegia petals, all contain one trace which in development matures basipetally. In all cases the stele in this portion of the flower gives the impression of being made up entirely of the aggregation of appendage traces.

7. From the point of view of vascular development and relation to the stelar tissue, carpellary dorsals are in each case identical to stamen traces.

8. Carpellary ventrals, in each case the last major traces to appear, mature in most cases to join a trace supplying an upper stamen.

The accuracy of Melville's observations on mature flowers of Caltha palustris is questioned. His comment on variability in the points of attachment of "ovuliferous branches" in mature flowers is incontestable but it cannot be said that the lateral traces from adjacent carpels join below the carpels more frequently than they display any other arrangement. Such an arrangement undoubtedly does occur but it is comparatively rare for such fusing laterals not to show evidence of their

essential independence again, a little further down the stele (fig. 6.6). At earlier stages these strands do appear as separate entities (fig. 6.16) and it is here contended that fundamentally, three strands are associated with each carpel. The flower, and as far as is known the floral bud of the two New Zealand species of Caltha lend the contention support while the origin of carpel vasculature in Helleborus appears in development to be very similar to Caltha palustris (compare fig. 6.27c with 6.16d and e). It would be difficult to believe that lateral traces from adjacent carpels in Aquilegia even at anthesis could ever be in direct continuity (fig. 6.28). Fraser (1937) examined follicles from many genera and apart from Caltha palustris species of Eranthus are the only ones in which fusion of laterals from adjacent carpels seems noteworthy. Fusion of lateral traces from adjacent appendages is in any case not an uncommon occurrence and various diagrams illustrating this have been published (e.g. Eames and MacDaniels 1951 pp. 149-151). Even therefore if the phenomenon did occur regularly among folliculate carpels it would be quite unnecessary to evoke Melville's interpretation.

8. THALICTRUM AQUILEGIFOLIUM

The genus Thalictrum, a member of the Ranunculoideae contains a large number of species each of which is characterized by a few to many carpels and stamens, and by a single perianth whorl. In T. aquilegifolium there are usually 6 or 7 tepals.

There are the same number of vascular strands in the pedicel as there are tepals and each tepal receives three traces, a prominent midvein and a pair of lateral veins. At the base of the receptacle the strand below each tepal splits, usually into five, and the central branch together with the outer two pass out to supply a tepal. The two which are at first adjacent to each midvein continue up and comprise the stele in the upper portion of the flower. These stelar strands, of which there are usually twice as many as there are pedicel strands, rarely branch and are approximately parallel. From each of them there arise single branches to each of two or perhaps three stamens and terminally to one or two carpels. There is no apparent difference in the supply to stamen and carpel other than within the appendages. Except at its extremity where an anastomosis of traces is produced, each stamen trace is unbranched. The carpel trace, which is single in the stipe, divides at the base of the ovary to produce a branch which runs in the dorsal midline as the dorsal trace, two traces which run in the remaining angles of the triquetrous ovary, and another which ascends in the ventral midline. Near the top of the ovary this latter trace trifurcates, one

branch providing the ovular supply, the other two continuing to ascend on either side of the ventral midline. Melville records greater variation than has been observed in the present investigation noting especially, considerable variability in the level of bifurcation of the trace in the mid-ventral line, and in the fashion in which the ovular trace originates from this. There seems however no reason to question the validity of his observations especially as they give the impression of having been made with considerable care.

There is little change in disposition of bundles as the fruit ripens although those of the stele become larger and there is some degree of lateral approximation above the perianth.

Unfortunately, because of the smallness of the flower, it has not been possible to glean much information on vascular development. Certainly vascular tissue in tepals and the pedicel appears first and equally certainly ventral carpellary traces are the last to appear. The supply to the ovule is in fact clearly visible in cleared preparations before the more distal part of the ventral complex. Beyond this however no observations could be made with any degree of confidence.

One aspect not treated by Melville but worthy of mention in appraising his theory is the orientation of bundles in the carpel. Below its subdivision at the base of the ovary the single bundle contains xylem on its adaxial face. This orientation is unchanged throughout the course of the dorsal bundle. The bundles which run in each of the other corners of the carpel twist through 90° so that the phloem is nearest the outside of the carpel and as far as can be detected this position is maintained throughout their course. Shortly above the junction of the ventral and dorsal traces, the xylem is

found on the side of the bundle nearest the locule. It is not possible to detect the position occupied by xylem and phloem either above the characteristic bifurcation in the ventral trace or in the ovular trace.

9. RANUNCULUS

Floral anatomy of various species of Ranunculus has been investigated by Smith (1926), Kumazawa (1930), and Brouland (1935), while the account of Tepfer (1953) is a very complete one at the time of anthesis in R. repens. Largely because of the existence of this excellent work it was decided to concentrate on this particular species emphasizing the development of vascular anatomy, an aspect not covered by Tepfer. Fig. 6.29c is directly from Tepfer's paper and represents floral vasculature at anthesis. The only comment is that the vascular areas, indicated in black in this figure, are more extensive than has been noted for flowers in the present investigation although when fruits are approaching maturity, conducting tissue would certainly be of this extent.

Like Thalictrum, Ranunculus repens does not display the clear sequential development of vascular tissue characteristic of some members of the Helleboroideae although several distinct phases have been detected. It is certain that the first vascular tissue to appear is a single trace in each sepal and that this matures basipetally as a pedicel strand. In the next recognizable stage a single trace is present in each petal and this is usually connected by a strand to each of the nearest two pedicel bundles. In the specimen indicating this stage some vascular tissue was also found above the level of petals apparently always in association with a stamen. It was revealed in slightly older buds that in

fact stamen traces first appear at the base of stamens and differentiate both into the stamen and into the cortex. Carpellary dorsals evidently develop in the same way (fig. 6.29a). The lateral traces to each sepal appear much later than the midveins and they join the branches from pedicel bundles. The point of this junction is about or shortly below the fusion of each pedicel strand with the corresponding branch from the adjacent strand (fig. 6.29b). Ovular traces appear later than carpellary dorsals and join dorsal traces near the base of the carpel, though always definitely in the carpel rather than in the axis. Ventral carpellary traces are the last to become visible and the junction between these, the ovular traces and the dorsal trace is variable. Most commonly a single trace departs from the dorsal bundle and this very shortly divides into the two ventrals. The single ovular trace usually departs either very near the base of one of the ventrals or from the point at which ventrals become separate.

Orientation of xylem and phloem is very similar to that already noted in the carpel of Thalictrum.

10. ACHENE BEARING FORMS - DISCUSSION

With respect to the Gonophyll theory two points emerge from the present investigation.

1. Even during its early development, there is no sign of ventral bundles being independent of the rest of the carpel. In fairness it must be remembered that Melville claimed no instances in which there is even the slightest degree of separateness from other tissues of any part of the ventral complex, and that his theory was indeed established in the face of this lack of more positive indication. The fact that it has now been shown that there is no evidence of independence of the ventral system in development possibly weakens Melville's theory though in itself does not invalidate it.

2. The orientation of bundles in the carpel is consistent with the interpretation of the carpel as a folded leaf-like appendage - in cross section vascular tissue appears leaf-like rather than branch-like.

It could be added that the vasculature of Ranunculus repens follows a pattern strongly reminiscent of for example Caltha and Helleborus, and that early in their respective development (before the appearance of carpellary ventrals) they are almost identical (compare figs 6.16d and 6.29b). In view of this it would seem surprising if carpels were radically different in these two sub-families of the Ranunculaceae.

11. IS THE ACHENE A REDUCED FOLLICLE?

The firm opinion of Chute (1930) and Eames (1961) concerning the derivation of achene from follicle has already been mentioned in this thesis (p. 89). It was in addition pointed out that as far as is known, theirs is a view which no worker this century has questioned.

Eames (1961) figures in diagrammatic fashion the vascular pattern of fifteen carpels from follicle and achene bearing forms and this figure is reproduced as fig. 6.30. A - E are essentially folliculate in terms of vascular pattern and the remainder, which include four species of Ranunculus, are achenes. It could well be contended that the gap between E and F, between in fact Waldsteinia and Geum, has not been effectively bridged. Chute (1930) produced an even larger series of carpels comprising 30 species from 15 genera and seemed to be aware of the critical gap in the series, figuring what was termed an "unusual" follicle of Aquilegia between achene and follicle. The work of Tepfer (1953) however suggests that this might simply be a form taken as the fruit matures. Moreover, it is debatable whether or not a single "unusual" feature should be regarded as of critical phylogenetic importance, especially when several species of the genus have since been investigated without the feature being reported again. Despite the unequivocal nature particularly of Eames' statement, the present writer remains unconvinced.

With respect to both sets of figures, the possibility that the three traces of a follicle are indeed

linked below the point of insertion of carpels does remain. In flowers and fruits of Caltha palustris and Helleborus niger this does occur irregularly although probably in less than 15% of carpels while at the time of initial appearance of vascular tissue in all species examined, the phenomenon is virtually non-existent. It could be noted that A and B in Eames' figure themselves obviate the possibility of fusion of individual carpel traces, because what are presumably stelar traces are figured as appearing between those running to a carpel. This suggests that there are three gaps associated with each carpel. This situation however was not observed in the present investigation and neither can it be imagined. There are only five carpels in Helleborus niger, there is no vascular tissue above them on the floral axis, they are evenly distributed radially and at most there is 500 μ of vertical distance between the insertions of the highest and lowest of them.

Early in this investigation it was felt that Caltha novae-zelandiae and C. obtusa might have carpels which did in fact bridge the gap between achene and follicle. Detailed investigation however reveals that carpel vasculature in these species is fundamentally similar to that in C. palustris. Even when the three veins seem to arise at the one point it has been shown that this would almost certainly not be so earlier in trace development and that in any case the point would be in the stele, certainly not in the appendage as is the case with achenes.

It is strongly suspected that essentially, three traces run to each carpel in follicle bearing forms and one to each in achene bearing forms. Although leaf gaps of the classical type are not formed, the situation in Ranunculus for carpels, stamens and petals would prob-

ably be single trace - single gap, while sepals would perhaps be described as having three traces from a single gap. Vegetative nodes are trilacunar with three traces. Although also difficult to define in Caltha, one might logically describe each carpel as having three traces from a single gap, stamens and less certainly tepals, one trace and one gap. Vegetative nodes are again trilacunar with three traces.

Variable node anatomy in the one species, even on the one branch is probably not uncommon. Philipson (1948) for example has found that the nodal anatomy associated with the bracts of Hieracium varies from unilacunar to trilacunar according to position on the peduncle while Post (1958) has suggested a physiological explanation to account for the considerable variability in nodal anatomy in certain members of the Gentianaceae. Each of these authors has in addition found nodes which are effectively intermediate between those usually recognized, this suggesting that several of the classical nodal types can be placed on a continuum. This raises the question as to whether or not the nodes of achenes (unilacunar) and follicles (trilacunar) could also be regarded as part of a continuum - whether or not in fact it is valid to maintain the existence of a gap in Eames' (or Chute's) series.

Many achenes and follicles were observed by Chute and Eames and several have been looked at from the point of view of development of their vascular supply in the present inquiry. Follicle and achene are represented in fig. 6.31a and c. If intermediate types were to be found they would surely bear some resemblance to the situation diagrammatized in fig. 6.31b. But as has been stated, carpellary ventrals (laterals) either originate as branches from dorsals within the carpel (achenes) or

they originate from completely independent stelar strands (follicles). It is not possible to compare these directly with Philipson's figures for Hieracium as it is clear that in his drawings secondary tissue is involved in addition to the strictly primary tissue of the carpels described here. Nodes reported in Hieracium can be summarized as in fig. 6.31d, e, and f. The primary condition is not known but it is not impossible that it could be as represented in fig. 6.31g, h, and i.

Post has in fact shown precisely this type of variation in primary nodal anatomy and moreover has suggested that the addition of secondary tissue may create the appearance of a greater variety of nodes than existed in the primary condition. In Rhododendron williamsianum (Philipson and Philipson 1968) the type of node can be seen to depend on the origin of the "accessory" traces. These may come from the laterals themselves or from independent positions on the stele. In the Monimiaceae, Money, Bailey and Swamy (1950) have commented on variation in the level at which the two bundles from double leaf traces unite and in Coleus Balfour and Philipson (1962) have reported that union between such bundles occurs only after the bundles have first made their appearance. Bailey (1956) has noted a general increase in complexity of nodes from seedlings to mature shoots.

There seems no doubt that the sequence outlined by Philipson and others is a valid one and that the difference between nodal types is at least sometimes only one of degree. But achene and follicle vasculature seem quite distinct and this may even suggest a long period of phylogenetic separation of these types of floral node.

Post has suggested that the development of nodal

types may be in response to projected importance or size of the appendage. On this basis therefore it would be possible to maintain that the three traces of follicles were correlated with the presence of several ovules and usually larger size, while the single achene trace was associated with one ovule and an appendage of smaller size. An argument which can be advanced against this however is that Hydrastris and Waldsteinia (fig. 6.30 D & E) are positively folliculate in vascular supply yet only have one ovule. Subsequent work on these and perhaps other genera may yet provide intermediate forms but it is the present writer's contention that at least at our present state of knowledge, there remains a gap in Eames' series.

While achene and follicle nodes may be quite distinct, it is not of course contended that they are of radically different type. There is nothing to suggest that each is not equivalent to well known vegetative nodes which themselves can be regarded as contributing to a continuous sequence.

Finally, no support for the facets of the Gonophyll theory concerned with achene and follicle has become evident as a result of this inquiry but rather, the classical theory is generally supported.

PART FOUR

Chapter VII

DISCUSSION AND SUMMARY

1. DISCUSSION

1. Context of the Gonophyll Theory

As was stated in the prologue to this thesis, the primary object of the inquiry was to gather information which would enable the establishment of a platform from which the Gonophyll theory could be appraised, and an evaluation of some of the significant aspects of the theory. Although much of the relevant information has been discussed with the appropriate chapter, it remains to finally appraise the theory in the light both of other opinions and of the total of the evidence presented in these pages.

Usually given credit for the interpretation which is followed by the majority of present day morphologists is the German poet and metaphysicist J.W. von Goethe (1790) whose theory was essentially that such organs as cotyledons, foliage leaves, bracts, sepals, petals, stamens and carpels were all expressions of a leaflike appendage (Arber 1946). The early support lent by the great French botanist A.P. de Candolle (1813) probably provided the theory with considerable impetus and it did of course seem ready made for pro-Darwinian theorists. Foster and Gifford (1959) have stated that it has proven to have been "an extremely astute viewpoint" while Arber (1950) has written that a common basic scheme of organization underlying both the leafy and the reproductive shoot would "seem too obvious to stress were it not for the fact that sometimes in recent years it has been repudiated."

It is necessary at least briefly to mention some of these theories as many of them contain elements of the Gonophyll theory. Lam (1959) for example, who has in fact maintained that "doubt about the Goethean concept is very old indeed," referred to Schleiden (1849) and Payer (1857) who each suggested that certain parts of the flower should not be equated with vegetative leaves. Neumayer (1924) thought that stamens were phylloclades borne in the axils of leaves while Zimmermann (1930) held that the flower had originated from sporangial clusters and sporophylls from aggregations of branch systems. This is the basis of the telome theory which has more recently received strong support from Wilson (1953).

Thompson (1934, 1937, 1943-44) visualized the ancestral flower as a sporogenous axis devoid of obligate appendages and believed the modern flower to have been derived as a result of localized expansions of the receptacle which in time produced the various parts. The view of Grégoire (1938) that there was no homologous connection between a vegetative shoot and a flower, all organs being sui generis, was in some significant respects rather similar.

Hagerup (1936, 1938) believed that at least some Angiosperm carpels were phyllomes subtending ovules which were essentially of axial origin and his views have been echoed by stachyospor / phyllospory theorists among whom Fagerlind (1946) and Lam (1948, 1959) have been prominent.

Emberger (1949) declared the flower to be a biological rather than a morphological entity and envisaged it as a mixture of leaves and axial organs while Plantefol (1949) held that only sepals were direct homologues of leaves. It was the belief of Deyl (1955) that floral appendages were "not necessarily foliar in nature" (Lam

1959). For many years Thomas (e.g. 1958) maintained that floral organs were "new structures due to changes in the growth of reproductive axes and not to modification of pre-existing leaves."

The abundant recent writings of Meeuse (e.g. 1963, 1965) display his strong opposition to the foliar interpretation and his approximate alignment with those who have maintained that axial components are involved in the modern flower. The systematist Croizat (1964) is another modern worker who may be described as a "polyaxial" theorist.

Melville's Gonophyll theory is also fundamentally a polyaxial theory and therefore certainly not unique. It has particularly strong resemblances to the theory of Neumayer and also recalls several interpretations adopted by Hagerup, Fagerlind, and Lam. However, Melville's ingenious and methodical synthesis, together with the extensive recollection of examples from present day floras, renders the theory outstanding at least from the point of view of its clarity of presentation. It seems clear that the theory must stand or fall on the applicability of its author's chosen examples.

It must be emphasized that the foregoing paragraphs do not pretend to cover all non-foliar theories of the flower nor do they provide any real indication of apparent measures of support. The literature on this is quite voluminous. Similarly, no attempt has been made to record opposition to these various viewpoints nor has any effort been made to evaluate the multitudinous reports which lend support to the classical theory. An attempt has simply been made to set the Gonophyll theory against the background of other theories which have offered opposition to the classical interpretation.

Some of the principles which underly the Gonophyll

theory but which have not been specifically considered in this thesis may now be briefly examined.

ii. The Axillary Bud Question

Many morphologists have evidently been concerned at the apparent lack of axillary buds which might be expected to be associated with floral appendages and seemingly this fact has provided the stimulant for many to postulate non-foliar origin of floral parts. Ovules have been supposed to be derived from axillary buds and stamens have been considered to have at least an axial component. The Gonophyll interpretation is of course essentially one emanating from a quest for axillary structures in the flower.

It can fairly be pointed out however that even apart from floral appendages, not all leaves have axillary buds. Philipson (1946) has demonstrated their absence in the inflorescence bracts of Bellis and this phenomenon is possibly widespread in the Compositae. Buds have been reported in cotyledonary axils (Yarbrough 1957) although they are probably not common in such a position but this, together with their absence from sepal and petal axils has apparently not always been sufficient to dispel the presumption that leaves must have buds associated with them. This axiom is also belied by the fact that just as some leaves exist without buds, so do some adventitious buds exist without associated leaves.

It is then viewed by the present writer as surprising that so many authors, of whom Melville is an outstanding example, should have argued so strenuously and so deviously in their efforts to prove at least to their own satisfaction, that axillary buds are fundamentally present in the flower.

Melville and others before him have also been

anxious to demonstrate that axillary buds arise in some cases upon leaflike organs. It is incontestable that there are examples in which this is true although the comment of Esau (1965) is noteworthy. With specific reference to the axillary bud she states ". . . the term axillary is somewhat inaccurate because the buds generally arise on the stem . . ." (present author's italics).

Esau continues that buds may "become displaced closer to the leaf bases or even onto the leaf itself by subsequent growth adjustments . . ." The findings of Ezelarab and Dormer (1963) concerning nodes in the Ranunculaceae could be added to those authors cited by Esau in this regard. Moreover, as has been pointed out by Philipson and Philipson (1968), in Rhododendron the bud may come to be located appreciably above the subtending leaf.

In view of the variety of locations for axillary buds, Melville's postulation remains not implausible although it is unfortunate that he is unable to cite intermediate conditions (where stamen "branches" for example in the Magnoliaceae arise near to or in the axil of perianth members) and it is particularly unfortunate that he has claimed no support from morphogenesis. If the present suggestion that leaf equivalents need not have axillary shoots associated with them is accepted, the support for Melville's unsubstantiated hypothesis that axillary branches may arise in a most unusual situation in the flower, is surely diminished.

iii. The Stamen Question

It is not intended to review Melville's evidence pertaining to Angiosperm stamens in entirety, but some of the significant features can appropriately be mentioned.

In support of the postulation that stamens can be

equated with branches, Melville and others have drawn evidence from ontogeny. It has been claimed, and certainly this seems true in some cases, that while petals, sepals and leaves are initiated by periclinal divisions in one of the tunica layers, stamens, like branches, originate by proliferation in the corpus. In fact however, this is only a generalization. Boker (1948, 1949) has reported the virtually identical initiation of stamens, petals and sepals in Vinca and Tepfer (1953) and Tucker (1959) have remarked similarly on this situation in the Ranunculaceae and the Winteraceae respectively. Wilson and Just (1939) evidently regarded this as the normal occurrence. On the other hand Foster (1936) stated that both tunica and corpus are each frequently involved in initial divisions concerning leaf primordia and Boker (1940) has reported specifically on the occurrence of this in Acacia. As for the deeper seated origin of axillary bud (branch) meristems it need only be said that while this usually appears to be so, axillary buds have on at least one occasion been reported as involving initial divisions in the outermost tunica layer (Champagnat 1961). It remains true of course that leaves are generally initiated in the tunica but it seems as misleading to suggest that this is invariably the case as it is to imply a deepseated origin for all, or even the majority of stamens.

Melville rather tentatively elicits support for his Gonophyll interpretation from the centrifugal stamens which are known from several families. He admits however (1963) that "further study of floral ontogeny is necessary before a complete explanation can emerge." Eames (1961) refers to the phenomenon simply as a "reversal of sequence of development (which) has doubtless occurred more than once, as have all other advanced floral characters." He

compares this with various other "departures from normal sequence in development."

iv. The Foliar Primordia Question

The fact that foliar primordia are separate in apocarpous forms and that there is no evidence for the congenital fusion necessary for the Gonophyll theory, has already been pointed out by Corner (1963). His belief which seems generally to be supported by evidence from several quarters, is that outgrowths cannot consolidate - the primordia involved must first become one entity. In an earlier paper (Corner 1958) it was shown how sepals may "capture" petal traces although the petaloid sepals so produced are not dual structures in the sense of unification of sepal and petal primordia.

In his later article Corner also asserts a lack of appreciation by Melville of the fact that all floral primordia grow basipetally and venation is therefore "phyllodic," not palmate as would occur with acropetal growth.

Once again, these are criticisms which apply to theories advanced by more than one opponent of the classical theory.

2. SUMMARY

The primary object of this work was an investigation of some of the important aspects of Melville's Gonophyll theory.

Firstly, many of Melville's findings and presumptions concerning the Magnoliaceae are gravely questioned. He appears to be incorrect in his assertion that the cortical vascular system in this group begins at (in fact upon) one of the upper foliage leaves. At least sometimes it originates in an internodal position. The fact that cortical strands have been shown sometimes to bypass axillary buds and the fact that more than a pair of cortical strands can originate from the supply to a leaf (and associated stipules) are deemed quite irreconcilable with the Gonophyll interpretation. Melville's interpretation of carpel vasculature in the same family is also considered incorrect. There is no developmental evidence to indicate that ventral traces arise on dorsal traces. Rather, ventrals essentially originate in the cortical system and dorsals in the stele. It is also contended that in order to explain the continuity of the cortical system in the gynoeceal region, Melville has evoked a form of development unknown to ontogeny. The evidence presented herein concerning the Magnoliaceae suggests strong essential similarity of vascular supply to bracts, perianth members, carpels and in some cases, stamens. It is submitted that the Gonophyll interpretation of the Magnoliaceous flower is erroneously based and fundamentally implausible.

