OCCURRENCE AND DEVELOPMENT OF EPIPHYLLOUS INFLORESCENCES

OCCURRENCE AND DEVELOPMENT OF EPIPHYLLOUS INFLORESCENCES: Consequences for their Morphological Interpretation, with special reference to Phyllonoma integerrima (Turcz.) Loes. and Helwingia Japonica (Thunb.) Dietr.

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ABSTRACT

The ontogenies of two epiphyllous inflorescences (in the genera Phyllonoma Willd. and Helwingia Willd.) have been studied, and found to involve contrasting patterns of growth. In the first case, a fertile axis is initiated on the leaf primordium, well above the axil, apparently through remeristematization of cells of the adaxial side of the primordium. In the second case initiation occurs at the base of the leaf primordium, near the axil, and the resulting inflorescence primordium is carried up by zonal growth beneath its base and that of the leaf. These two patterns appear to account for a majority of the epiphyllous branch systems whose development has been studied. Previous studies and interpretations of epiphylly are reviewed and the present data discussed with reference to these earlier interpretations. It is suggested that epiphylly can be better understood in terms of changes in the position of organ and organ-system initiation, and zonal growth.

ABSTRACT:

L'étude du développement ontogénique de deux inflorescences épiphylles (le genre Phyllonoma Willd. et le genre Helwingia Willd.) révèle des processus de croissance différents. Dans le premier cas, l'initiation de l'axe fertile se fait sur le primordium foliaire bien au-dessus de l'aisselle par une differentiation méristématique des cellules du coté adaxial du primordium. Dans le second cas, l'initiation de l'axe fertile s'effectue à la base du primordium foliaire, près de l'aisselle. Le primordium de l'inflorescence, qui en résulte, se déplace au-dessous de sa base et de celle de la feuille par croissance intercalaire. Ces deux processus de développement se retrouvent chez la majorité des systèmes d'axes épiphylles étudiés jusqu'à présent. L'auteur présente un résumé des études et des interprétations traitant des Epiphylles. Il discute les résultats de cette étude en fonction des interprétations antérieures.

"I gave him a vivid picture of the metamorphosis of of plants and, with many a characteristic stroke of the pen, conjured up a symbolic plant before his eyes. He watched with great interest, showing a decided grasp of the subject. But when I had finished, he shook his head and said: 'That is not experience - it is an idea.'"

Goethe, describing a conversation with Schiller.
Quoted in <u>Goethe as a Scientist</u>, by R. Magnus, 1961.

"If Blake could do this when he rose up from a shite,
What might he not do if he sat down to write."

William Blake. "When Klopstock England defied."

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Reviews of the occurrence and anatomy of epiphylly, accompanied by their authors' interpretations of the phenomenon, have been published, often on the occasion of the description of a new species with epiphyllous inflorescences (Planchon, 1853; Duchartre, 1853, 1887, 1886; Schumann, 1890; Velenovsky, 1907; Harms, 1917; Croizat, 1960; Melville, 1962; and Jong, 1970).

The first developmental study was made by Payer (1857b), who from dissections described the development of the male inflorescence of Tilia. In 1890, Casimir de Candolle made the first comparative study of the occurrence, vascular anatomy and development of epiphyllous inflorescences. Like Payer, however, his developmental studies - of Phyllonoma and Helwingia - were based principally only on dissections. Schumann (1890) also reported the results of developmental studies, but only in limited detail, and unillustrated. Velenovsky (1907) made a fairly detailed morphological study of Helwingia, which denigrated the developmental and anatomical aspects of the problem. Finally, Stork (1956) also studied the development of the inflorescence of Phyllonoma integerrima, but although he described its ontogeny from sectioned material, he apparently only observed relatively old leaf primordia, and not initiation of the inflorescence. Furthermore, he did not, unfortunately, publish either photographs or drawings of his sections. To date, there have been no detailed morphogenetic studies of epiphyllous inflorescences; epiphyllous shoots and buds have attracted much attention (see reviews by Dormer, 1973 and Tomlinson, 1973).