It is also held that vasculature in the Gnetum inflorescence is fundamentally dissimilar to the Magnolia flower and that attempts to equate the two are not consistent with the facts.

As far as floral vasculature is concerned, distinct similarity exists between the Magnoliaceae and at least one member of the Winteraceae although the cortical system is undoubtedly less strongly developed in the latter family. There is no evidence to suggest any basic similarity between the Winteraceae and Gnetum.

While the cortical vascular system is well developed in the Calycanthaceae, its strands are inverted and it does not extend beyond the perianth. Despite the suspicion that may be entertained concerning relationship between Magnoliaceae and Calycanthaceae, when facts are viewed objectively there is very little to support this. Within the family there is a strong suggestion of similarity of perianth members, bracts and leaves although the evidence is not as convincing with respect to stamens and carpels.

Much evidence conflicting with that cited by Melville concerning fusion of lateral traces of adjacent folliculate carpels has been revealed, and quite apart from present findings, the accumulated work of others indicates that his claims concerning the frequency of the junction, present an exaggerated picture. Evidence from development indicates that during early stages this union may be rare indeed. Moreover, the reported occurrence of such a union in vegetative stems suggests that even if it did occur regularly the situation would not be so unusual as to demand such a startling explanation. Melville's interpretation of the Ranunculaceous follicle is therefore deemed fallacious.

His interpretation of the achene is less assailable

although it is the present author's contention that in early stages of floral vascular development (before the appearance of follicle laterals) follicles and achenes display marked similarity at least with respect to their relation with strands below them. At appropriate stages this similarity extends in each case to stamens.

At the same time, it is contended that on the evidence of the course of traces, especially during their development, achenes and follicles comprise distinct carpel types, of undoubted common origin although as far as is known there are no forms genuinely intermediate between the two.

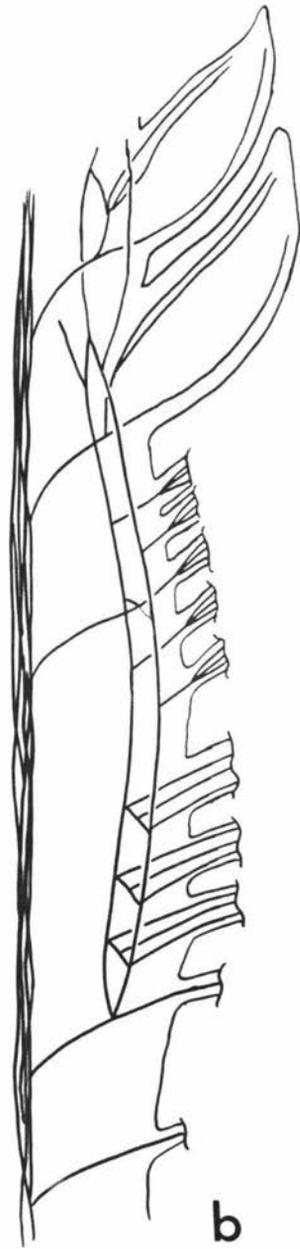
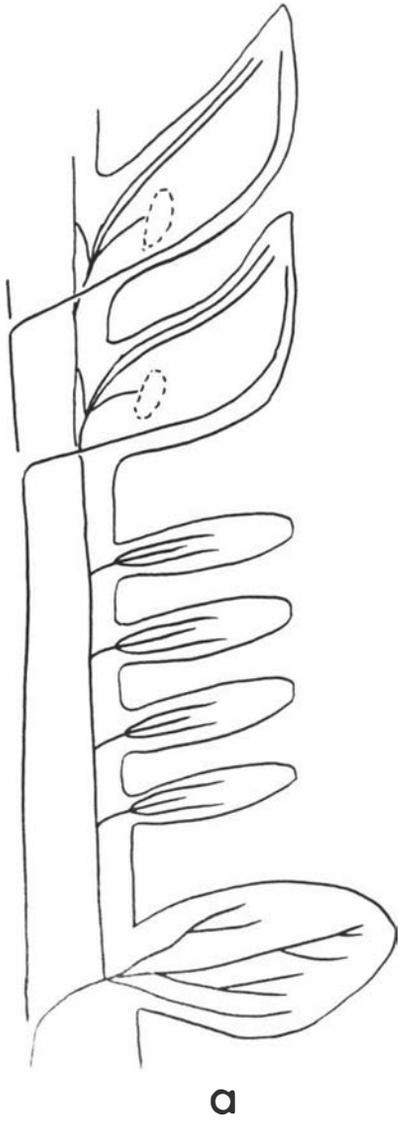
The second major aim outlined in the prologue emanated from the suggestion that components of the vascular system of the flower may display different inter-relationships at different stages of development. This hypothesis is considered to have been abundantly substantiated. In several instances, adjacent stelar strands in the flower are at first straight and approximately parallel but they later assume undulating courses and finally fuse at various points to produce a reticulation. Whatever other significance may be attached to this observation it must be regarded as one, the consequence of which generally presents considerable opposition to the Gonophyll theory.

It has not been practicable to subject all facets of the Gonophyll theory to scrutiny but it is submitted that the theory is so seriously weakened by the total of the evidence presented in these pages that it might well be considered to have been disproved in principle.

PART FIVE

ILLUSTRATIONS

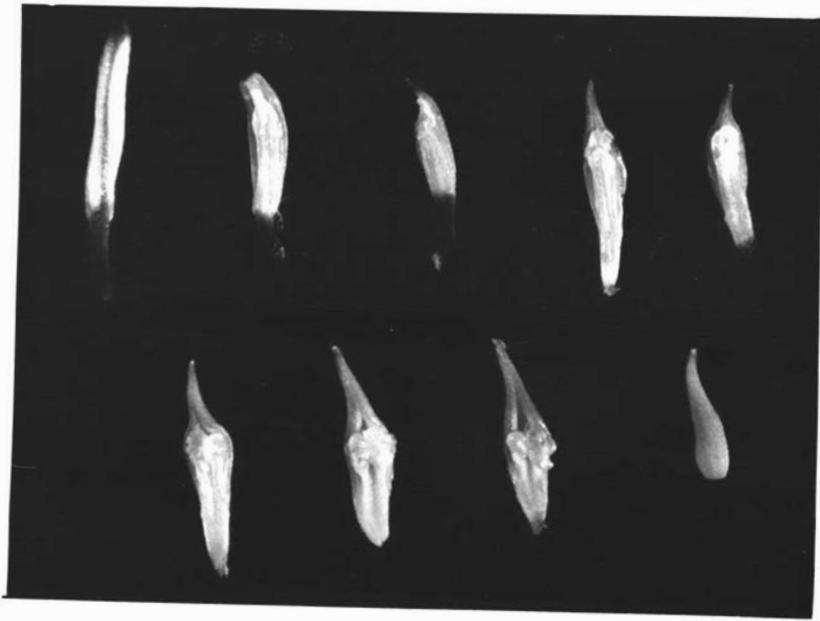
FIG. 2.1



- FIG. 2.1 (a) Diagrammatic representation of Magnolia flower
(b) Detailed vasculature of Magnolia stellata

Both after Melville (1963), illustrate the gonophyll interpretation of the Magnolia flower.

The cortical system is seen originating as a branch of a tepal trace and providing most of the vasculature of stamens. Carpel vasculature is seen as involving a midvein from the stele and ventrals from the cortical system. Ventrals are also linked vertically. By such an interpretation a carpel is regarded as equivalent to a bract plus the bifurcating branch system which arises upon it. Melville sees such a carpel as equivalent to a perianth member (bract) plus stamens (vascularized by the bifurcating branches associated with that bract).



a

FIG. 2.2

b

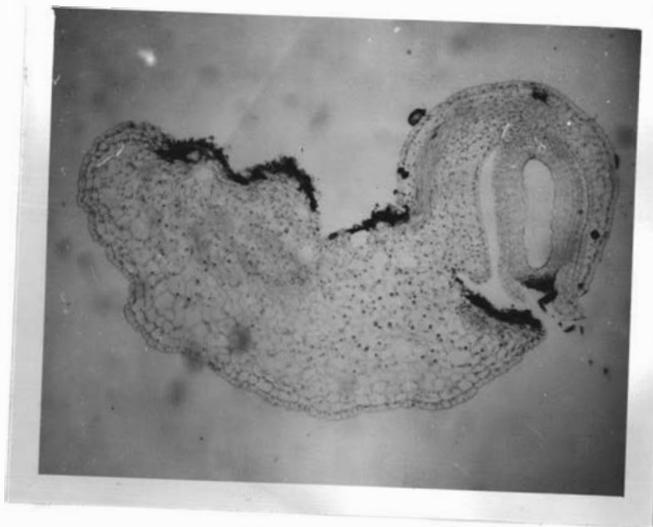


FIG. 2.2 (a) Photograph of carpelloid stamens -
Michelia fuscata (x10)

Arrangement is in approximate sequence from a stamen at upper left through various intermediate forms to a true carpel at lower right.

(b) Photomicrograph of transverse section of a carpelloid stamen - Michelia fuscata (x50)

The ovule appears to be completely exposed. There is evidence of integuments and of female gametophyte.

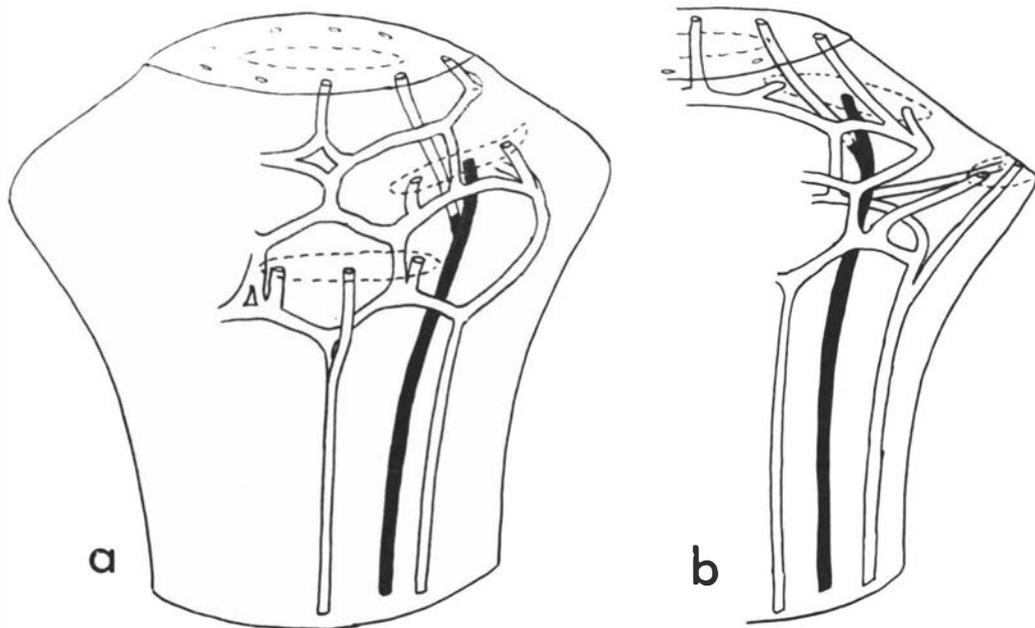


FIG. 2. 4

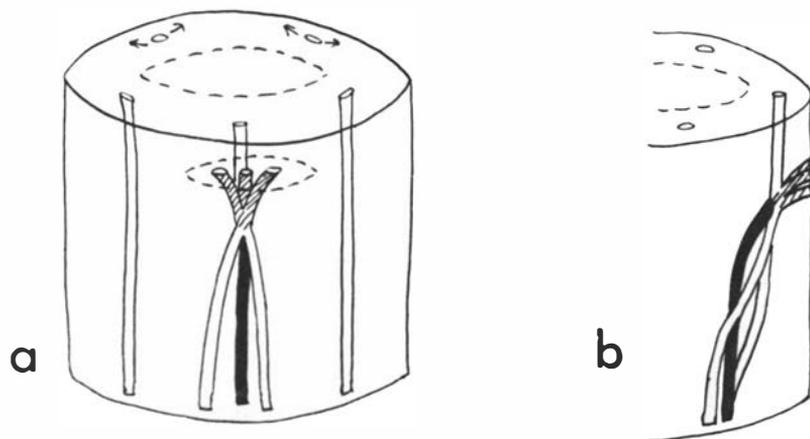


FIG. 2. 3

FIG. 2.4 (a) Three dimensional reconstruction indicating disposition of a portion of the cortical (unshaded) and stelar (black) systems in the lower part of the receptacle of Michelia fuscata

Areas of attachment of perianth members appear as long ovals (delimited by a dotted line) through which three traces are depicted as passing. The nature of the cortical reticulation can be seen. The shading of traces to the appendages indicates the system in which the particular component arose. The dotted circle near the centre of the exposed upper surface represents the position of the stele.

(b) Three dimensional reconstruction of the same conducting tissue as depicted in (a) but with the receptacle 90° displaced.

FIG. 2.3 (a) Three dimensional reconstruction of the portion of the pedicel of Michelia fuscata from which the bracteole arises

The cortical system is unshaded, the stele black, and traces to the bracteole cross hatched. On the exposed upper surface arrows indicate tendency for cortical traces to subdivide shortly above this level, while the position of the stele is dotted.

(b) Three dimensional reconstruction of the same conducting tissue as depicted in (a) but with the receptacle 90° displaced

The origin of cortical strands from between stelar components is indicated at the bottom.

FIG. 2.6

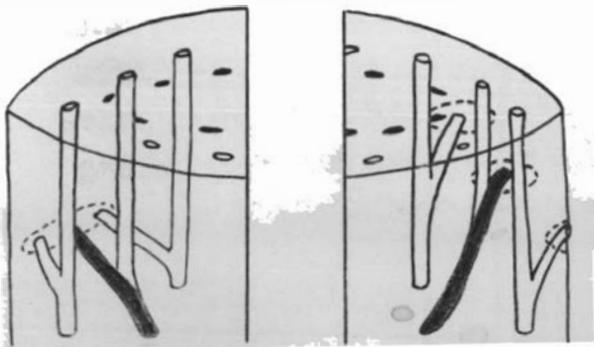
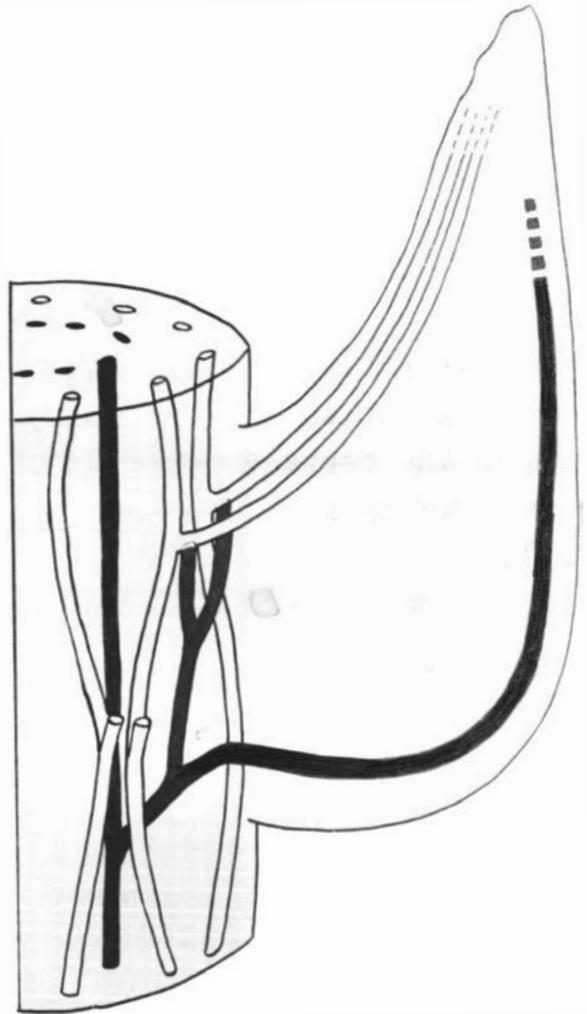


FIG. 2.5

FIG. 2.6 Three dimensional reconstruction indicating vascular supply to a carpel in Michelia fuscata

The stelar strand (and the dorsal trace and ascending stelar bundle) are shaded black while cortical strands and ventral traces are unshaded. This pattern is remarkably constant for carpels throughout the family.

FIG. 2.5 Three dimensional reconstruction indicating vascular supply to stamens in Michelia fuscata

The stele and its branches are shaded black, while the cortical system and branches therefrom are unshaded. Branches from the supply to each stamen are seen to ascend in the cortical system. On the left is depicted a case where three traces contribute to a stamen while on the right one trace runs to each of three stamens although both stelar and cortical systems contribute.

The figure is idealized in that the undulating courses of strands have not been depicted.

FIG. 2.7

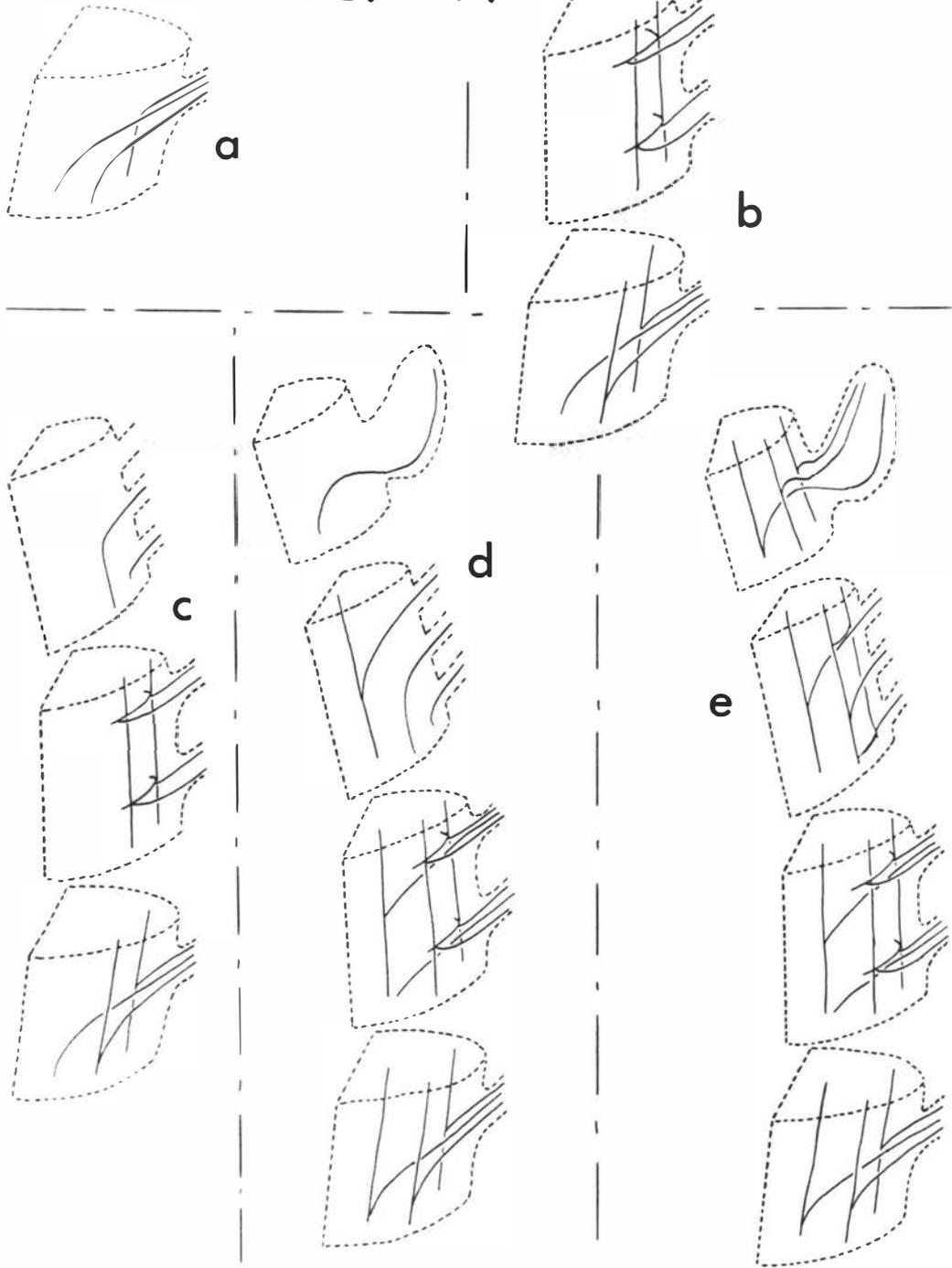


FIG. 2.7 Diagrammatic representation of the development of floral vasculature in Michelia fuscata as illustrated by three dimensional views of parts of the vascular system in various portions of the receptacle

(a) Contributions of cortical and stelar systems to the bract. No traces extend above this level at an early stage.

(b) Bract and perianth portions with cortical strands (which originate as branches of traces to bracts) shown as linked between two perianth levels. From these "rings" traces to appendages are seen to arise. No stelar system is present above the level of the bract at this time.

(c) Bract, perianth and androecial portions with branches from the cortical system extending into some stamens. No stelar system is evident above the level of the bract.

(d) Bract, perianth, androecial and gynoecial portions with stelar components now evident in all portions but with the cortical component as yet absent from the gynoecium.

(e) The same portions as shown in (d) but with cortical components now evident in the gynoecial portion and with cross connections between cortical strands in the androecial portion.

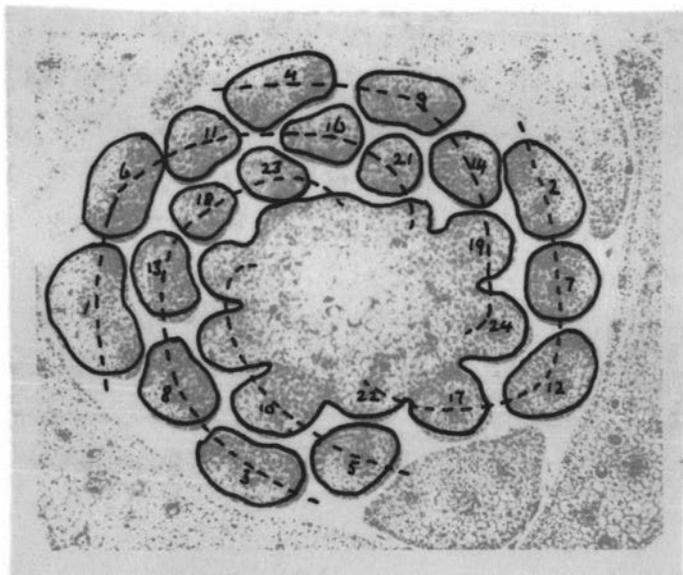


FIG. 2.8

FIG. 2.8 Photomicrograph of transverse section through gynoecial region of young floral bud of Michelia fuscata (x40)

On the overlying transparency a number is placed over each carpel, 1 being the lowest on the axis. The only constant parastichies are those indicated by dotted lines which in fact connect carpels five plastochrons apart. Whether or not there is any relationship between dorsal traces of carpels in any one parastichy has not been determined. Because of irregularity it seems not possible to determine phyllotaxis from vertical superimpositions although Tucker's method, based on the number of turns in the genetic spiral between successive members of the same parastichy would give $2/5$.

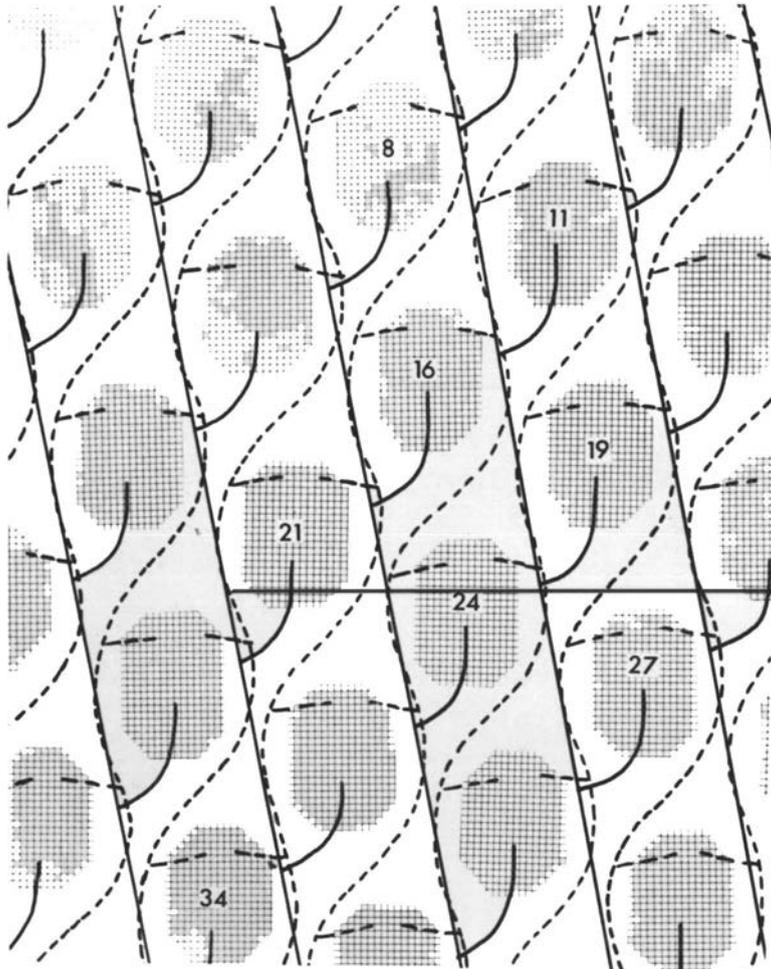


FIG. 2.9

FIG. 2.9 Relationship between carpels, stelar system and cortical system in Michelia fuscata

Carpel bases are cross hatched, the cortical system and ventral traces dotted, and the stelar system and dorsal traces represented by unbroken lines. For the sake of clarity ascending stelar bundles have been omitted. The carpel nearest the apex was numbered 1 and some of the others are indicated.

The members of one of the contact parastichies ($x, x+8, x+8+8, \text{etc. e.g. } \dots 11, 19, 27, \dots$) are connected by their dorsal traces to the same stelar strands while members of the other ($x, x+5, x+5+5, \text{etc. e.g. } \dots 11, 16, 21, \dots$) are associated with cortical strands, each strand in fact supplying alternately left and right ventrals of carpels. Carpels of another parastichy ($x, x+13, x+13+13, \text{etc. e.g. } \dots 8, 21, 34, \dots$) receive ventrals from an identical source.

If for example carpels 8 and 16 were regarded as being vertically superimposed it can be seen that there would be three turns in the genetic spiral between these two appendages. The phyllotaxis fraction would in this case therefore be $3/8$.

FIG. 2. 10

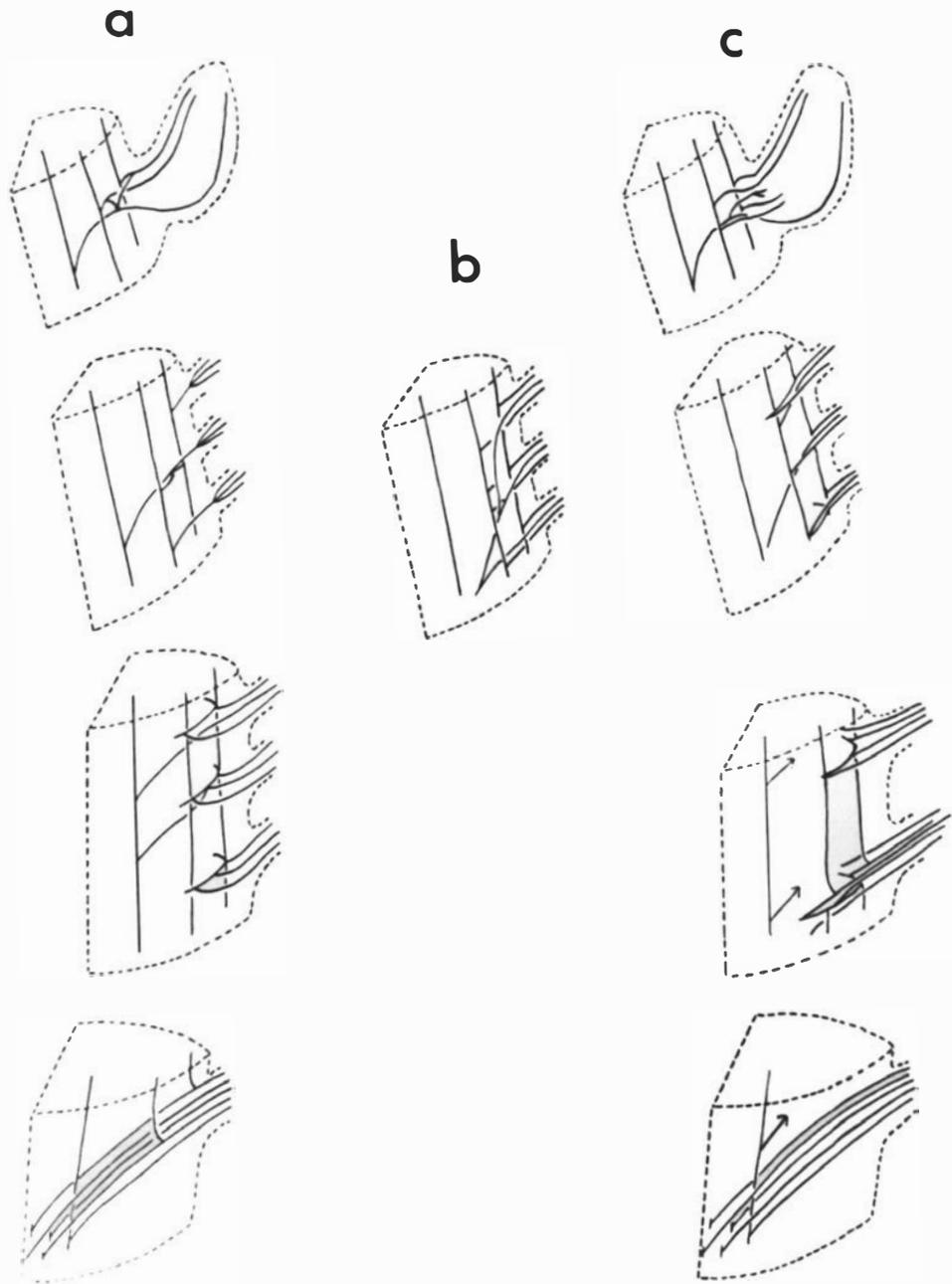


FIG. 2.10 Diagrammatic representations of the floral vascularization in three Magnoliaceous species illustrated by three dimensional views of parts of the vascular system in various portions of the receptacle.

(a) Magnolia stellata

The supply to a bracteole is indicated in the lowermost portion. Two strands comprising part of the cortical system ascend as branches from some of the bracteolar traces. In the perianth (second portion) cortical strands are connected by rings from which appendage traces depart. Branches from the stelar system may or may not be joined to the rings and if they contribute to vasculature of an appendage it is always as a midvein. In the third portion the vasculature of stamens can be seen to originate as a single trace either from a cortical strand, or from a connection between adjacent cortical strands to which a branch from the stelar system is joined. In the uppermost portion a carpel is depicted and this receives its vasculature in a fashion virtually identical with carpels of Michelia fuscata.

(b) Magnolia soulangiana (stamen portion)

Stamens each receive three traces, laterals from cortical strands, and a midvein either directly or indirectly from the stelar system.

(c) Liriodendron tulipifera

The supply to bracts is again indicated in the lowest portion. A strand of the cortical system is shown originating from the stelar system above this level. In

the perianth (second portion), cortical strands are joined by a ring and from this traces to perianth members depart. A midvein from the stele is shown as present in the lower member. In the stamen portion the supply to appendages can be seen to originate either entirely from cortical strands (or connections between them) or from both cortical and stelar systems the former providing laterals and the latter, midveins. Carpel vasculature (upper portion) involves ventrals from separate cortical strands and a dorsal from a stelar strand. Ascending stelar bundles connecting ventral and dorsal traces in the one carpel do not exist in this species.

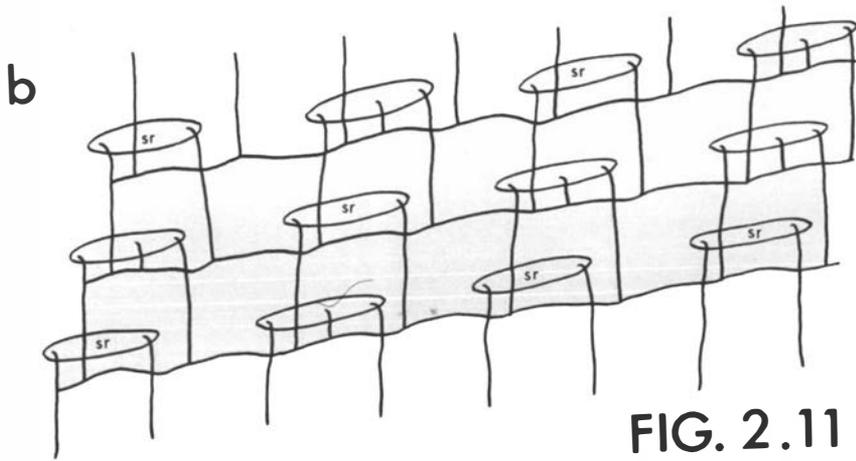
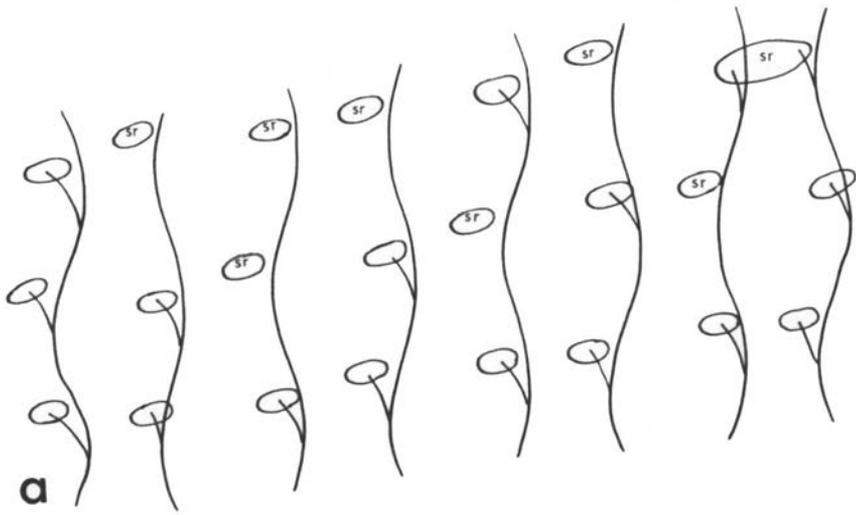


FIG. 2.11

FIG. 2.12

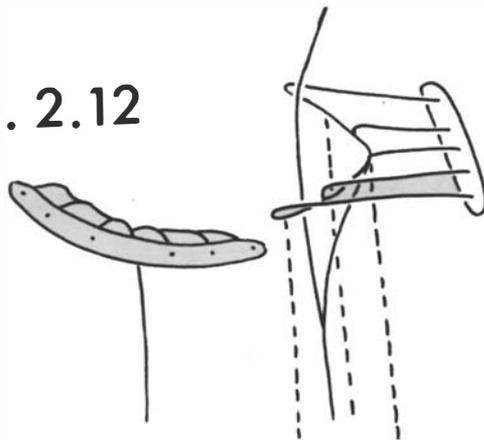


FIG. 2.11 (a) Stamen vasculature of Magnolia stellata

Cortical strands are shown as undulating lines. Most of the stamens (indicated as small ovals) receive their trace from the cortical system although some, as indicated by the letters "sr" receive their trace from the stele. In one of the stamens a midvein is shown from the stele while laterals originate from separate cortical strands.

(b) Perianth vasculature of Magnolia stellata

The cortical system and its contributions to appendages is indicated as in (a). Letters "sr" indicate a contribution from the stele which in fact only involves some of the midveins.

FIG. 2.12 Development of perianth vasculature in Liriodendron tulipifera

Solid lines to the appendage (base indicated by an oval on the left) indicate established traces at an early stage. All can be seen to originate from one stelar strand and not to be connected to the other perianth member indicated. Dotted lines represent the positions in which cortical strands will develop.

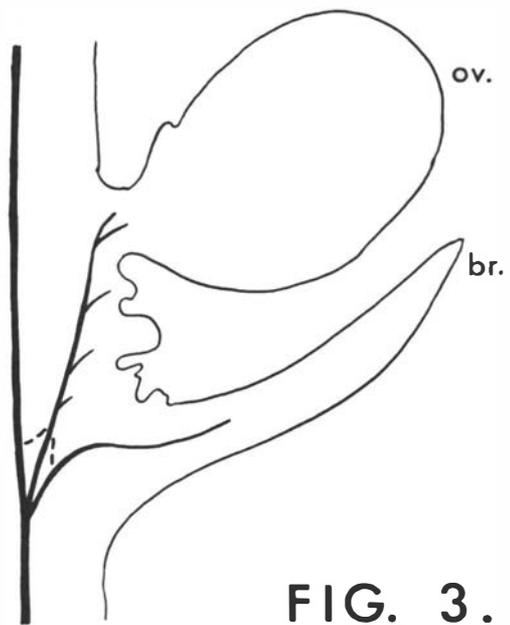


FIG. 3.1

FIG. 3.1 Portion of a female inflorescence of Gnetum gnemon indicated diagrammatically

The trace to the bract (br) is indicated departing from the stele and the trace to the single functional ovule (ov) leaves in a position axillary to this bract trace. Branches to nonfunctional ovules depart from the ovule trace. The dotted lines mark alternative positions for departure of the ovule trace.

FIG. 4. 1

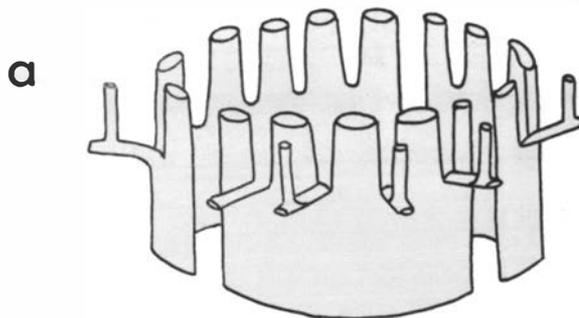
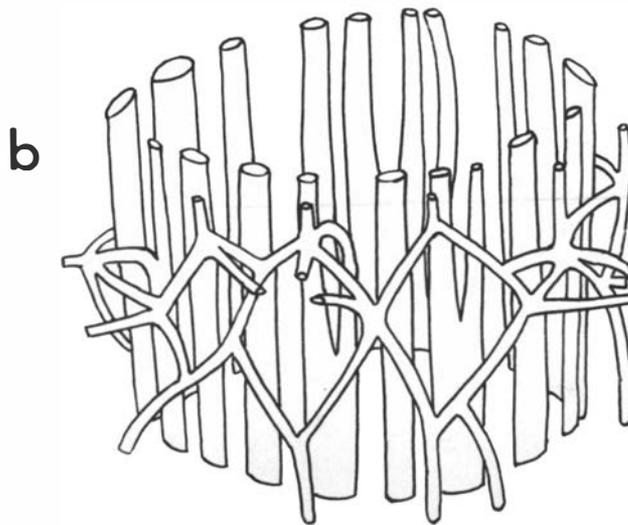
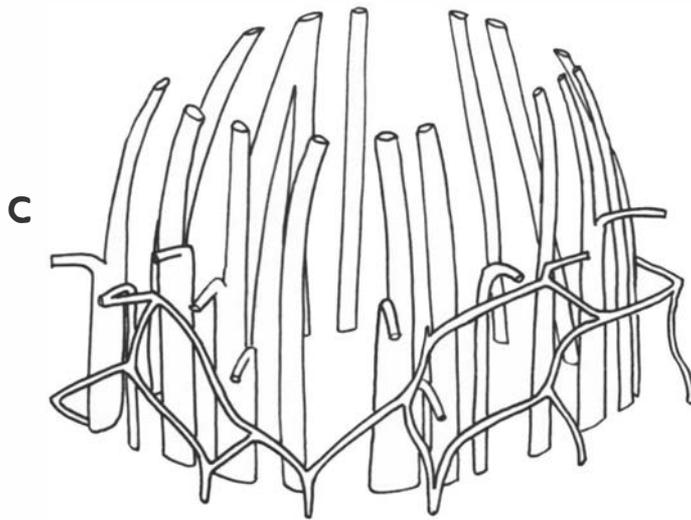


FIG. 4.1 Three dimensional partial reconstruction of vasculature of mature flower of Belliolum crassifolium

The stele consists of a number of approximately parallel strands and the cortical system of a network of finer surrounding strands.

(c) Androecial region

Some stamens are supplied from the cortical system and others directly from the stele. In one case, two traces from the cortical system can be seen to contribute to a single stamen. The cortical system seems not to extend above this level.

(b) Corolla region

Three traces run to each petal, the laterals from the cortical system and the midveins from the stele (usually) although this latter trace is joined to the cortical network as it passes through.

(a) Calyx region

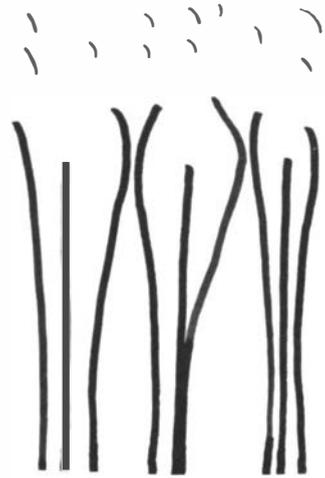
Strands of the cortical system can be seen originating as branches from traces which run to the calyx. Below the departure of calyx traces, the stele can be seen to consist of only three strands.



a



b



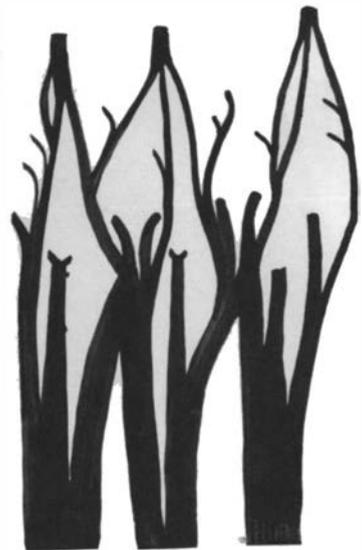
c



d



e



f

FIG. 4.2

FIG. 4.2 Diagrammatic representation of buds and flowers opened out and indicating six stages in the development of floral vasculature in Drimys winteri var. chilensis

(a) Very young bud - pedicel strands and branches of calyx traces.

(b) Petal traces and associated strands appearing.

(c) Strands associated with perianth well developed. Those associated with stamens appearing.

(d) Continuous strands established above perianth in androecial region.

(e) Appearance of carpel traces, depicted at this stage as consisting of three traces to each carpel.

(f) At anthesis. Loss of identity of three traces to each carpel and increase in size of all vascular bundles.

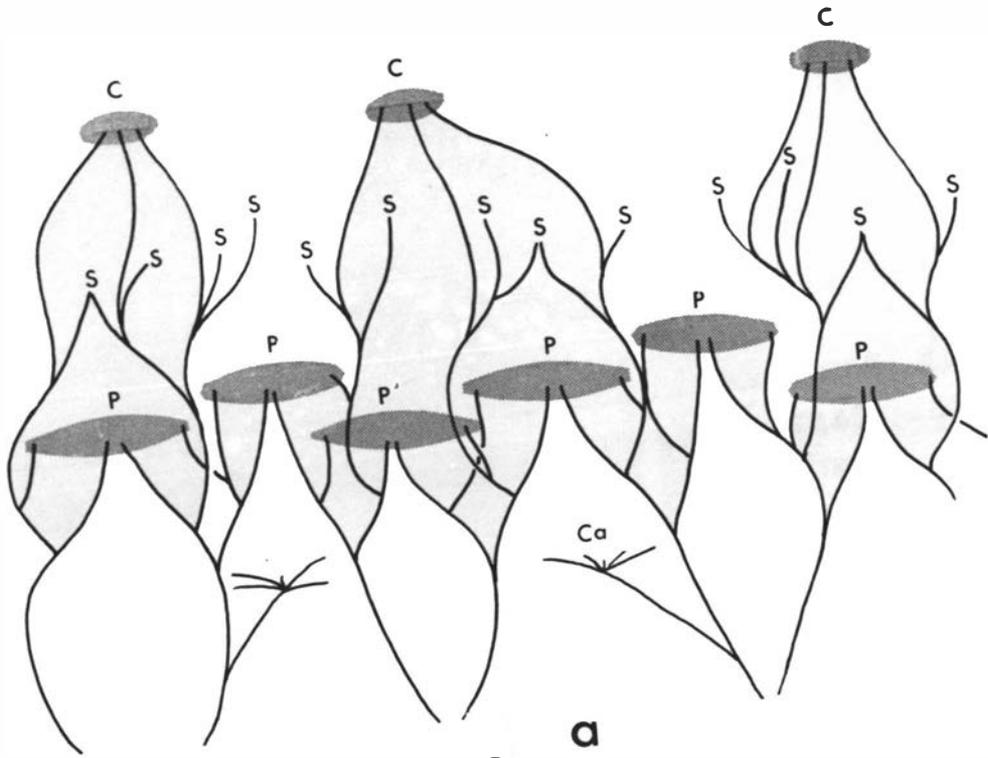


FIG. 4. 3

a
b

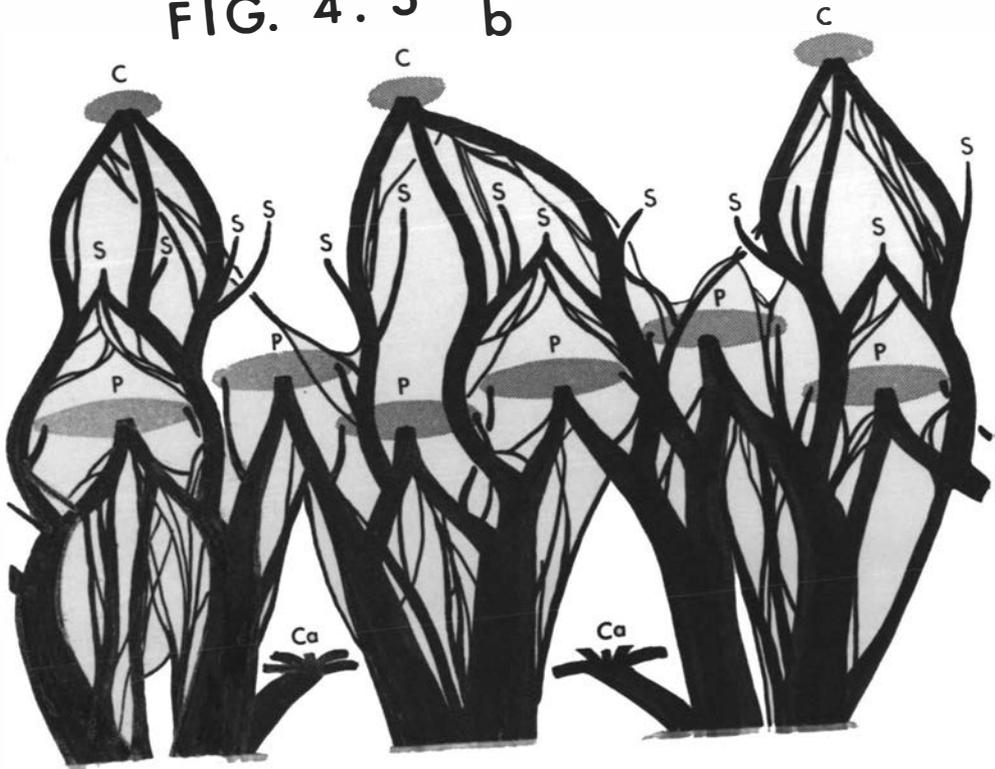


FIG. 4.3 Representation similar to fig. 4.2 of two stages in development of floral vascular system of Pseudowintera axillaris

(a) Young bud with all major strands and traces initiated. A double supply to each petal and to several of the stamens is evident. Three independent traces can be seen running to each carpel.