II. ACKNOWLEDGEMENTS

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Plate I is reproduced through the courtesy of Prof. R. Bernier of the University of Montreal, whose microfilm of Turpin's 'Equisse d'Organographie végétale...' held by the Bibliothèque Nationale, Paris, I used. I would like to thank Mr. U. Posluszny for the photograph of <u>Turnera ulmifolia</u> used as Fig. 1 of Plate II. Plate X was copied through the courtesy of Ms. Pat Hall, Librarian, the Gray Herbarium, from whose copy of Humboldt, Bonpland and Kunth's 'Nova Genera et Species Plantarum' it was made. I would like also to thank Ms. M. de Sèves for her assistance with translations into french, especially

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III. INTRODUCTION

A. Review of Epiphylly.

A.1 Terminology and Purpose.

1.1 By "epiphyllous" is meant the observed occurrence of the organ or organ-system so described upon a leaf (in any position - adaxially, abaxially, or marginally). This entire study is conceived of dialectically, within the "classical theory of the shoot", and as a contribution toward a critique of the same theory. This theory, referred to and described repeatedly in what follows, is the concept of shoot organization which originated with, among others, Goethe and A.P. de Candolle, and continues today as the more or less unquestioned basis of comparative plant morphology. This theory is set forth, with different emphases, by writers such as Troll (1937), McLean and Ivimey-Cook (1951) and Eames (1961).

1.2 The present study has been undertaken also in conjunction with the concurrent development of a "new conception of the shoot of higher plants" by my supervisor, Dr. Rolf Sattler (1971 and in press). In this new conception, the fundamental categories of organs recognized classically are also recognized, in addition to intermediates between those categories. However, the rules by which these organs may be combined, and by which real organs must be described in terms of them, are changed. Thus, in this thesis, for purposes of practicality, the classical concepts of leaf and stem, and of the homology between vegetative stems and inflorescence axes are accepted. However, what I have endeavoured to demonstrate, from the literature as well as my data, is that the classical "rules" governing these organ categories in situations like epiphylly become counterproductive to scientific progress. They necessitate pseudo-explanations and distortions which get in the way of true understanding. Yet at the same time, there are considerably more useful explanations available.

1.3 One such pseudo-explanation is the concept of "congenital" or "phylogenetic" fusion. It is a crucial adjunct of the classical theory (Sattler, in press), and, like the classical theory, will be discussed repeatedly in the course of this study. It can be used, for example, to explain the insertion of an inflorescence upon a leaf, a situation not recognized by the classical theory, in such a way that the classical theory is not violated. If the organ in question is truly a leaf, then a fusion must have occurred such that an inflorescence originating on the stem, and a leaf on the same stem have become joined over part of their respective lengths. If this fusion is not observable during the life-history of a single individual of the species in question (for which the condition is characteristic), it must then have occurred "congenitally", or "phylogenetically", i.e., in the course of the phylogeny of the species (for discussion of this aspect of the concept, see also Puri, 1962).

1.4 In other words, the leaf and epiphyllous inflorescence are homologized with a leaf and an axillary inflorescence, by invoking an unobservable process of fusion. It has been pointed out by Jardine (1969) that even the common evidence of phylogeny, i.e. fossils, in a chronological sequence of similar forms cannot adequately substantiate the hypothesis of phylogenetic fusion without detailed information about the ontogenetic processes of the organs involved. Thus, part of the purpose of this study is to this end, to provide ontogenetic data for hypothetically fused organs, i.e. leaves and their epiphyllous inflorescences. Kaplan

(1971: 138) has suggested that this, "the elucidation of the mechanisms of morphological change", is the most useful objective of comparative developmental studies.

1.5 Finally, it was also mentioned that in situations such as epiphylly the rules of the classical theory necessitate distortions, by means of interpretations, of observations. By describing the ontogeny of certain epiphyllous inflorescences, it should be possible to provide a coherent set of observations, the "interpretation" of which, according to the classical theory, should make clear the distortions involved. Thus it has been shown here and elsewhere that stems and their homologues developing normally do in fact, in these cases, occur upon leaves, even in the embryonic state. That this situation should be accepted as such, rather than interpreted as something else, seems abundantly clear.