(b) At anthesis. Substantial thickening of many traces and loss of identity of others. Numerous random secondary connections can be seen.

FIG. 5.1

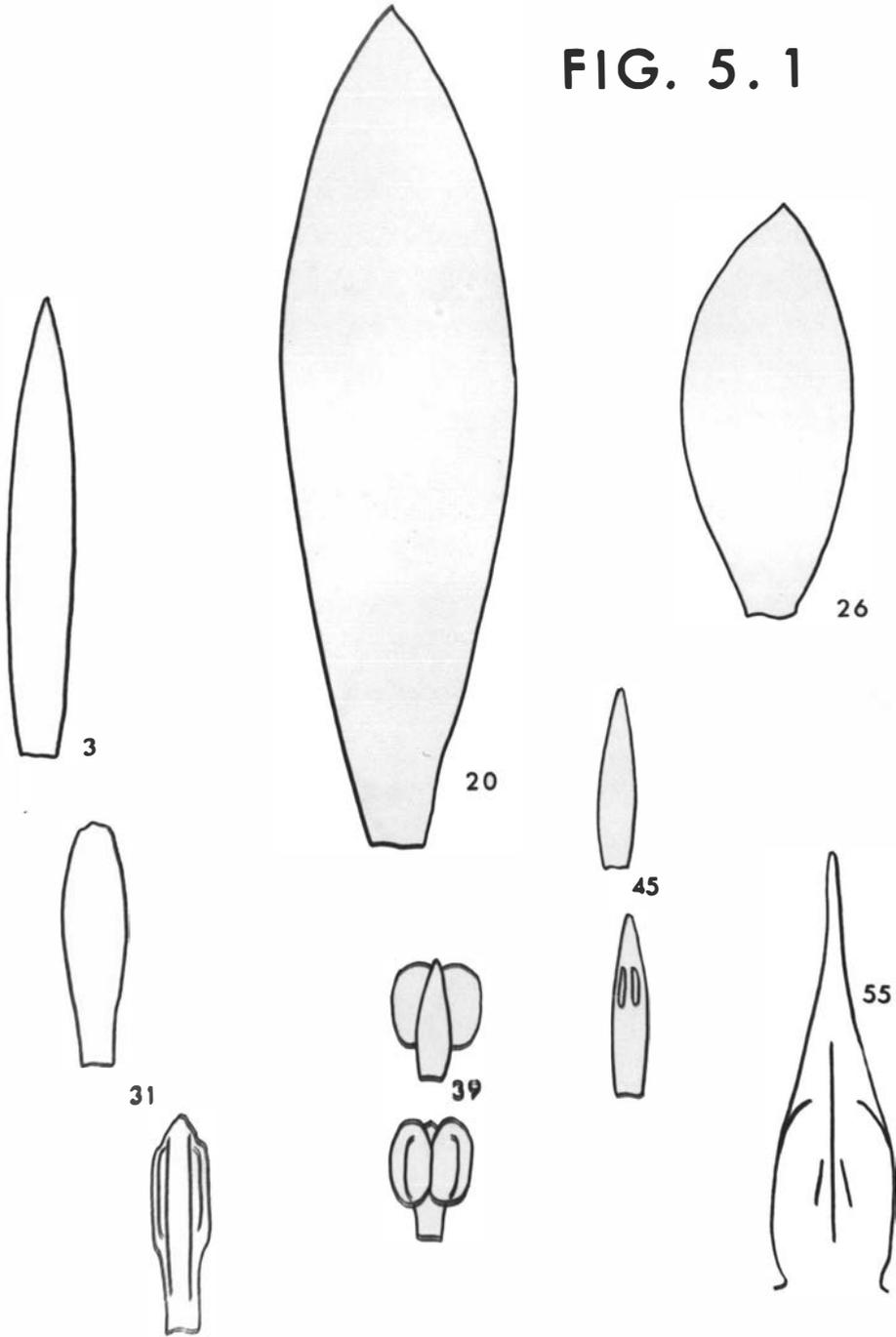


FIG. 5.1 Calycanthus occidentalis Outlines of some of the floral appendages indicating change in shape as the axis is ascended

Appendages were labelled from 1 (nearest the bracts) to 61 (innermost in this case). 3, 20, 26 and 55 are drawn from the adaxial view while both abaxial (upper outline) and adaxial (lower outline) views of appendages 31, 39 and 45 are indicated. 3, 20 and 26 would all be tepals, and 31 and 45 nonfunctional stamens between tepals and functional stamens, and between functional stamens and functional carpels respectively. 39 is a functional stamen and 55 a functional carpel.

FIG. 5. 2

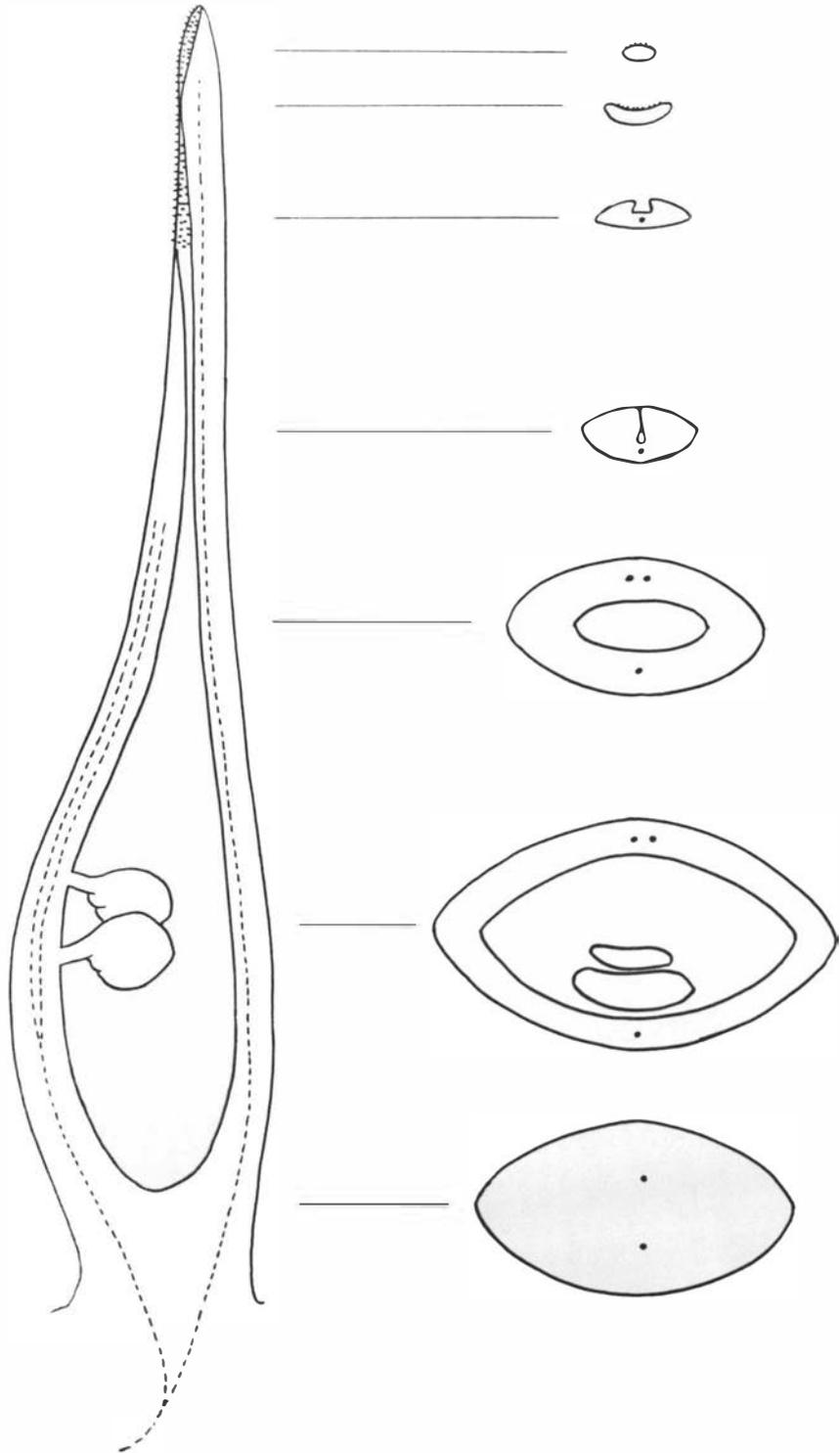


FIG. 5.2 *Calycanthus occidentalis* Young functional
carpel

On the left a carpel is depicted as if slit longitudinally near the dorsi-ventral midline. Stigmatic surface, stylar canal and two ventrally attached ovules are indicated. Traces are represented by dotted lines.

On the right, the series of outlines are of transverse sections cut at the levels indicated.

b

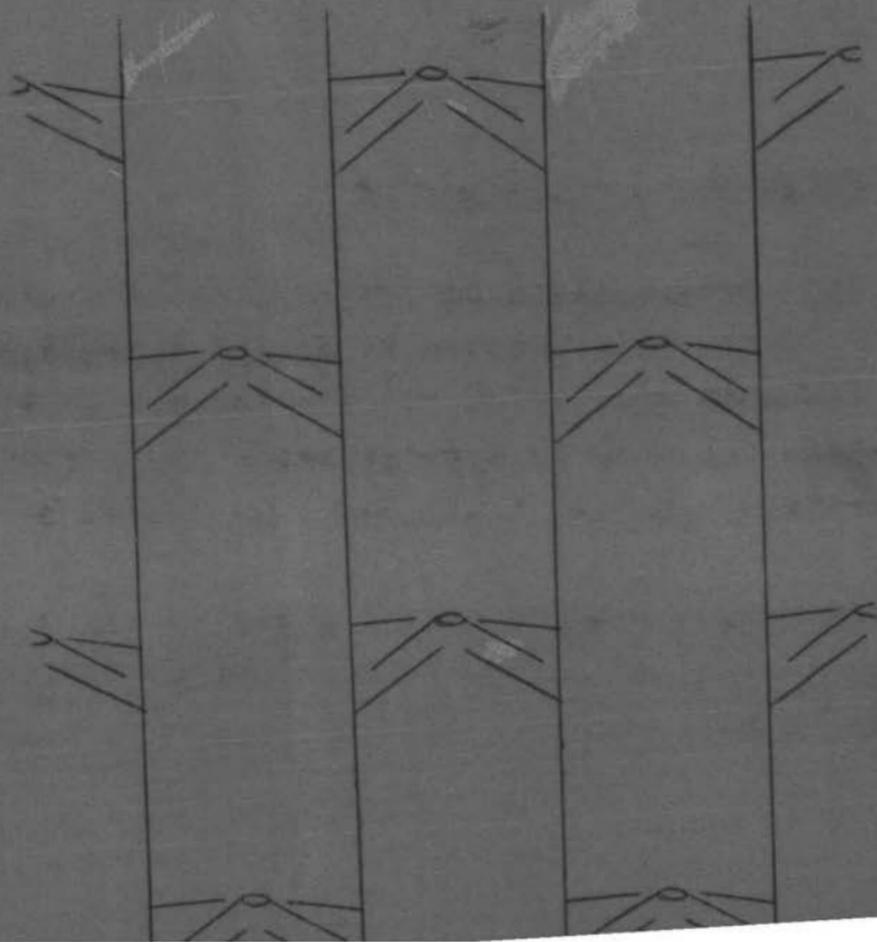


FIG. 5. 3_a

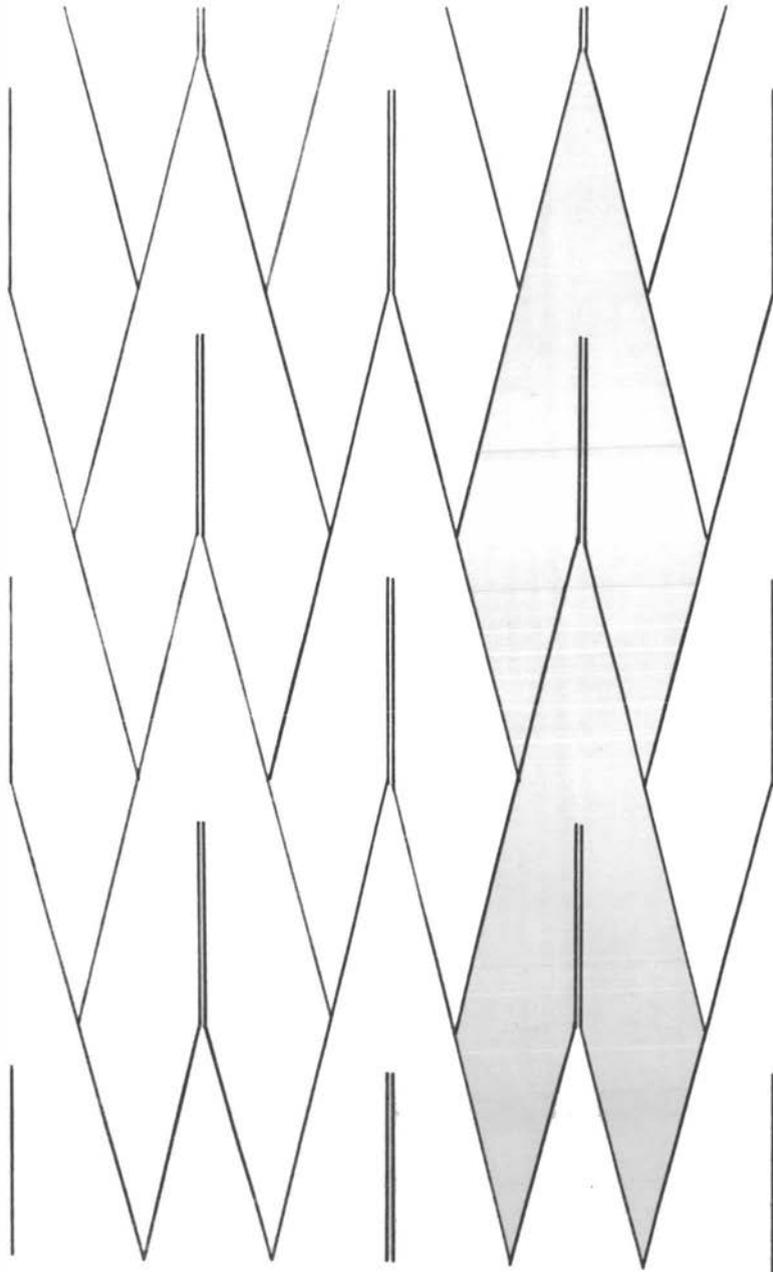


FIG. 5.3 Calycanthus occidentalis

(a) Diagrammatic representation of contribution
of stelar system to foliar appendages

The distance over which two strands are parallel
and very close together is approximately one internode
and is immediately prior to departure of traces to leaves.

(b) In the superimposed transparency the
cortical system is red and strands of the axillary
shoot system green.

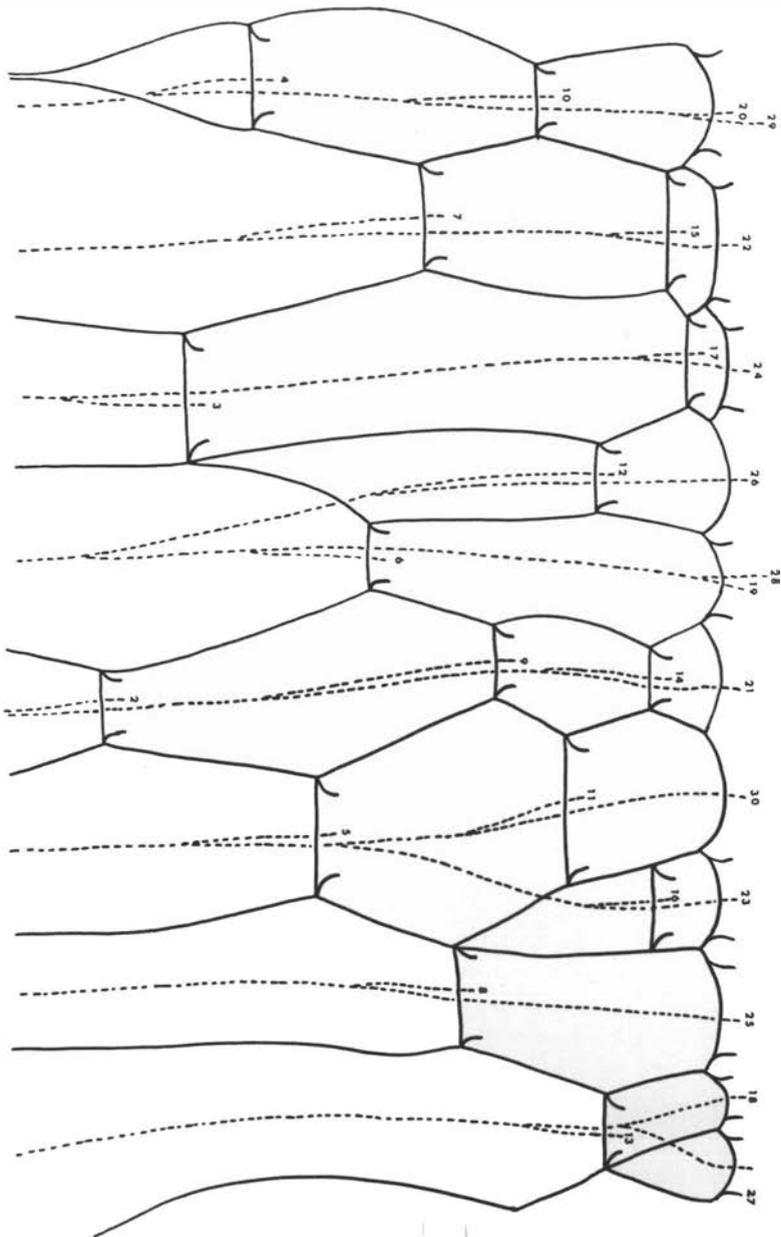


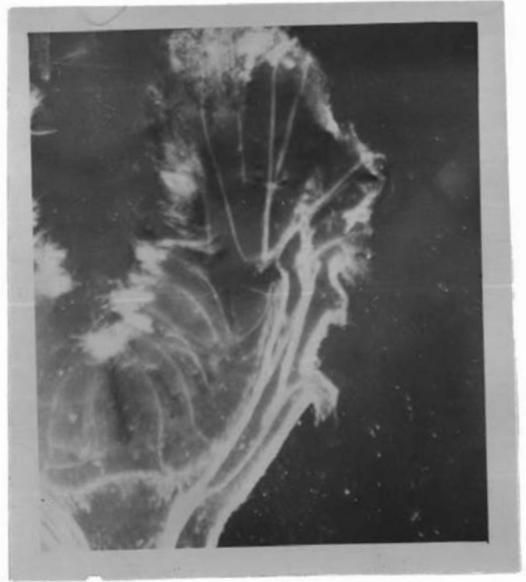
FIG. 5. 4

FIG. 5.4 Calycanthus occidentalis Vascular supply of tepals depicted as if flower were slit down one side, opened out and reduced to one plane

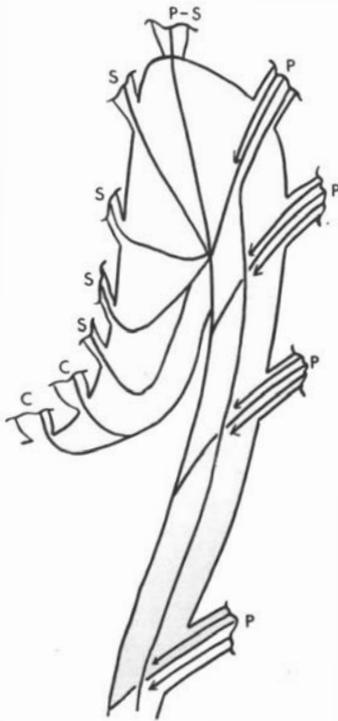
Cortical system and its branches (tepal laterals) indicated by solid lines and stelar system and midveins as broken lines in appendages 2-30.

Considerable similarity between this cortical system and that of the vegetative portion (fig. 5.3b) will be noted although there is subdivision of cortical strands, and the connections between adjacent cortical strands occur at the points of departure of traces. There is less similarity between this stelar system and that of fig 5.3a, the dual origin of midvein traces not being evident. In most cases the midvein, as it passes through the cortex, is joined to the connection between cortical strands.

It will be seen that some of the higher tepals (20, 21, 26, 28, 29 and 30) lack a lateral supply.

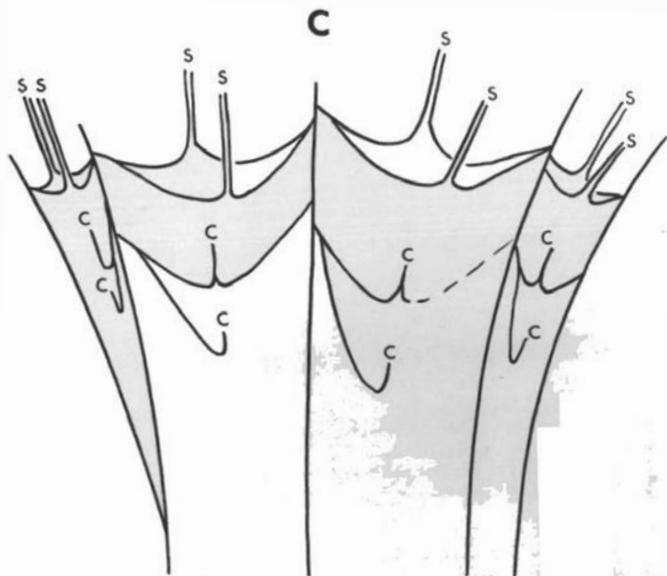


a



b

FIG. 5.5



c

FIG. 5.5 Calycanthus occidentalis Floral vasculature

(a) Photomicrograph of one side of cleared flower indicating floral vasculature

(b) Diagrammatized interpretation of fig. 5.5a

P = perianth member (tepal) - indicated with lateral supply from cortical system and midvein from stelar system.

P-S = appendage of character intermediate between tepal and stamen (e.g. 31 in fig. 5.1). One trace only is evident and this is from the stelar system.

S = stamen - indicated in this view as receiving one of the usually two stamen traces from the stelar system.

C = carpel - each also seen in this view to receive one trace from the stelar system.

(c) Stelar vascular system of cleared half flower as seen from the inside of the cup (compare fig. 5.5b) with supply to stamens and carpels indicated.

Each stamen is seen to receive one trace from each of two adjacent strands. Some carpels are also vascularized in this fashion (although traces are completely fused in the carpel base) while other carpels receive only one trace.

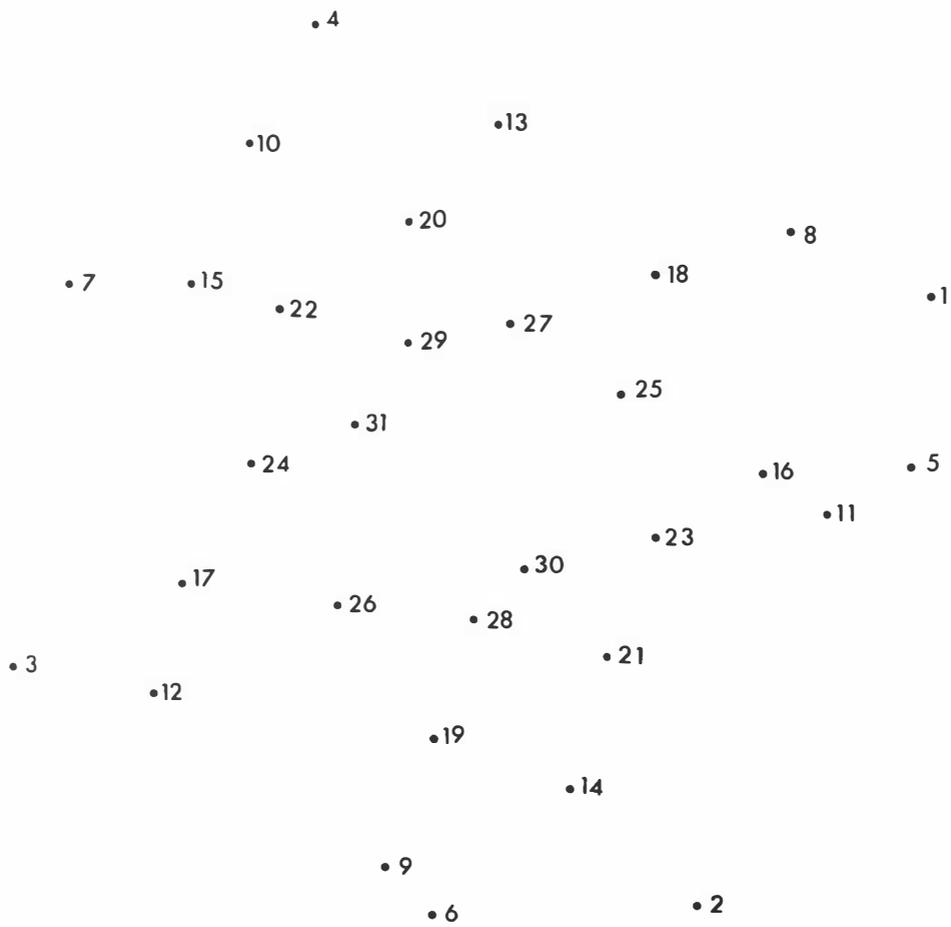


FIG. 5. 6

FIG. 5.6 Calycanthus occidentalis Phyllotaxis of
perianth members

The numbered dots are the positions of midveins where appendages leave the receptacle. The diagram has been conventionalized with lower members indicated outermost. In fact there is an increase rather than a decrease in the diameter of the receptacle as this portion of the floral axis is ascended.

Appendages are numbered from 1 (first above bracts) to 31. The opposite (bijugate) arrangement is evident in bracts and foliar members and may be said to persist a short distance into the perianth (i.e. 1 and 3, 2 and 4, 5 and 7 are almost opposite). Thereafter oppositeness is lost (e.g. 8 and 10, 10 and 12 etc.). The higher members seem in fact to be arranged in spiral fashion although the angle between them is variable. Parastichies, at least in any accepted sense, do not appear to exist and with the general tendency for the angle between successively initiated appendages to increase as the axis is ascended, a constant phyllotaxis fraction is not present.

N.B. Figs 5.4 and 5.6 have been compiled from the same flower.

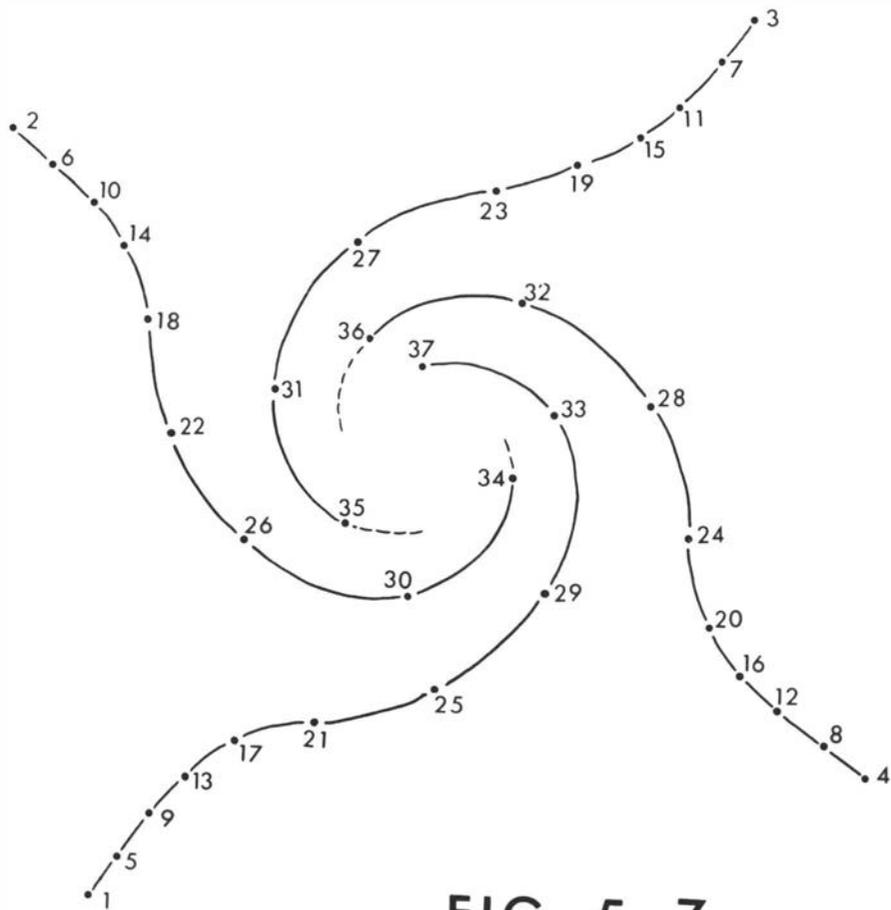


FIG. 5. 7

FIG. 5.7 Chimonanthus fragrans Phyllotaxis of perianth members

Notation as in fig. 5.6 although there are 37 members indicated.

The opposite arrangement of bracts and foliar members extends into the perianth, a bijugate tendency becoming evident after the first ten or twelve members. This latter arrangement continues throughout the higher perianth members although the highest members could as well be considered as being on a spiral. Again it does not seem possible to determine a constant phyllotaxis fraction by accepted methods. It is possible to simply regard the opposite (bijugate) arrangement as changing to a spiral arrangement more quickly in Galycanthus occidentalis than in Chimonanthus fragrans, and this is effected by larger angles developing between successively initiated appendages in the former species.

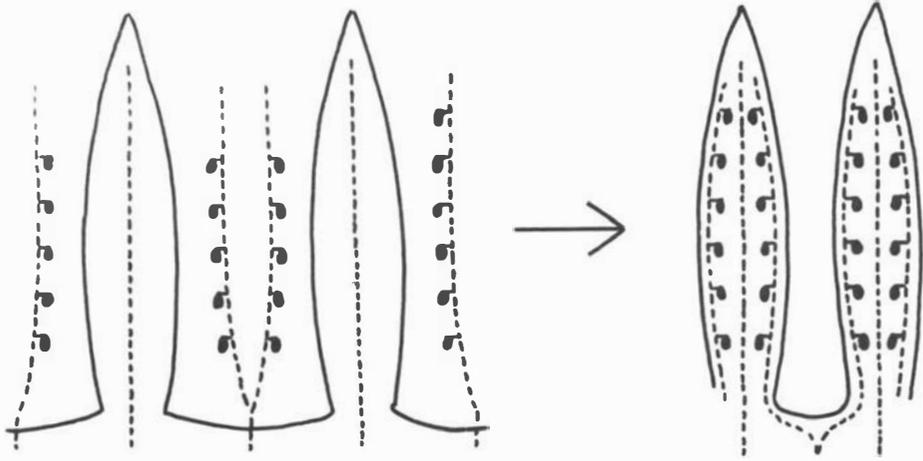


FIG. 6. 1

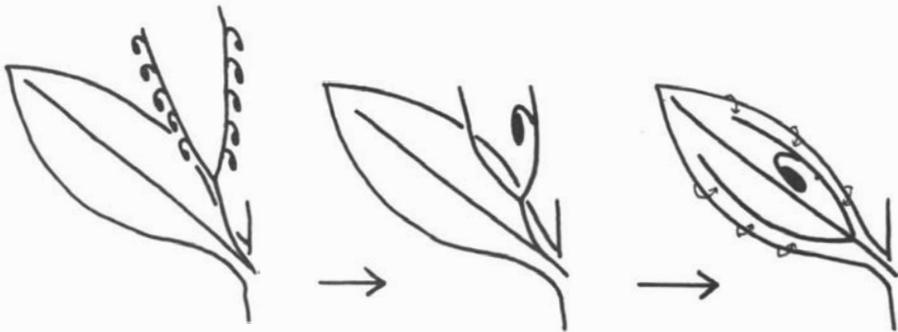


FIG. 6. 2

FIG. 6.1 Origin of follicles according to the Gonophyll theory

Dotted lines represent vascular bundles. On the left two tegophylls are indicated and between them a bifurcating ovuliferous branch. The fusion of the branches to adjacent tegophylls is represented on the right.

FIG. 6.2 Origin of an achene according to the Gonophyll theory

The sterile tegophyll with its associated bifurcating ovuliferous branch is depicted on the left, reduction in number of ovules in the centre, and adnation of the fertile branch to the tegophyll followed by rolling of the tegophyll margins on the right.

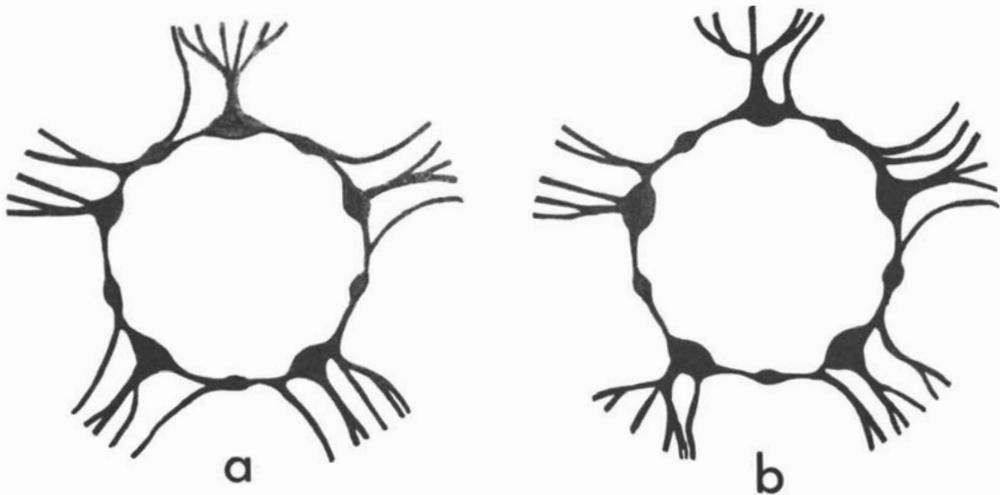


FIG. 6.3

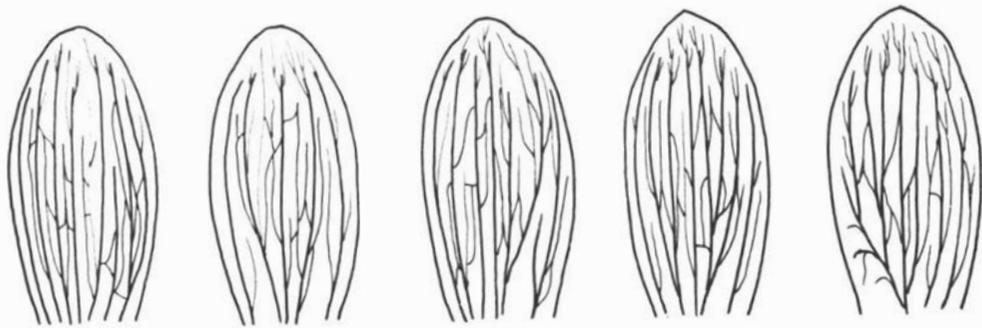


FIG. 6.4

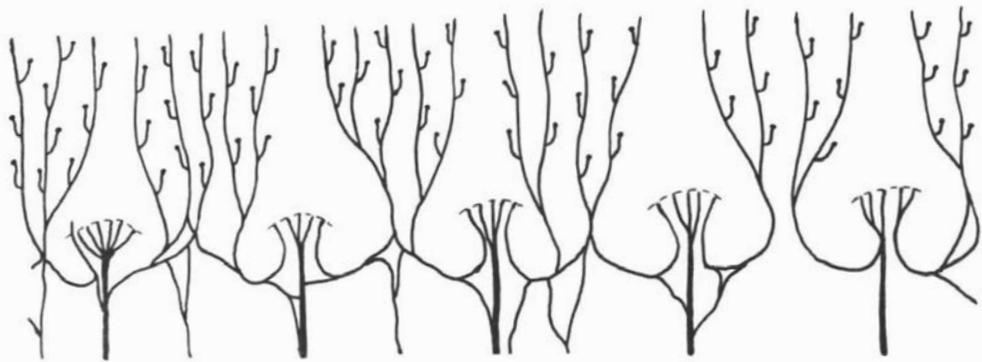


FIG. 6.5

FIG. 6.3 Reconstruction of transverse section from the base of two flowers of Caltha palustris

Each embodies the vascular system included in ten successive sections cut at 10 μ . The "ring" is obvious and the base of the tepal supply is also depicted. It can be seen that in no two tepals is the vascular supply identical.

FIG. 6.4 Venation of the five tepals whose bases appear in fig. 6.3a.

The tepal represented on the left is uppermost in the earlier figure and the others in order to the right correspond to those in clockwise sequence in fig. 6.3a. Only occasional anastomoses between lateral traces and others are evident.

FIG. 6.5 Schematic representation of main traces (other than carpellary) in a whole flower of C. palustris

This is again based on the flower of fig. 6.3a with the upper tepal of that figure on the left in fig. 6.5. The course of traces which ascend beyond tepals - which tend to bifurcate shortly above tepals and thereafter retain approximately parallel courses - can be seen.

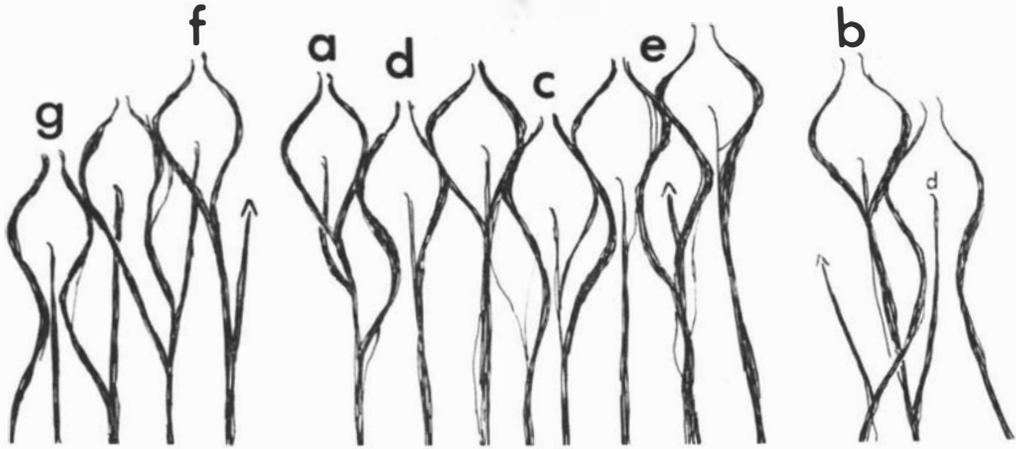


FIG. 6.6

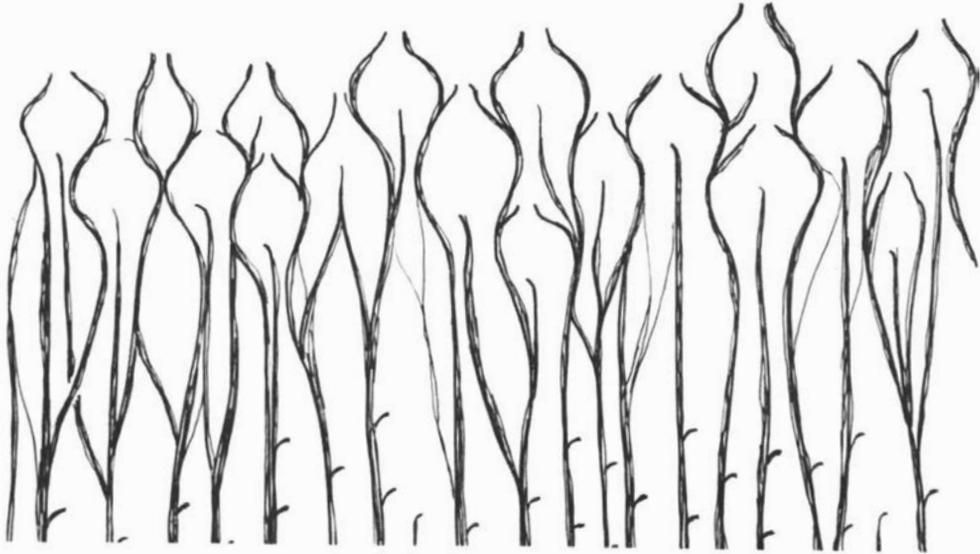


FIG. 6.7

FIG. 6.6 Some of the lower carpels from three separate flowers of Caltha palustris

The drawings indicate the various types of relationship between the carpel traces as mentioned in the text. The tendency for dorsal traces to leave appreciably below ventrals is indicated.

Reconstructions based on cleared preparations at the time of anthesis.

FIG. 6.7 Vascular supply to all of the carpels of a single flower of C. palustris.

Part of the androecial supply is also indicated. Reconstruction of a cleared flower at anthesis.

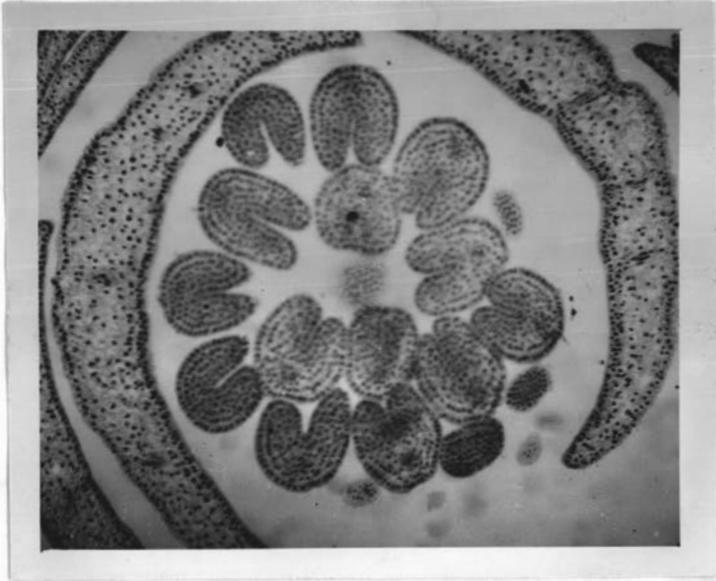


FIG. 6.8

FIG. 6.9

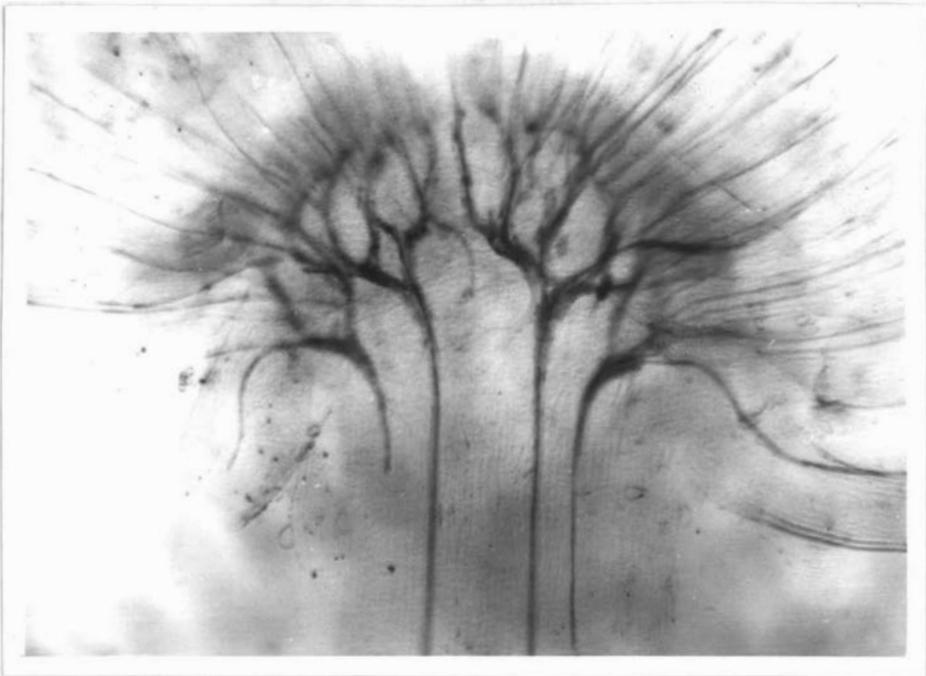


FIG. 6.8 Photomicrograph of floral bud of Caltha palustris indicating residual apex above carpels (x50)

FIG. 6.9 Photomicrograph of cleared half flower of C. palustris taken shortly after vascular tissue has first appeared in the bud (x25)

Three pedicel traces and portions of a fourth can be seen. Centrally, traces can be seen to be diverging from two adjacent tepals though not meeting.