(III) A.2 Historical Background

2.1 In 1790, in his essay on metamorphosis in plants ("Versuch die Metamorphose der Pflanzen zu erklären", English translation by Arber, 1946), J.W. von Goethe referred to 'the fertility that is latent in the leaf', in describing how in the bract-borne inflorescence of Tilia, as in the fertile phylloclades of Ruscus and the fronds of some ferns, leaves, or leaf-like organs, give rise to reproductive structures. From this description of leaf-fertility, he proceeded to identify carpels as fertile leaf-homologues, as part of an overall identification of leaves as the fundamental (appendicular) units of all (serial) plant structure, reproductive as well as vegetative. Similar analyses had also been made earlier by C.F. Wolff and others (Arber, 1950; Blunt, 1950). Its result, in Goethe's mind, was the conception of an archetypal plant ("Urpflanze"; cf. Troll, 1937, Fig. 12, McLean & Ivimey-Cook, 1951: I, Fig. 845) embodying all the stages of leaf-metamorphosis along a single shoot-axis.

2.2 In 1804, the french artist and botanist P.J.F. Turpin on returning from Hispaniola independantly designed a plate (Plate I) depicting his own impression of the vast range of leaf form in both vegetative and reproductive plant structures. This was subsequently published as an illustration for a French translation of Goethe's essay (Turpin, 1837). Although he illustrates different kinds of vegetative epiphyllous propagules, in 1804 he apparently had not encountered epiphyllous inflorescences, and did not, unfortunately, illustrate this aspect of leaf morphology until he came to design the plates for Humboldt, Bonpland, and Kunth's Nova Genera et Species Plantarum (e.g. Plate X).

2.3 In 1827, A.P. de Candolle made a comprehensive interpretation of plant structure along similar lines, stressing the leaf-identity of all appendicular organs. This interpretation has become the classical theory of shoot organization, referred to above (III. A. 1.) and adhered to generally even now (Troll, 1937; Eames, 1961). According to this model, the entire diversity of aerial plant structure is comprised of two mutually exclusive, discontinuous organ-types, caulome and phyllome, in obligate positional relationships to each other (for critiques of the classical model, see e.g. Arber, 1950; Croizat, 1960; Jong, 1970; and Sattler, 1971, and in press). Thus, while on the one hand, St. Hilaire (1840, cited by Croizat, 1960: fn. p. 1029) could describe epiphylly as simply one of many types of pedunculation, the type of thinking embodied in the classical theory led him and de Candolle (1827, 1835) as well as Payer (1857b) nevertheless to ascribe epiphylly exclusively to the process of congenital fusion of a leaf and an axially-inserted inflorescence (see pp. 26-29 and 33-34). In this way only one of the consequences of Goethe's original concept of leaf-fertility, suggested to him by the epiphyllous inflorescence of <u>Tilia</u>, was accepted by later botanists. The leaf-identity of all appendicular organs, particularly of flowers, became enshrined in classical morphological theory. But the quality of "fertility" which Goethe saw in leaves as the source of epiphyllous conditions was completely ignored.

2.4 Similarly, although until the beginning of the nineteenth century botanists had described the inflorescence-bearing, leaflike structures of <u>Ruscus</u> as "leaves" (cf. Willdenow's specific epithets for species of <u>Phyllonoma</u> and <u>Helwingia</u>, pp. 65 and 73), the position of these structures, as well as the occurrence of inflorescences on them, required that they be redefined as a type of caulome, e.g. "phylloclade", as they were, then, by Martius and successive authors (cited by Duval-Jouve, 1877).

2.5 Planchon (1853, NB. This title, in its discussion, is almost completely identical with Planchon & Linden, 1853), in his observations on epiphylly à propos Erythrochiton hypophyllanthus described of leaves ("appendices"), "la faculté d'être normalement prolifères, ... de produire eux-memes directement d'autres appendice ou des axes". However, this was only by way of contradiction, in stating the argument that leaf and (axillary) inflorescence in E. hypophyllanthus and other species were instead congenitally fused.

2.6 Meanwhile Duchartre (1886), as well as possibly Meisner (1838, quoted by Goebel, 1902), in their descriptions of the morphology and/or anatomy of epiphyllous branches and inflorescences of certain Begonias maintained the notion of truly epiphyllous inflorescences, i.e. inflorescences which arose directly from the leaf, rather than from the stem. On the basis of their vascular anatomy (cf. pp. 26-29) Duchartre distinguished the unique case of B. ameliae from all other epiphyllous inflorescences described, which according to him resulted from congenital fusion (e.g. Helwingia, Phyllonoma). C. de Candolle, in his 'Recherches sur les Inflorescences Epiphylles', however, concluded that all epiphyllous inflorescences were leaf-products. His study of the ontogeny and vascular anatomy of the fertile and sterile leaves of Helwingia and Phyllonoma suggested that in both cases the inflorescence arose epiphyllously, and that the presence or absence of the inflorescence on leaves amounted to an example of heterophylly.