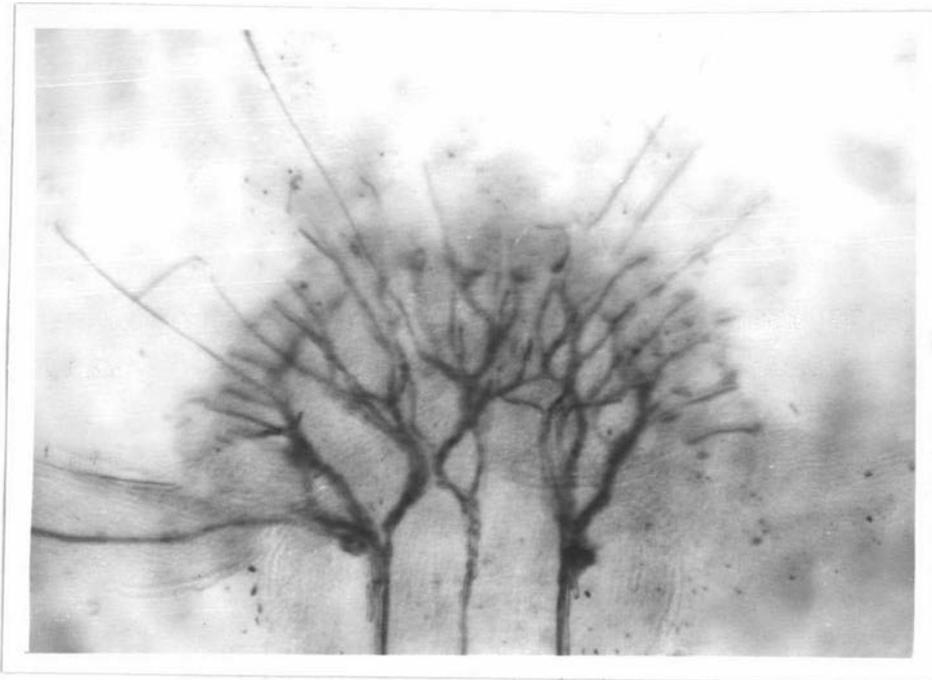


FIG. 6.10

FIG. 6.11

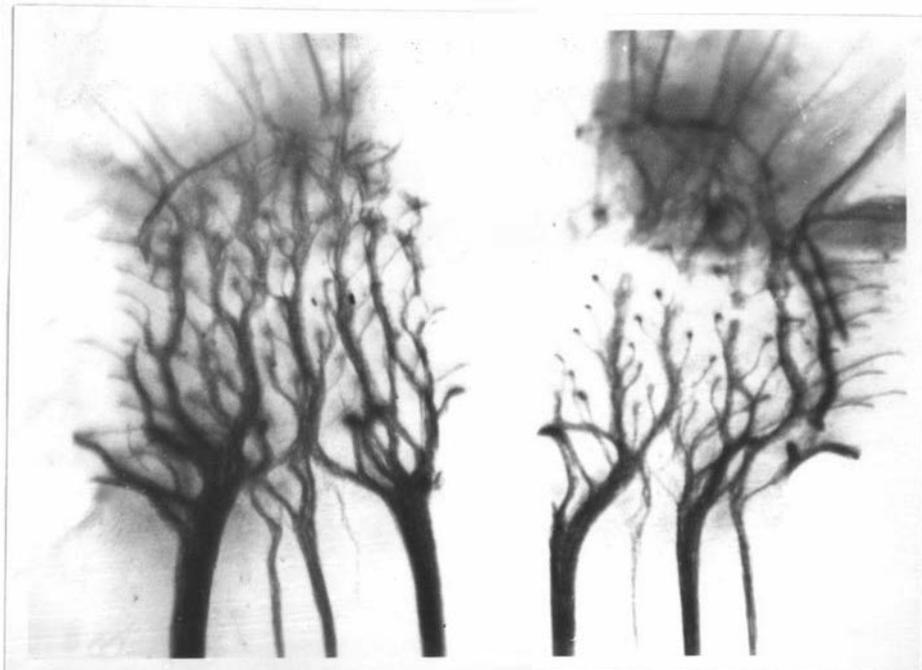


FIG. 6.10 Cleared half flower of Caltha palustris at a slightly later stage than fig. 6.9. (x25)

This shows diverging pedicel traces much closer, in fact probably fused.

FIG. 6.11 Cleared half flower of C. palustris about the time of anthesis (x25)

The secondary pedicel traces have appeared and the diverging pedicel traces are now definitely fused.

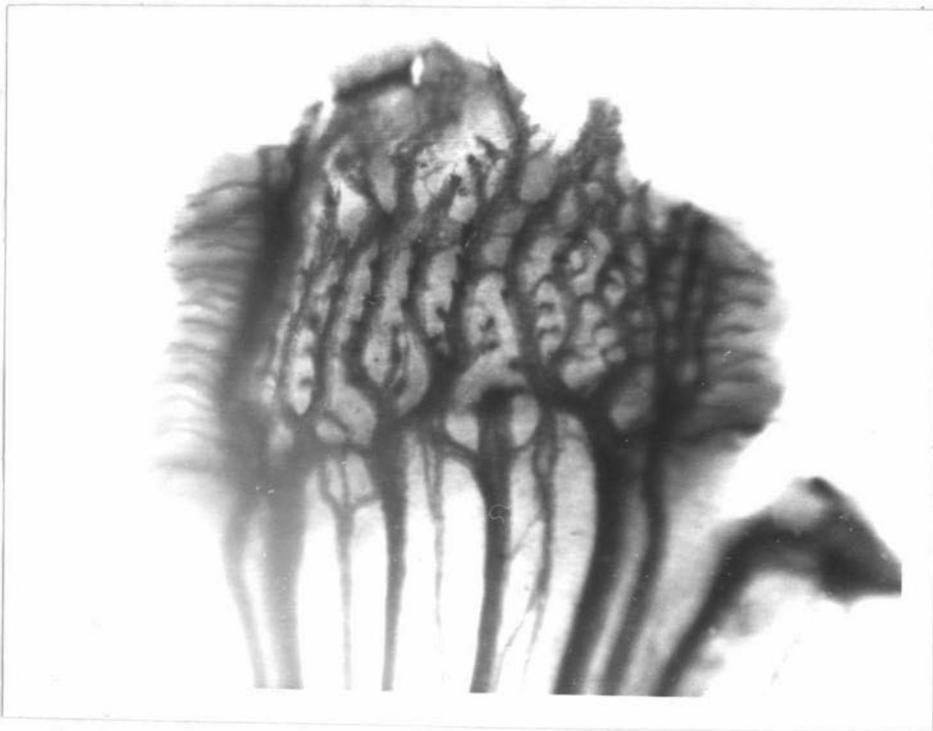


FIG. 6.12

FIG. 6.13

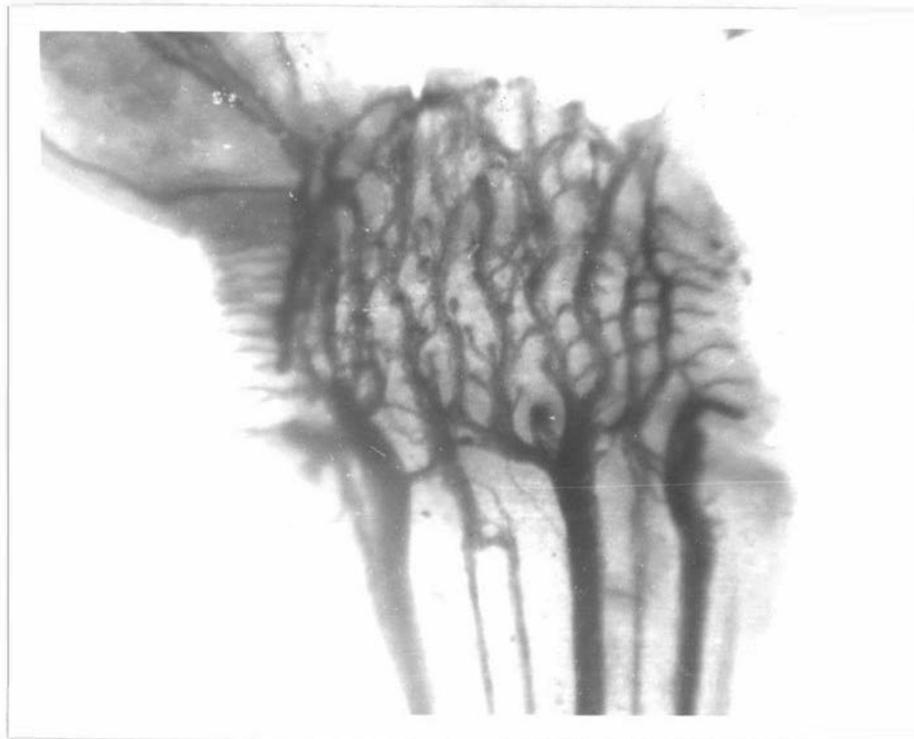


FIG. 6.12 Cleared half flower of Caltha palustris shortly after anthesis (x15)

Compared to fig. 6.11 greater thickness of traces, more branching from secondary pedicel traces and connections between ascending traces above the tepals are evident.

FIG. 6.13 Similar to fig. 6.12 although probably slightly older (x15)

Note more communication between ascending traces in the androecial region. Traces to a carpel remain at upper left. The two ventrals in close proximity near the carpel base can be seen some distance above the dorsal trace.

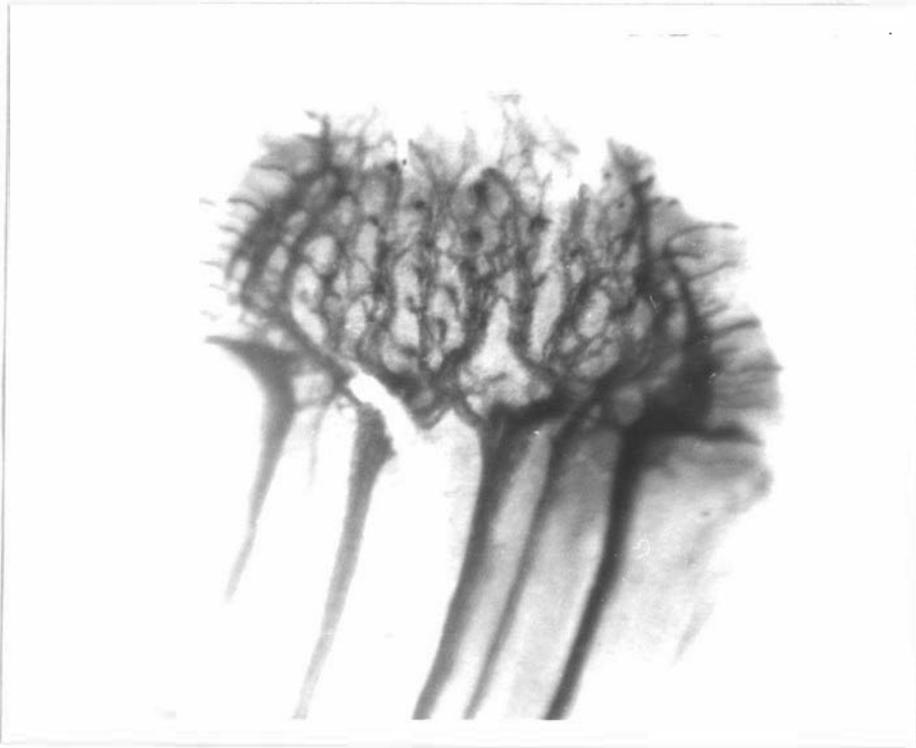


FIG. 6.14

FIG. 6.15



FIG. 6.14 Cleared half flower of Caltha palustris when
fruit is approaching maturity (x15)

The reticulation above the perianth is increasing.

FIG. 6.15 Cleared half of the mature fruit of C. palustris
(x15)

The reticulation in the androecial region is typical
and here is of its maximum extent.

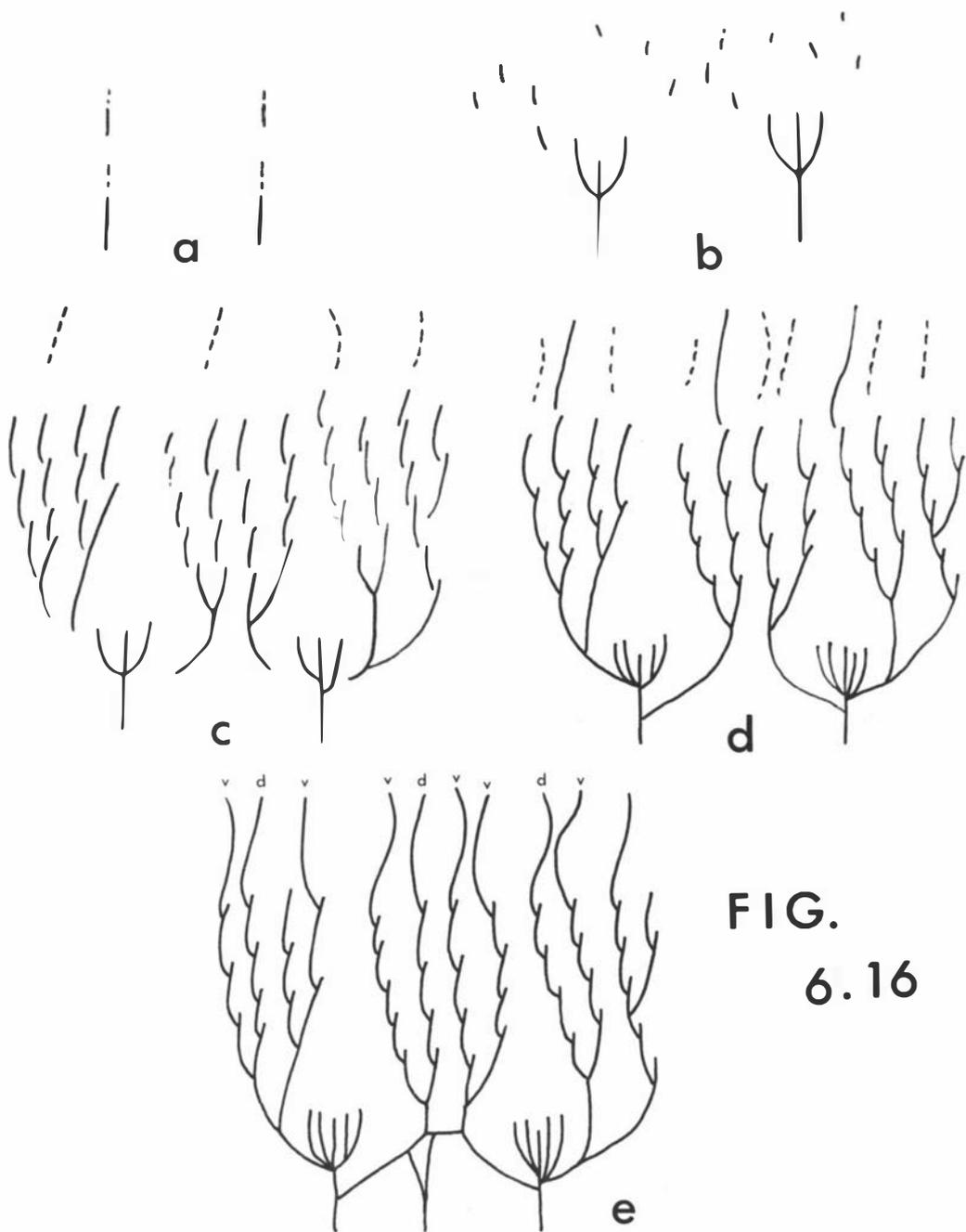


FIG.
6.16

FIG. 6.16 Diagrammatic representation of five stages in development of vascular system in flower of Caltha palustris

(a) Evidence of vascular tissue in tepals and perianth.

(b) Vascular tissue well developed in tepals and pedicel. Development commencing in stamens.

(c) Stamen traces well developed but not yet basally connected. The connection of upper stelar regions to the pedicel strands is incomplete although carpellary dorsals are appearing.

(d) The stele above the perianth is complete and continuous although carpellary dorsals are not yet joined to the stele. Carpellary ventrals are appearing. This is approximately equivalent to fig. 6.8.

(e) Floral vasculature at anthesis. All major components are present. Subsidiary pedicel strands are evident and branches from adjacent strands are fused. This is approximately equivalent to fig. 6.11.

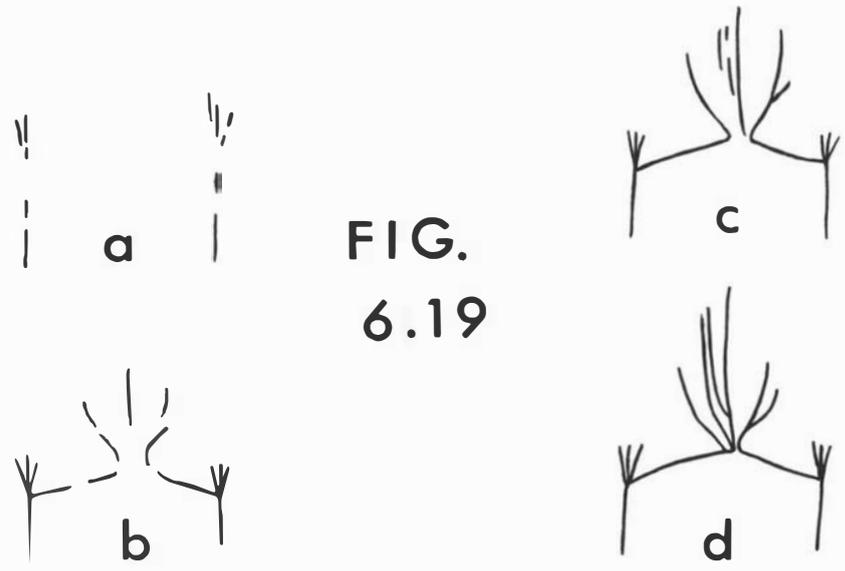
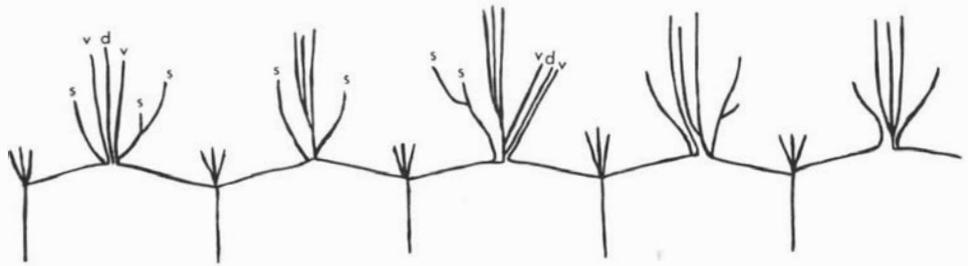


FIG. 6.17 (a) General outline of L.S. flower of Caltha novae-zelandiae at anthesis indicating shape of receptacle

(b) Similar outline of C. palustris

FIG. 6.18 Diagrammatic representation of vasculature of flower of C. novae-zelandiae

s = stamen trace

d = carpellary dorsal

v = carpellary ventral

FIG. 6.19 Four stages in the development of the vascular system in a sector of the flower of C. novae-zelandiae

The carpel depicted is that second from right in fig.6.18

(a) Evidence of vascular tissue in tepals and pedicel.

(b) Elements of vascular tissue appearing in stamens and as a dorsal trace in the carpel.

(c) Carpellary ventrals appearing.

(d) At anthesis.

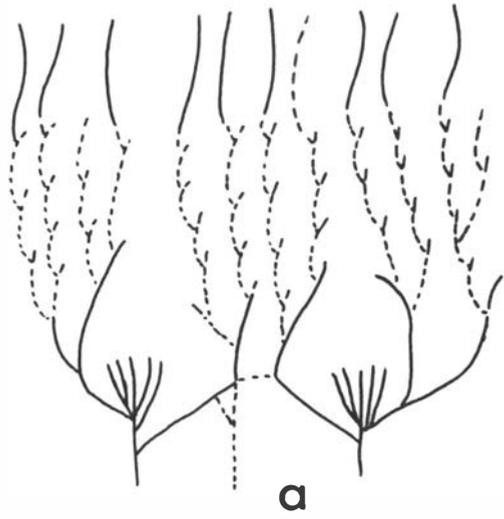


FIG. 6.20

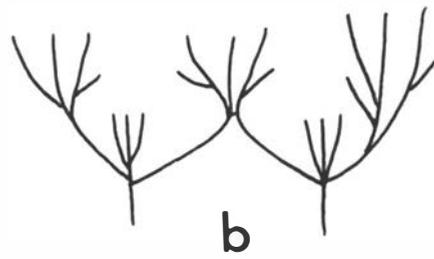


FIG. 6.21

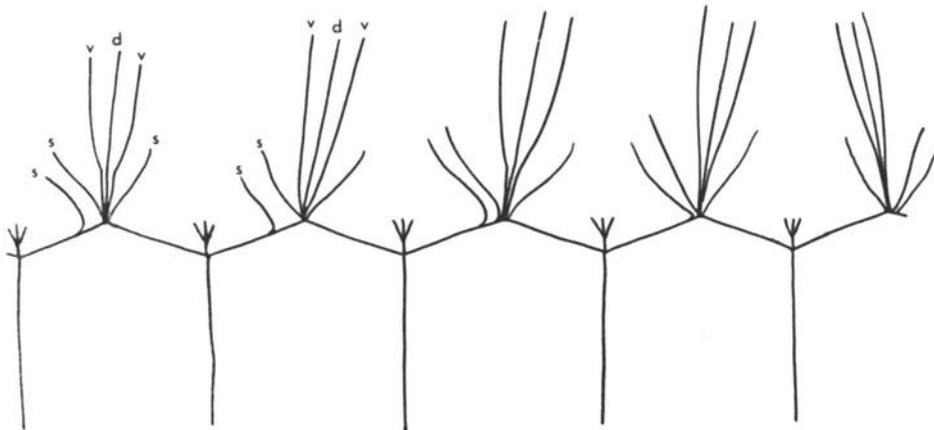


FIG. 6.20 (a) Floral vascular system of Caltha palustris
(also figured in fig 6.16)

Dotted lines represent vascular bundles which if deleted would result in the pattern represented in (b).

(b) Derived from (a) this corresponds very closely to the situation depicted for C. novae-zelandiae (fig. 6.18).

FIG. 6.21 Diagrammatic representation of vasculature of flower of C. obtusa

s = stamen trace

d = carpellary dorsal

v = carpellary ventral

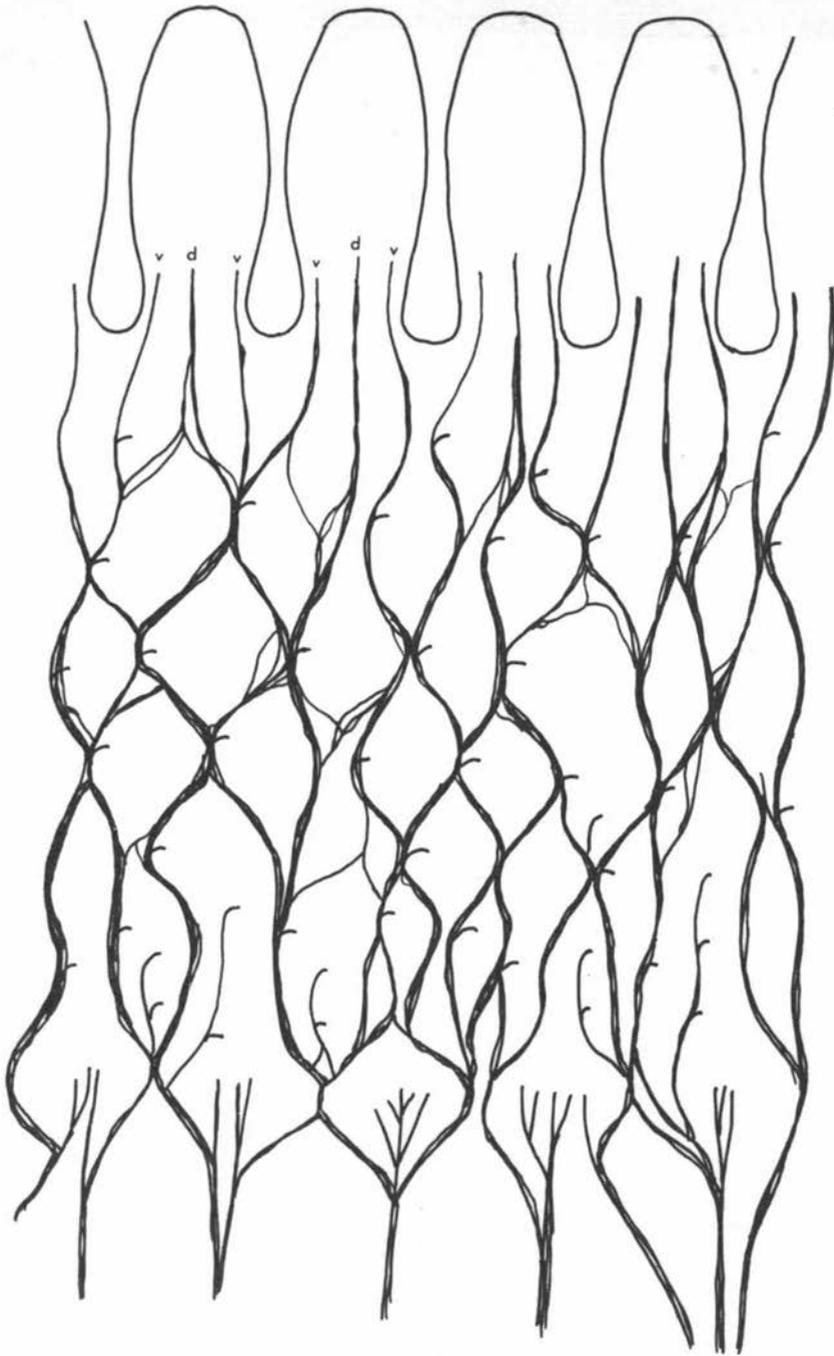


FIG. 6.22

FIG. 6.22 Reconstruction of vasculature of whole flower
of Helleborus niger at anthesis

A reticulation of traces is clearly visible in the androecial region and variability of carpellary trace origin is also evident. This is at a stage approximately equivalent to fig. 6.26.

d = carpellary dorsal

v = carpellary ventral

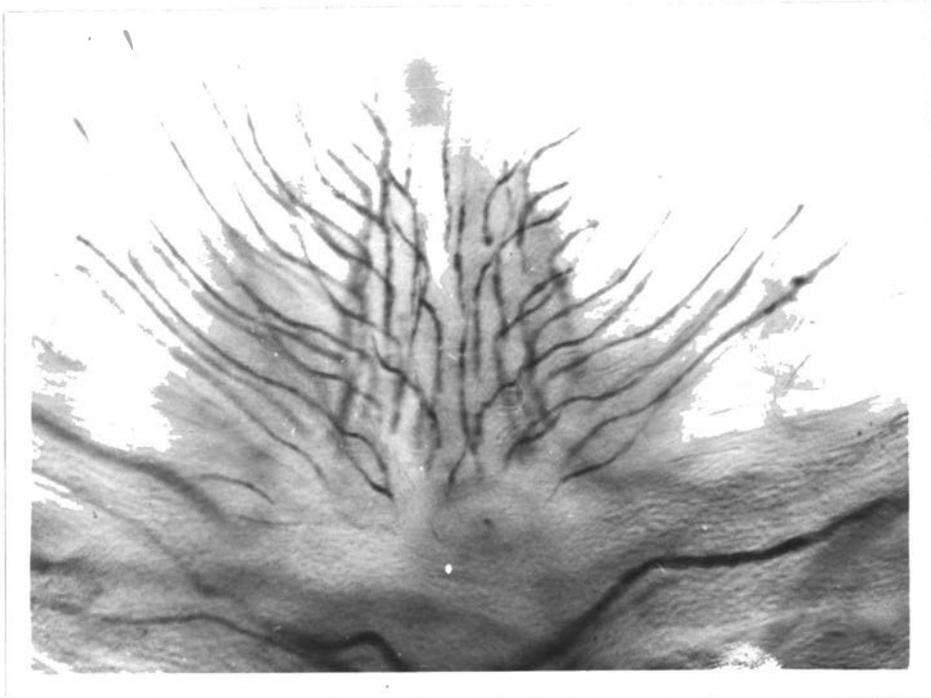


FIG. 6.23

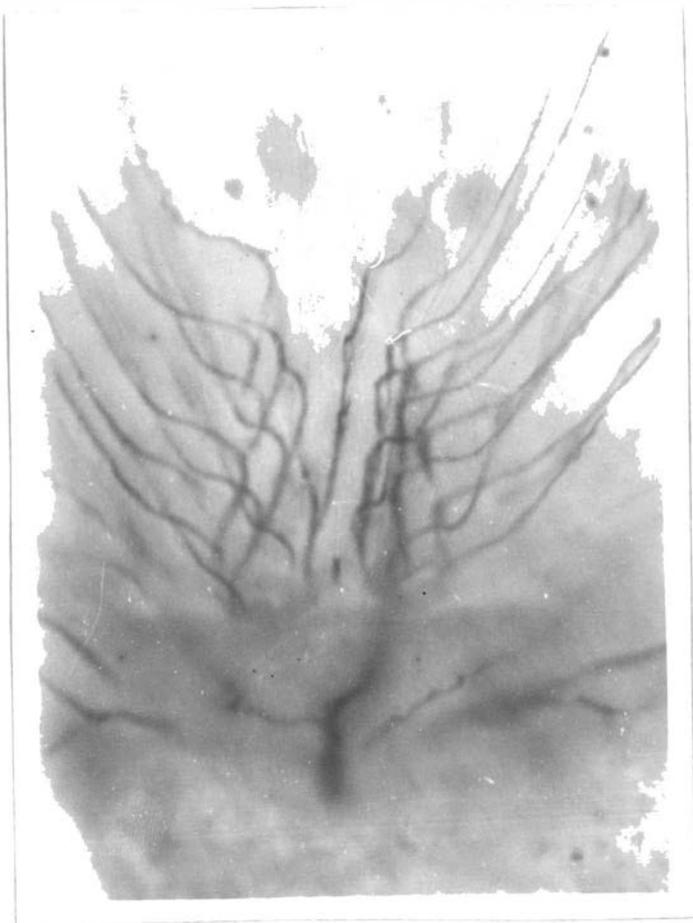


FIG. 6.24

FIG. 6.23 Photomicrograph of cleared half flower of
Helleborus niger (x15)

At this stage traces have not long been established
and the bases of stamen traces are not yet fused.

FIG. 6.24 As with 6.23 but with bases of stamen traces
now fused to form essentially straight parallel
traces in the androecial region (x15)

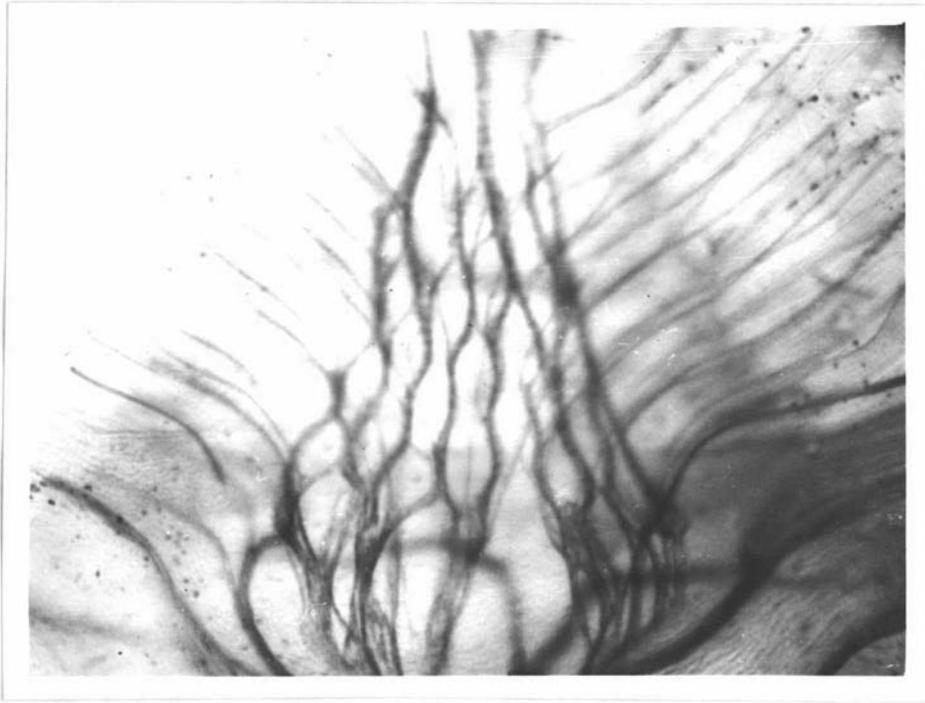


FIG. 6.25

FIG. 6.26

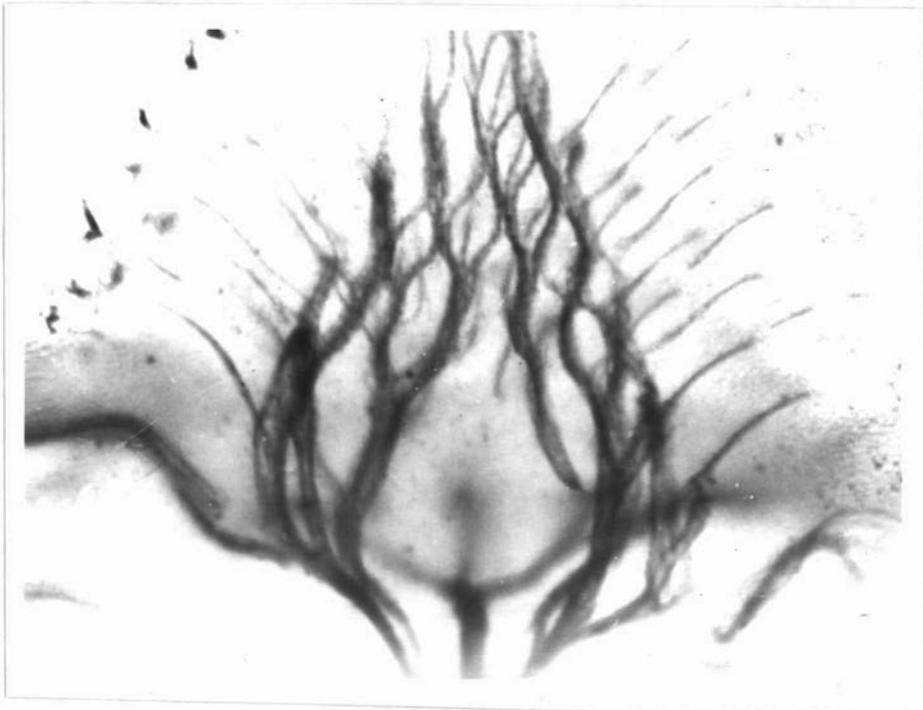


FIG. 6.25 Cleared half flower of Helleborus niger just prior to anthesis (x10)

Undulations of stelar strands in the androecial region are especially obvious.

FIG. 6.26 As 6.25 although at anthesis (x10)

A reticulation of vascular strands in the androecial region is now evident.

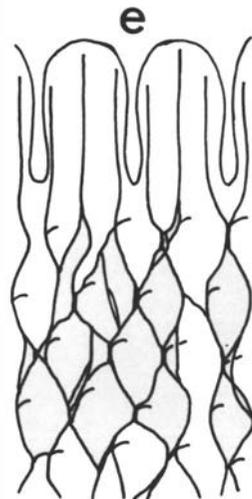
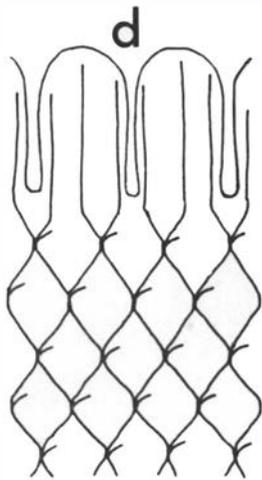
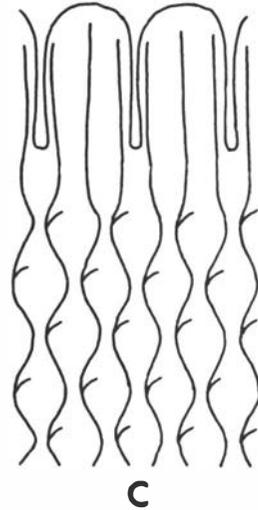
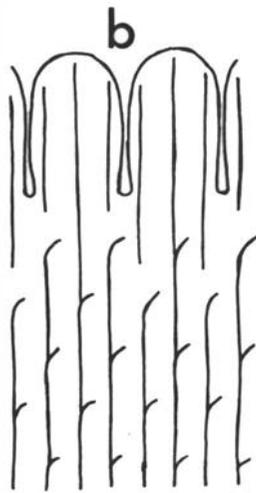
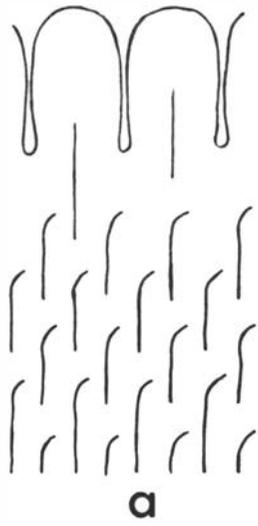


FIG.
6.27

FIG. 6.27 Diagrammatic representations of five stages in the development of the upper portion of the floral vascular system of Helleborus niger

(a) Stamen and dorsal carpellary traces appearing. (Approximately equivalent to fig. 6.23)

(b) Stamen and dorsal carpellary traces fused to produce a recognizable stele. (Approximately equivalent to fig. 6.24)

(c) Undulations appearing in stelar bundles in androecial region. (Approximately equivalent to fig. 6.25)

(d) Situation at anthesis. (Approximately equivalent to fig. 6.26)

(e) Same stage as (d) but drawn from an actual cleared half flower.

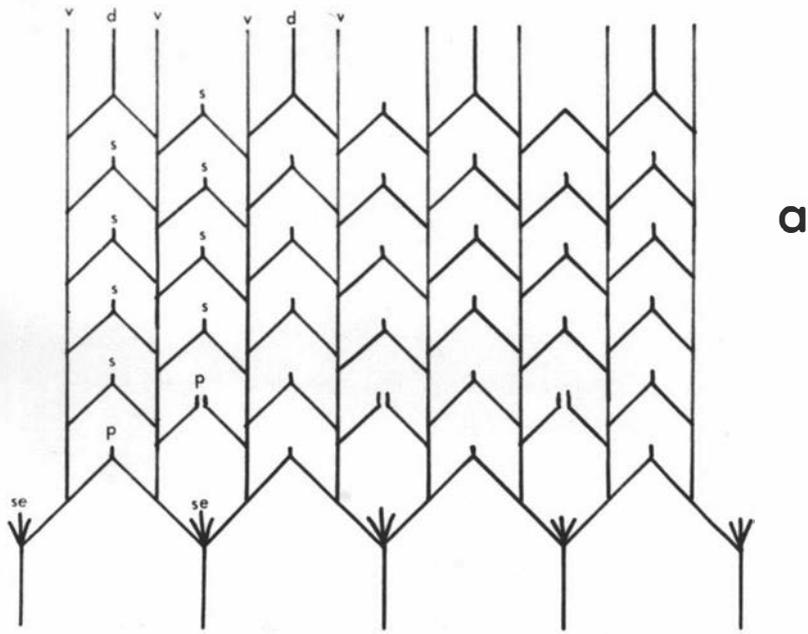


FIG. 6.28

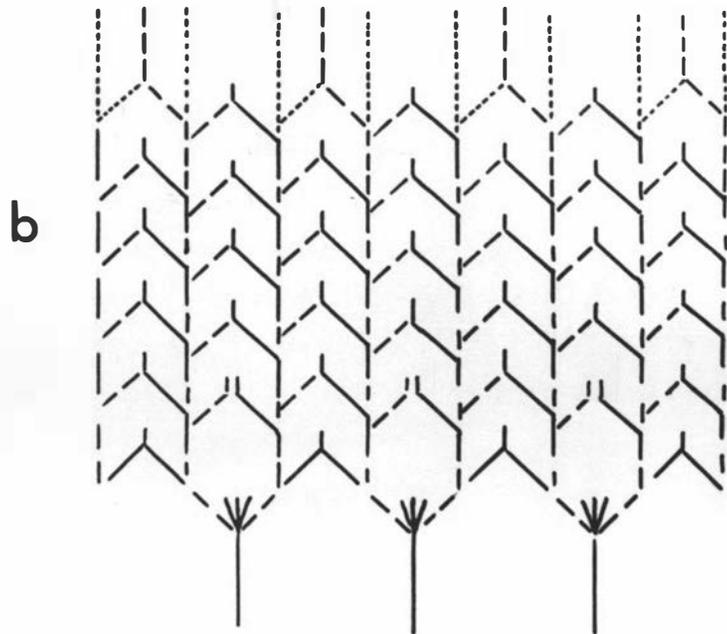


FIG. 6.28 (a) Diagram of floral vasculature of Aquilegia vulgaris compiled from half flowers cleared at anthesis

One trifurcating trace can be seen to contribute to each sepal (se), two (which may or may not remain distinct in the appendage) to each petal (p), and two (which become fused in the appendage) to each stamen (s). The dorsal carpellary trace (d) has origins like stamen traces while carpellary ventrals (v) appear to be direct continuations of stelar strands.

(b) Similar diagram to (a) but compiled in order to emphasize sequence of appearance of major vascular components

Solid lines indicate first tissue to appear, long dotted broken lines that which appears second, and short dotted broken lines that which appears last.

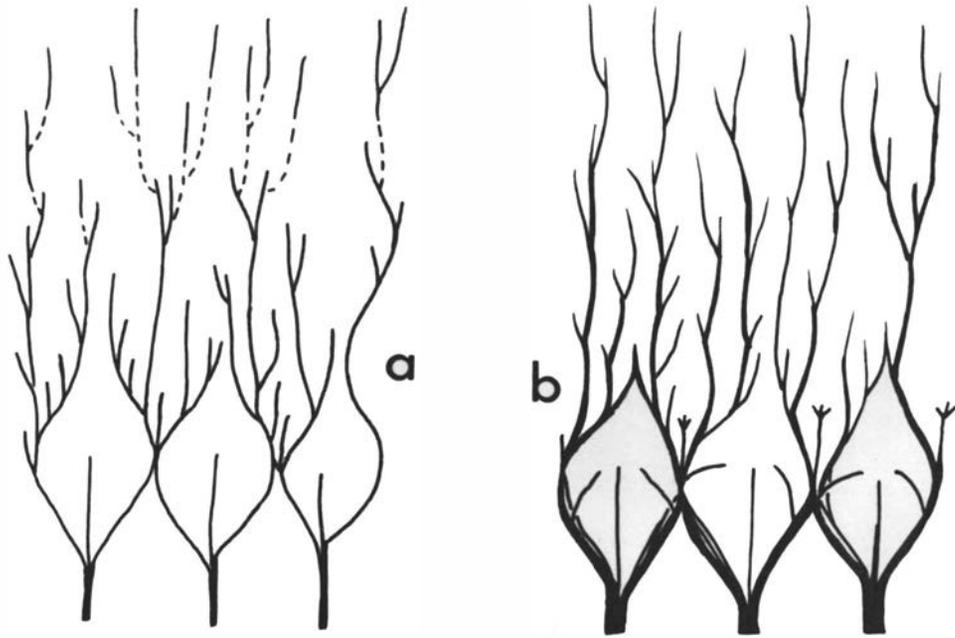


FIG. 6.29



FIG. 6.29 Development of the floral vascular system of
Ranunculus repens

(a) and (b) are based on young cleared half flowers,
(c) is after Tepfer 1953.

(a) Shortly after vascular tissue has appeared in the floral bud. A single trace is visible in each sepal, petal and stamen. Dotted lines indicate developing strands, (i.e. basal connections of carpellary traces are not yet established).

(b) Just prior to anthesis. Three traces can be seen running to each sepal, one (trifurcating) in each petal and one in each stamen and each carpel.

(c) Young fruit stage. Considerable thickening of lower strands tends to obscure precise nature of sepal, petal and stamen trace origins. The ventral carpellary bundles are not shown.

c = carpel

s = stamen

p = petal

se = sepal

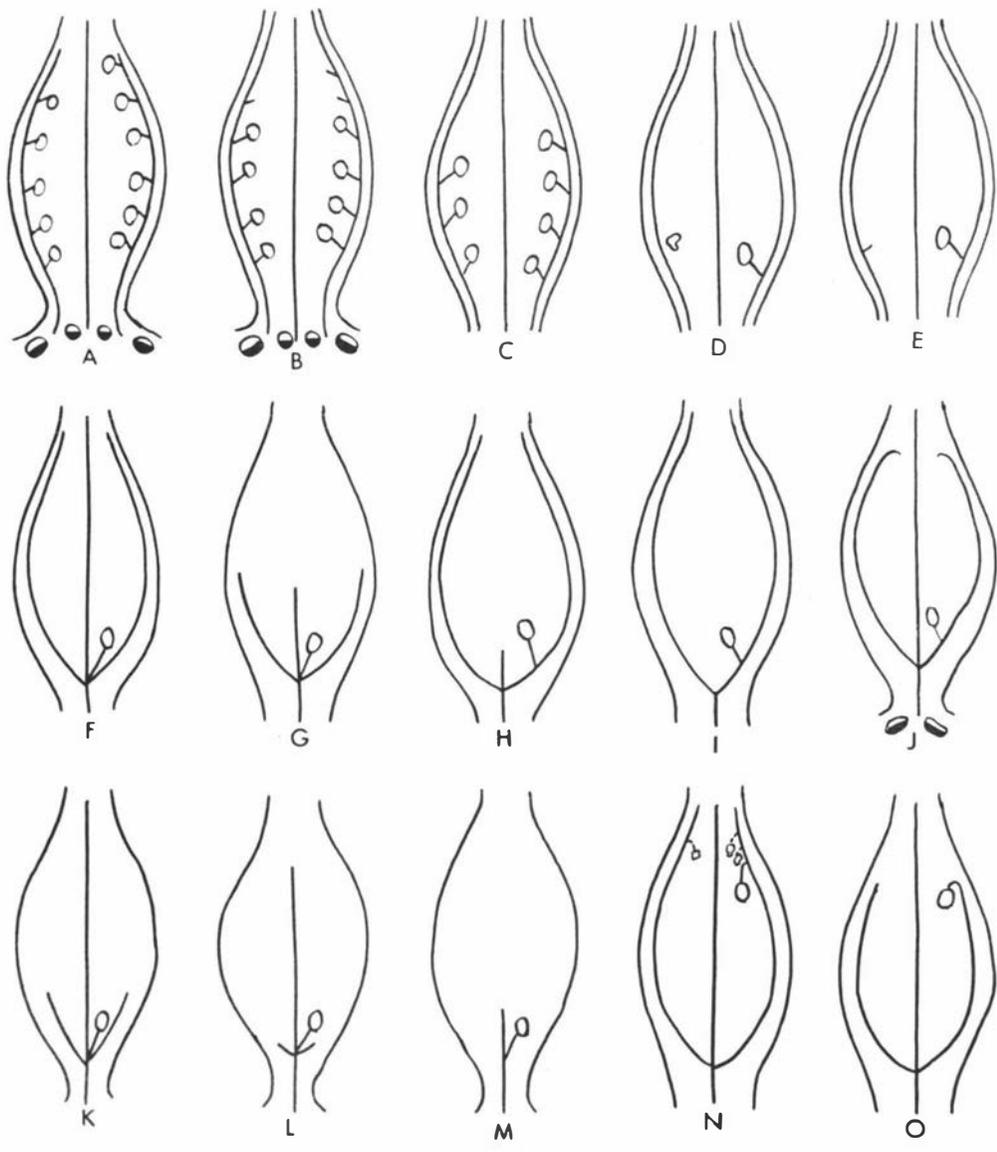


FIG. 6. 30

FIG. 6.30 Vasculature of follicles (A-E) and of achenes (F-O) after Eames (1961)

As commented in the text, the existence of stelar bundles between the three running to a carpel in Helleborus (A) would be most surprising and may indeed be an error. It is also commented that the gap between the most reduced follicle shown (E Waldsteinia) and the first achene (F Geum) is not effectively bridged either in this drawing or in Eames' accompanying description.