2.7 Subsequent workers tended to disagree with de Candolle's conclusions, preferring alternative developmental explanations for epiphyllous inflorescences, whether or not they invoked congenital fusion (invoking congenital fusion: van Tieghem, 1897; Barth, 1896; Velenovsky, 1907; Troll, 1937; rejecting it: Schumann, 1890; Schinz, 1894; Goebel, 1898, 1933). With the exception of Leavitt (1909), and Cooper's (1932) study of Bougainvillea, North American and British workers appear to have ignored epiphyllous inflorescences (Good, 1956; Bierhorst, 1971; Bold, 1973) or dismissed them in accordance with the classical theory of the shoot (cf. Stork, 1956; Eames, 1961). While vegetative propagation from leaves received considerable attention (for reviews, see Priestley & Swingle, 1929; McVeigh, 1937; Dormer, 1972; Tomlinson, 1973; cf. pp. 22-24), directed at morphology, anatomy, and ontogeny, there were no comparable studies of epiphyllous inflorescences until Stork's (1956) work on Phyllonoma, Melville (1962), that of Stebbins and Yagil (1966 etc.) on Hordeum, and Jong's (1970), on Streptocarpus.

2.8 Arber (1950) refers in passing to a few instances of epiphyllous shoot production (in Brassica, Bryophyllum (as Kalanchöe), Nymphaea, and tomato, as described in the next section), in setting forth her concept of the leaf as a "partial shoot... arising laterally from a parent whole-shoot". This phrase in turn summarizes the conclusions reached earlier by C. de Candolle in his 'théorie de la feuille' (1868). Arber develops this idea further, to suggest that a partial shoot 'has an inherent urge towards the development of whole-shoot characters'. Thus, situations such as epiphylly she sees as successful manifestations of this "urge" toward complete shoot-like behavior (e.g. continued growth, radial symmetry, flowering, etc.). Even more striking manifestations would be the epiphyllous initiation of organs discussed below for Phyllonoma, Chrysalidocarpus, as well as Cardamine, tomato, et al.

2.9 A leaf and an epiphyllous branch have been suggested by Melville (1962) to constitute the fundamental unit of construction (= "Gonophyll") of angiospermous flowers, as well as of angiosperm vegetative structures. Thus carpellate gynoecia are supposed to consist of sterile phyllomes (tegophylls) bearing ovuliferous branches (cf. placentae). In modern angiosperms where fertile and sterile branches occur on the foliage leaves and bracts, it therefore appears 'that the gonophyll structure has been retained throughout the evolutionary history of these plants'. Thus, the epiphyllous inflorescences of Tilia, Phyllonoma, Helwingia, Polycardia, the Dichapetalaceae, etc., which Melville discusses at some length are considered to be primitive structures, homologous apparently with the leaf-opposed reproductive structures of the Glossopteridales, as well as Botryopteris, as reconstructed by Melville, and with the epipetiolar branches found in the coenopterid ferns (cf. Troop & Mickel, 1968; and pp. 30-31).

2.10 In a similar vein, Stebbins (in press) suggested that angiospermous carpels are derived from structures similar to the ovuliferous leaves of Lidgettonia (cf. Bierhorst, 1971).

2.11 In contrast to these more or less speculative evaluations of epiphylly, Bugnon (1958) has treated the subject in the course of a discussion of 'les déformations nodales de la pousse par croissance intercalaire chez les plantes à fleurs'. According to Bugnon, epiphyllous inflorescences may result from intercalary growth occurring beneath the primordia of adjacent leaves and inflorescences. Bugnon coins the term "hypophylloclade" to describe the intercalation on which the definitive leaf and inflorescence are inserted (cf. Text - figure 1).

2.12 With Bugnon (1958) and Melville (1962) one of the few recent detailed discussions of epiphylly is that of Croizat (1960; also, personal communication). Like Bugnon, his concern is principally with processes of growth, as well as with the recognition of the "intermediateness" of real plant organs, with respect to fundamental categories. He emphasizes the importance of epiphylly as 'a phase of branching and growth of direct interest to inflorescence, leaf, shoot as one, that is, as a phase of the morphogenetic and phylogenetic setup fundamental for the plant body as a whole'. In his discussion, he makes extensive and enthusiastic use of the concepts of the Dijon school "hypoclades", (Kursner, 1955; cf. "hypophylloclades", Bugnon, 1958) to describe epiphyllous and related situations.

2.13 Finally, Sattler (1971, and in press) has proposed a new model of the shoot in which positional relationships between plant organs such as the insertion of stems or their homologues upon leaves is accepted as such. He modifies the classical conception of the shoot so that real plant organs may correspond to the fundamental organ categories (leaf, stem, emergence, root) that it recognizes, regardless of the positional relationship to each other in which they occur. Alternatively, real organs may correspond to intermediates between the fundamental organ categories. Thus, epiphylly may be due not only to deformations of orthodox positional relationships by intercalary growth, but also to initiation of branch or inflorescence primordia on leaves or leaf primordia.

2.14 Sattler's revision of the classical shoot concept consists in part of a rejection of the concept of congenital fusion. Other authors, among them Croizat (1948, 1960, 1973) instead associate (congenital) "fusion" with the non-individualization of primordia, applying the term to a wholly ontogenetic process. In a detailed discussion of the development of the concept, Bugnon (1958), like Sattler, also rejects the use of congenital fusion, in favor of the ontogenetic process of intercalary growth. Recently, however, this view of his has been criticized (Vieth & Lamond, 1973) for failing to differentiate "ontogenetic", or "post-genital" fusion from congenital fusion.

2.15 As Macdonald and Sattler (1973) suggest, not only classically-oriented workers, but also heterodox ones, use the concept of congenital fusion 'to rescue the general applicability of the (fundamental) categories...'. Thus Melville (1962) disagrees with the use of congenital fusion to explain the epiphyllous inflorescences which he discusses, but only because he explains them as primitive structures instead; he uses the term "fusion" himself to describe a process affecting plant parts in the course of phylogeny.

2.16 Arber (1925, 1950), on the other hand, appears to use the concept of congenital fusion in a much more idealistic sense, to describe a process intervening not so much between actual organs, as between human concepts of organs. She describes (1925) how the phylloclade of <u>Ruscus</u> results from the complete fusion of an axillary bud with its prophyll, in such a way that the prophyll dominates, with respect to dorsiventrality and determinate growth, while the axillary shoot expresses itself in the position of the phylloclade, subtended by a leaf, and its capacity to produce flowers.

Plate I

"Végétal type idéal, appendiculé; parties supérieures, composant l'Hémisphère supérieure;" portion of Plate 3 of P.J.F. Turpin's 'Equisse d'Organographie végétale...' (1837). Reproduced from the copy held by the Bibliothèque Nationale, Paris. The original, as pointed out by Arber (1950), is more than 19 inches high.

Figure 7': 'Embryon gemmaire axillaire, fixes, développée en tige fasciée, munie de noeuds-vitaux réguliers et de petites feuilles, sur les deux côtés desquels noeuds-vitaux sortent de petits bouquets de fleurs. Exemp. Xylophylla'.

Figure 8 : 'Feuille productrice d'embryons reproducteurs, adventifs sur ses deux faces et ses bords, comme celles de l'*Ornithogalum thyrsoides* que nous avons publiées.'

Figure 10: (on left side) 'Feuille lobée sur laquelle se trouve deux *nodus* ligneux, embryons gemmaires, formés d'abord entre les deux épidermes, analogues à ceux corticaux que M. Dutrochet a fait connaître. Nous avons trouvé de ces feuilles détachées dans les forêts de St.-Domingue. Plusieurs de ces embryons germaient.'

Figure 11: 'Feuille dont l'extrémité s'allonge en vrille, se recourbe en a vers la terre, y prend racine en b et reproduit, par ce moyen, un nouvel individu c. Ce mode de reproduction est connu dans l'*Asplenium rhizophyllum*.'