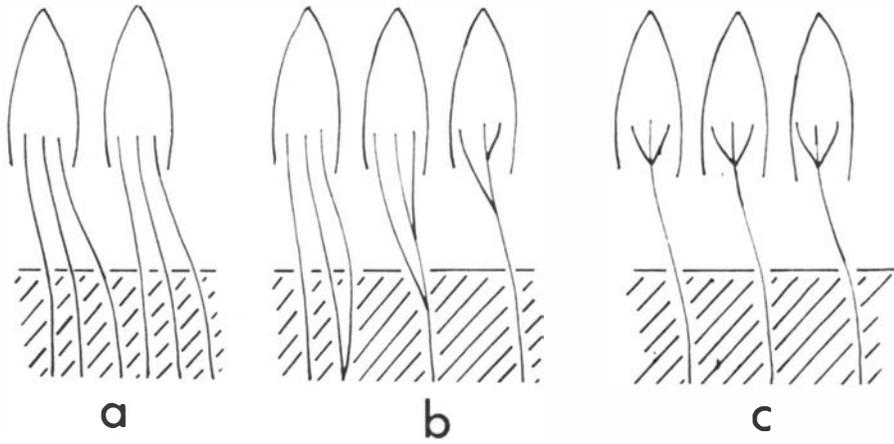


FIG. 6.31

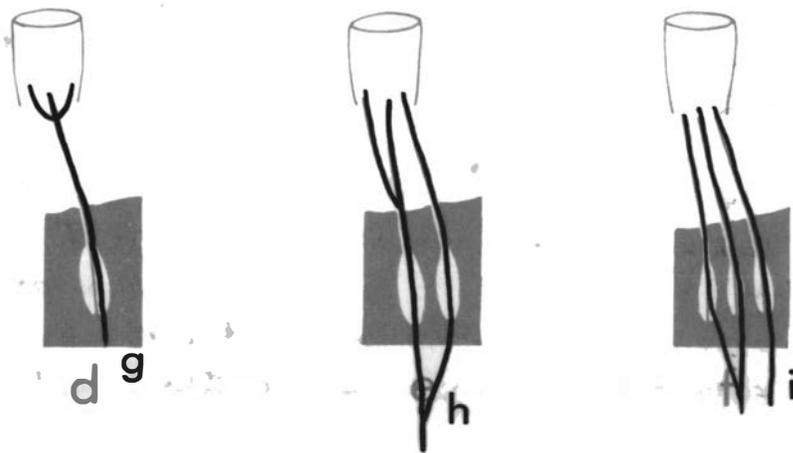


FIG. 6.31 Diagrams indicating possible relationship between unilacunar and trilacunar nodes (achene and follicle respectively)

- a. Follicle type vasculature after secondary thickening has occurred. (Stele cross hatched)
- b. Some of the hypothetical types which could be intermediate between follicle and achene.
- c. Achene type vasculature.
- d. } Types of node in Hieracium after secondary
- e. } thickening has taken place. (Stele black)
- f. } d could be regarded as achene type, f as follicle type and e as an intermediate (after Philipson).
- g. } The transparency superimposed on d, e, and f
- h. } indicates the increased variety which
- i. } might be evident if only primary tissues were considered. Such intermediate types seem unknown among follicles and achenes.

PART SIX

REFERENCES

REFERENCES

Titles of periodicals abbreviated in accordance with "The World List of Scientific Periodicals," 4th ed. 1963-65.

References marked + not seen.

- ALLAN, H.H. 1961: "Flora of New Zealand." Vol. 1.
Government Printer, Wellington.
- ARBER, A. 1946: Goethe's botany. Chronica Bot. 10:
67-124.
- ARBER, A. 1950: "The Natural Philosophy of Plant Form."
Cambridge University Press, Cambridge.
- ARBER, E.A.N. and PARKIN, J. 1907: On the origin of
angiosperms. J. Linn. Soc. (Bot.) 38: 29-80.
- BAILEY, I.W. 1956: Nodal anatomy in retrospect. J.
Arnold Arbor. 37: 269-287.
- BAILEY, I.W. and NAST, C.G. 1943a: The comparative
morphology of the Winteraceae. I. Pollen
and stamens. J. Arnold Arbor. 24: 340-346
- BAILEY, I.W. and NAST, C.G. 1943b: The comparative
morphology of the Winteraceae. II. Carpels.
J. Arnold Arbor. 24: 472-481.
- BAILEY, I.W. and NAST, C.G. 1945: The comparative
morphology of the Winteraceae. VII. Summary
and conclusions. J. Arnold Arbor. 26: 37-47.
- BAILEY, I.W., NAST, C.G. and SMITH, A.C. 1943: The
family Himantandraceae. J. Arnold Arbor. 24:
190-206.
- BAILEY, I.W. and SMITH, A.C. 1942: Degeneriaceae, a new

- family of flowering plants from Fiji. J. Arnold Arbor. 23: 356-365.
- BALFOUR, E.E. and PHILIPSON, W.R. 1962: The development of the primary vascular system of certain dicotyledons. Phytomorphology 12: 110-143.
- BENSON, L. 1957: "Plant Classification." Heath, Boston.
- BERSIER, J.-D. and BOCQUET, G. 1960: Les méthodes d'éclaircissement en vascularisation et en morphogénie végétales comparées. Arch. Sci. (Genève) 13: 535-556.
- BESSEY, E.A. 1898: The comparative morphology of the pistils of the Ranunculaceae, Alismaceae and Rosaceae. Bot. Gaz. 26: 297-313.
- BOKE, N.H. 1940: Histogenesis and morphology of the phyllode in certain species of Acacia. Am. J. Bot. 27: 73-90.
- BOKE, N.H. 1948: Development of the perianth in Vinca rosea L. Am. J. Bot. 35: 413-423.
- BOKE, N.H. 1949: Development of the stamens and carpels in Vinca rosea L. Am. J. Bot. 36: 535-547.
- BROULAND, M. 1935: Recherches sur l'anatomie florale des Renonculacées. Botaniste 27: 1-278.
- CANRIGHT, J.E. 1952: The comparative morphology and relationships of the Magnoliaceae. I. Trends of specialization in the stamens. Am. J. Bot. 39: 484-497.
- CANRIGHT, J.E. 1953: The comparative morphology and relationships of the Magnoliaceae. II. Significance of the pollen. Phytomorphology 3: 355-365.
- CANRIGHT, J.E. 1955: The comparative morphology and relationships of the Magnoliaceae. IV. Wood and nodal anatomy. J. Arnold Arbor. 36: 119-140.

- CANRIGHT, J.E. 1960: The comparative morphology and relationships of the Magnoliaceae. III. Carpels. Am. J. Bot. 47: 145-155.
- CHAMPAGNAT, M. 1961: Recherches de morphologie descriptive et experimentale sur le genre Linaria. Annls Sci. nat. (Bot.) Ser. 12, 22: 1-170
- CHUTE, H.M. 1930: The morphology and anatomy of the achene. Am. J. Bot. 17: 703-723.
- CORNER, E.J.H. 1958: Transference of function. J. Linn. Soc. (Bot.) 56: 33-40.
- CORNER, E.J.H. 1963: A criticism of the Gonophyll theory of the flower. Phytomorphology 13: 290-292.
- CROIZAT, L. 1964: Thoughts on high systematics, phylogeny and floral morphogeny, with a note on the origin of Angiospermae. Candollea 19: 17-96.
- ⁺DANDY, J.E. 1927: The genera of the Magnolieae. Bull. Misc. Inform. Kew: 257-264.
- DE CANDOLLE, A.P. 1813: "Théorie Élémentaire de la Botanique." Paris.
- ⁺DEYL, M. 1955: The evolution of the plants and the taxonomy of the monocotyledons. (In Czech.) Sb. nár. Mus. Praze 11B: 3-143.
- DOUGLAS, G.E. 1944: The inferior ovary I. Bot. Rev. 10: 125-186.
- EAMES, A.J. 1931: The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Am. J. Bot. 18: 147-188.
- EAMES, A.J. 1961: "Morphology of the Angiosperms." McGraw-Hill, New York.
- EAMES, A.J. and MACDANIELS, L.H. 1951: "Introduction to Plant Anatomy." 2nd ed. McGraw-Hill, London.
- EMBERGER, L. 1949: La valeur morphologique et l'origine de la fleur. Colloques int. Cent. natn. Rech. scient. 4: 279-295.

- ESAU, K. 1943: Vascular differentiation in the vegetative shoot of Linum. II. The first phloem and xylem. Am. J. Bot. 30: 248-255.
- ESAU, K. 1965: "Plant Anatomy." 2nd ed. Wiley, New York.
- EZELARAB, G.E. and DORMER, K.J. 1963: The organization of the primary vascular system in Ranunculaceae. Ann. Bot. 27: 21-38
- FAGERLIND, F. 1946: Strobilus und Blüte von Gnetum und die Möglichkeit, aus ihrer Struktur den Blütenbau der Angiospermen zu deuten. Ark. Bot. 33A: 1-57.
- FAHN, A. and BAILEY, I.W. 1957: The nodal anatomy and the primary vascular cylinder of the Calycanthaceae. J. Arnold Arbor. 38: 107-117.
- FOSTER, A.S. 1936: Leaf differentiation in Angiosperms. Bot. Rev. 2: 349-372.
- FOSTER, A.S. and GIFFORD, E.M. 1959: "Comparative Morphology of Vascular Plants." Freeman, San Francisco.
- FRASER, M.S. 1937: A study of the vascular supply to the carpels in the follicle-bearing Ranunculaceae. Trans. R. Soc. Edinb. 59: 1-56.
- GIROLAMI, G. 1953: Relation between phyllotaxis and primary vascular organization in Linum. Am. J. Bot. 40: 618-625.
- GOEBEL, K. VON 1887: "Outlines of Classification and Special Morphology of Plants." Clarendon Press, Oxford.
- ⁺GOETHE, J.W. VON 1790: "Versuch die Metamorphose der Pflanzen zu erklären." Ettlinger, Gotha.
- ⁺GRÉGOIRE, V. 1935: Les anomalies florales des Primula et la valeur du placenta central. Ann. Soc. sci. Brux 60: 297.
- GRÉGOIRE, V. 1938: La morphogénèse et l'autonomie morphologique de l'appareil floral. I. Le carpel.

Cellule 47: 287-452.

- HAGERUP, O. 1934: Zur Abstammung einiger Angiospermen durch Gnetales und Coniferae, I. Biol. Meddr 11: 1-83.
- HAGERUP, O. 1936: Zur Abstammung einiger Angiospermen durch Gnetales und Coniferae, II. Biol. Meddr 13: 1-60.
- HAGERUP, O. 1938: Zur Abstammung einiger Angiospermen durch Gnetales und Coniferae, III. Biol. Meddr 14: 1-34.
- HALLIER, H. 1905: Phylogenetic studies of flowering plants. New Phytol. 5: 151-162.
- HIEPKO, P. 1965: Vergleichend-morphologische und Entwicklungsgeschichtliche Untersuchungen über das Perianth bei den Polycarpicae. Bot. Jb. 84: 359-426.
- HILL, A.W. 1918: The genus Caltha in the Southern Hemisphere. Ann. Bot. 32: 421-435.
- HOLM, T. 1909: Liriodendron tulipifera L. Merk's Rep. 18: 198-201.
- ⁺HUTCHINSON, J. 1921: The family Winteraceae. Kew Bull. 185-190.
- HUTCHINSON, J. 1948: "British Flowering Plants." Gawthorn, London.
- HUTCHINSON, J. 1959: "The Families of Flowering Plants." 2nd ed. Oxford University Press, London.
- JOHANSEN, D.A. 1940: "Plant Microtechnique." McGraw-Hill, New York.
- KUMAZAWA, M. 1930: Studies on the structure of Japanese species of Ranunculus. J. Fac. Sci. Tokyo Univ. Sec. 3, 2: 297-343.
- LAM, H.J. 1948: Classification and the new morphology. Acta biotheor. 8: 107-154.
- LAM, H.J. 1959: "Taxonomy general principles and Angio-

- sperms." In "Vistas in Botany I" ed. Turrill, W.B. Pergamon Press, London.
- LEINFELLNER, W. 1965: Wie sind die Winteraceen-Karpelle tatsächlich gebaut? I. Die Karpelle von Drimys, Sektion Tasmannia. Öst. bot. Z. 112: 554-575.
- LEINFELLNER, W. 1966a: Wie sind die Winteraceen-Karpelle tatsächlich gebaut? II. Über das Vorkommen einer ringförmigen Plazenta in den Karpellen von Drimys, Sektion Wintera. Öst. bot. Z. 113: 84-95.
- LEINFELLNER, W. 1966b: Wie sind die Winteraceen-Karpelle tatsächlich gebaut? III. Die Karpelle von Bubbia, Belliolum, Pseudowintera, Exospermum und Zygogynum. Öst. bot. Z. 113: 245-264.
- MAHESHWARI, P. and VASIL, V. 1961: "Gnetum." Botanical Monograph No 1. C.S.I.R., New Delhi.
- MARSDEN, M.P.F. and BAILEY, I.W. 1955: A fourth type of nodal anatomy in dicotyledons illustrated by Clerodendron trichotomum. J. Arnold Arbor. 36: 1-50.
- MCLAUGHLIN, R.P. 1933: Systematic anatomy of the woods of the Magnoliales. Trop. Woods 34: 3-39.
- MEEUSE, A.D.J. 1963: Stachyosporry, phyllosporry and morphogenesis. Adv. Fronts Pl. Sci. 7: 115-163.
- MEEUSE, A.D.J. 1965: Angiosperms - past and present. Adv. Fronts Pl. Sci. 11: 1-228.
- MELVILLE, R. 1960: A new theory of the Angiosperm flower. Nature, Lond. 188: 14-18.
- MELVILLE, R. 1962: A new theory of the Angiosperm flower. I. The gynoecium. Kew Bull. 16: 1-50.
- MELVILLE, R. 1963: A new theory of the Angiosperm flower. II. The androecium. Kew Bull. 17: 1-63.

- MONEY, L.L.I., BAILEY, I.W. and SWAMY, B.G.L. 1950: The morphology and relationships of the Monimiacae. J. Arnold Arbor. 31: 372-404.
- MORLEY, T. 1949: Staining of plant materials cleared in NaOH. Stain Tech. 24: 231-235
- MÜLLER, E. 1944: Die Nervatur der Nieder- und Hochblätter. Bot. Archiv. 45: 1-92.
- NAST, C.G. 1944: The comparative morphology of the Winteraceae. VI. Vascular anatomy of the flowering shoot. J. Arnold Arbor. 25: 454-466.
- NEUMAYER, H. 1924: Die Geschichte der Blüte. Abh. zool.-bot. Ges. Wien 14: 1-112.
- OZENDA, P. 1947: Structure du noeud foliaire des Magnoliacées et des Annonacées. C. r. hebd. Séanc. Acad. Sci. Paris 224: 1521-1523.
- OZENDA, P. 1949: Recherches sur les dicotylédones apocarpiques. Publ. Lab. École Norm. Sup., sér. biol. II. Paris 1-183.
- PARKIN, J. 1923: The strobilus theory of angiospermous descent. Proc. Linn. Soc. Lond. 135: 51-64.
- PAYER, J.B. 1857: "Traité d'Organogénie Comparée de la Fleur." Masson, Paris.
- PEARSON, H.H.W. 1912: On the microsporangium and microspore of Gnetum with some notes on the structure of the inflorescence. Ann. Bot. 26: 603-620.
- PHILIPSON, W.R. 1946: Studies in the development of the inflorescence. I. The capitulum of Bellis perennis L. Ann. Bot. 10: 257-270.
- PHILIPSON, W.R. 1947: Studies in the development of the inflorescence. II. The capitula of Succisa pratensis Moench. and Dipsacus fullonum L. Ann. Bot. 11: 285-298.
- PHILIPSON, W.R. 1948: Studies in the development of the inflorescence. IV. The capitula of Hieracium

- boreale Fries and Dahlia gracilis Ortg. Ann. Bot. 12: 65-76.
- PHILIPSON, W.R., and PHILIPSON, M.N. 1968: Diverse nodal types in Rhododendron. J. Arnold Arbor. 49: 193-224.
- PLANTEFOL, L. 1949: "L'ontogénie de la Fleur." Masson, Paris.
- ⁺POLLARD, C.L. 1908: Calycanthaceae in "North American Flora." Vol.22, pp.237-238. Ed. Britton, N.L. et al. New York Botanical Garden, New York.
- POST, D.M. 1958: Studies in Gentianaceae. I. Nodal anatomy of Frasera and Swertia perennis. Bot. Gaz. 120: 1-14.
- RICHARDS, F.J. 1948: The geometry of phyllotaxis and its origin. Symp. Soc. Expt. Biol. 2: 217-245.
- ROHWEDER, O. 1967: Karpellbau und Synkarpie bei Ranunculaceen. Ber. Schweiz. bot. Ges. 77: 376-432.
- SAMPSON, F.B. 1963: The floral morphology of Pseudo-wintera, the New Zealand member of the vesselless Winteraceae. Phytomorphology 13: 403-423.
- SCHAEPPPI, H. 1953: Morphologische Untersuchungen an den Karpellen der Calycanthaceae. Phytomorphology 3: 112-120.
- ⁺SCHLEIDEN, M.J. 1849: "Principles of Scientific Botany." London.
- SINNOT, E.W. 1914: Investigations on the phylogeny of the Angiosperms. Am. J. Bot. 1: 303-322.
- SKIPWORTH, J.P. 1962: The primary vascular system and phyllotaxis in Hectorella caespitosa Hook. f. N.Z. Jl Sci. 5: 253-258.
- SKIPWORTH, J.P. and PHILIPSON, W.R. 1966: The cortical vascular system and the interpretation of the Magnolia flower. Phytomorphology 16: 463-469.
- SKVORTZOVA, H.T. 1958: A contribution to the anatomy of

- the flower of Magnolia grandiflora L. (In Russian) Bot. Ž. 43: 401-408.
- SMITH, G.H. 1926: Vascular anatomy of Ranalian flowers. I. Ranunculaceae. Bot. Gaz. 82: 1-29.
- SMITH, G.H. 1928: Vascular anatomy of Ranalean flowers. II. Menispermaceae, Calycanthaceae, Annonaceae. Bot. Gaz. 85: 152-177.
- SNOW, R. 1955: Problems of phyllotaxis and leaf determination. Endeavour 14: 190-199.
- SPORNE, K.R. 1948: A note on a rapid clearing technique of wide application. New Phytol. 47: 290-291.
- SPORNE, K.R. 1958: Some aspects of floral vascular systems. Proc. Linn. Soc. Lond. 169: 75-84.
- SWAMY, B.G.L. 1949: Further contributions to the morphology of the Degeneriaceae. J. Arnold Arbor. 30: 10-38.
- TEPFER, S.S. 1953: Floral anatomy and ontogeny in Aquilegia formosa var. truncata and Ranunculus repens. Univ. Calif. Publs Bot. 25: 513-648.
- THODAY, M.G. 1911: The female inflorescence and ovules of Gnetum africanum with notes on G. scandens. Ann. Bot. 25: 1101-1135.
- THOMAS, H.H. 1958: Fossil plants and evolution. J. Linn. Soc. (Bot.) 56: 123-135.
- +THOMPSON, J.M. 1934: Studies in advancing sterility. VII. The state of flowering known as angiospermy (with special reference to placentation and the origin and nature of follicles and achenes). Publs Hartley bot. Labs Lpool Univ. 12: 5-47.
- THOMPSON, J.M. 1937: On the place of ontogeny in floral enquiry. Publs Hartley bot. Labs Lpool Univ. 17: 3-20.
- THOMPSON, J.M. 1943-44: Towards a modern physiological

- interpretation of flowering. Proc. Linn. Soc. Lond. 156: 46-49.
- TIAGI, Y.D. 1963: Vascular anatomy of the flower of certain species of the Calycanthaceae. Proc. Indian Acad. Sci. Sect. B 58: 224-234.
- TUCKER, S.C. 1959: Ontogeny of the inflorescence and the flower in Drimys winteri var. chilensis. Univ. Calif. Publs Bot. 30: 257-336.
- TUCKER, S.C. 1961: Phyllotaxis and vascular organization of the carpels in Michelia fuscata. Am. J. Bot. 48: 60-71.
- TUCKER, S.C. 1966: The gynoeceal vascular supply in Caltha. Phytomorphology 16: 339-342.
- WHITAKER, T.W. 1933: Chromosome number and relationship in the Magnoliales. J. Arnold Arbor. 14: 376-385.
- WILSON, C.L. 1942: The telome theory and the origin of the stamen. Am. J. Bot. 29: 759-764.
- WILSON, C.L. 1953: The telome theory. Bot. Rev. 19: 417-437.
- WILSON, C.L. and JUST, T. 1939: The morphology of the flower. Bot. Rev. 5: 97-131.
- WORSDELL, W.C. 1908: A study of the vascular system in certain orders of the Ranales. Ann. Bot. 22: 651-682.
- YARBOROUGH, J.A. 1957: Arachis hypogaea. The seedling, its epicotyl and foliar organs. Am. J. Bot. 44: 19-30.
- ⁺ZIMMERMANN, W. 1930: "Die Phylogenie der Pflanzen." Gust. Fischer, Jena.