Figure 13: 'Feuille productrice d'embryons reproducteurs, réguliers, du *Bryophyllum calycinum*.
Observation. - Ces singulières feuilles offrent de l'analogie avec les tiges aplaties, en forme de feuille, Cierges des Epiphylles, des pédoncules fasciées des *Xylophylla*, etc., en ce que, comme ceux-ci elles ont des noeuds-vitaux qui forme dentelures et de l'angle desquels sortent les embryons gemmaires reproducteurs de l'espèce. On voit quelquefois ces embryons, encore attachés sur la feuille-mère, pousser de petites radicelles latérales.'

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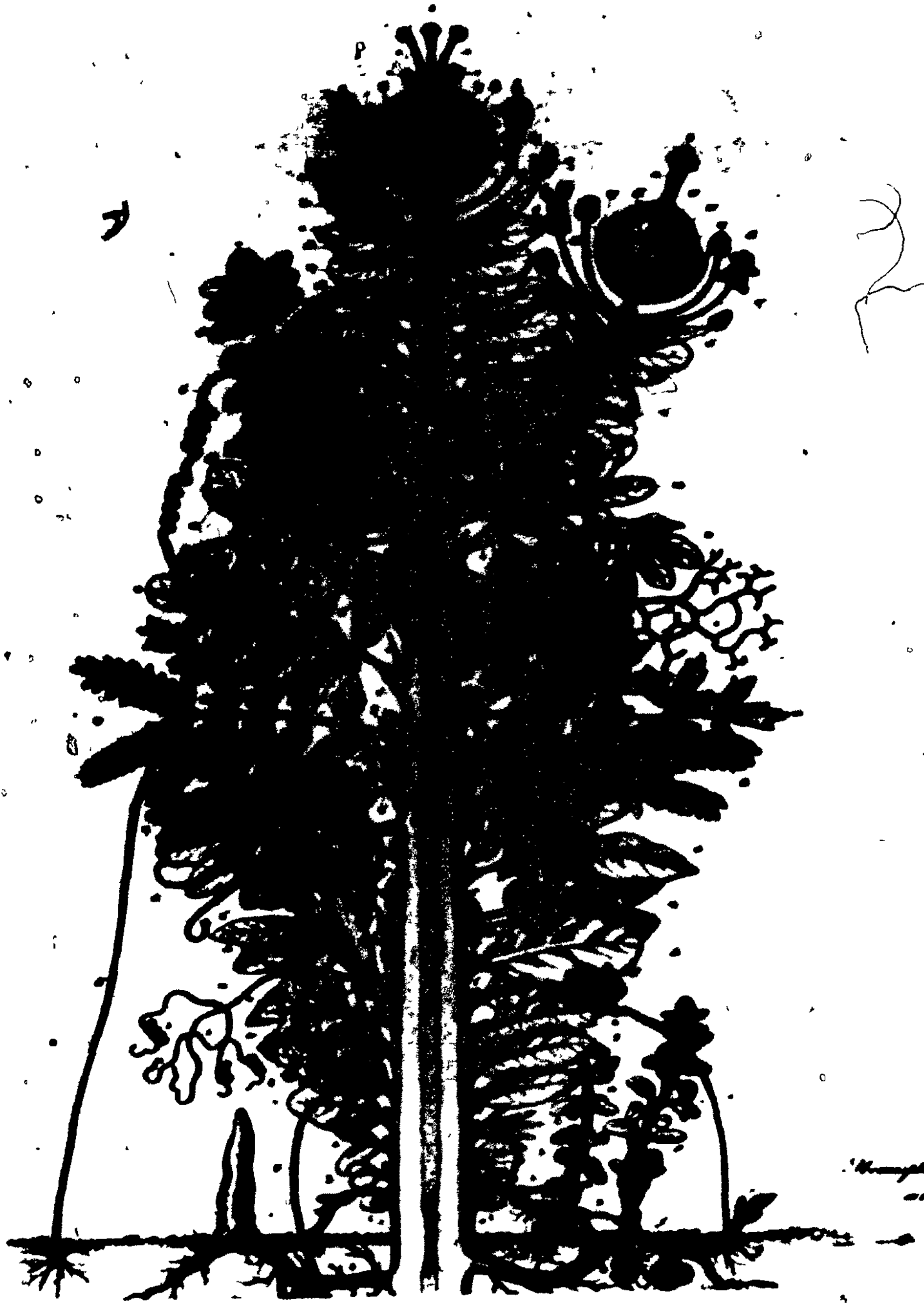

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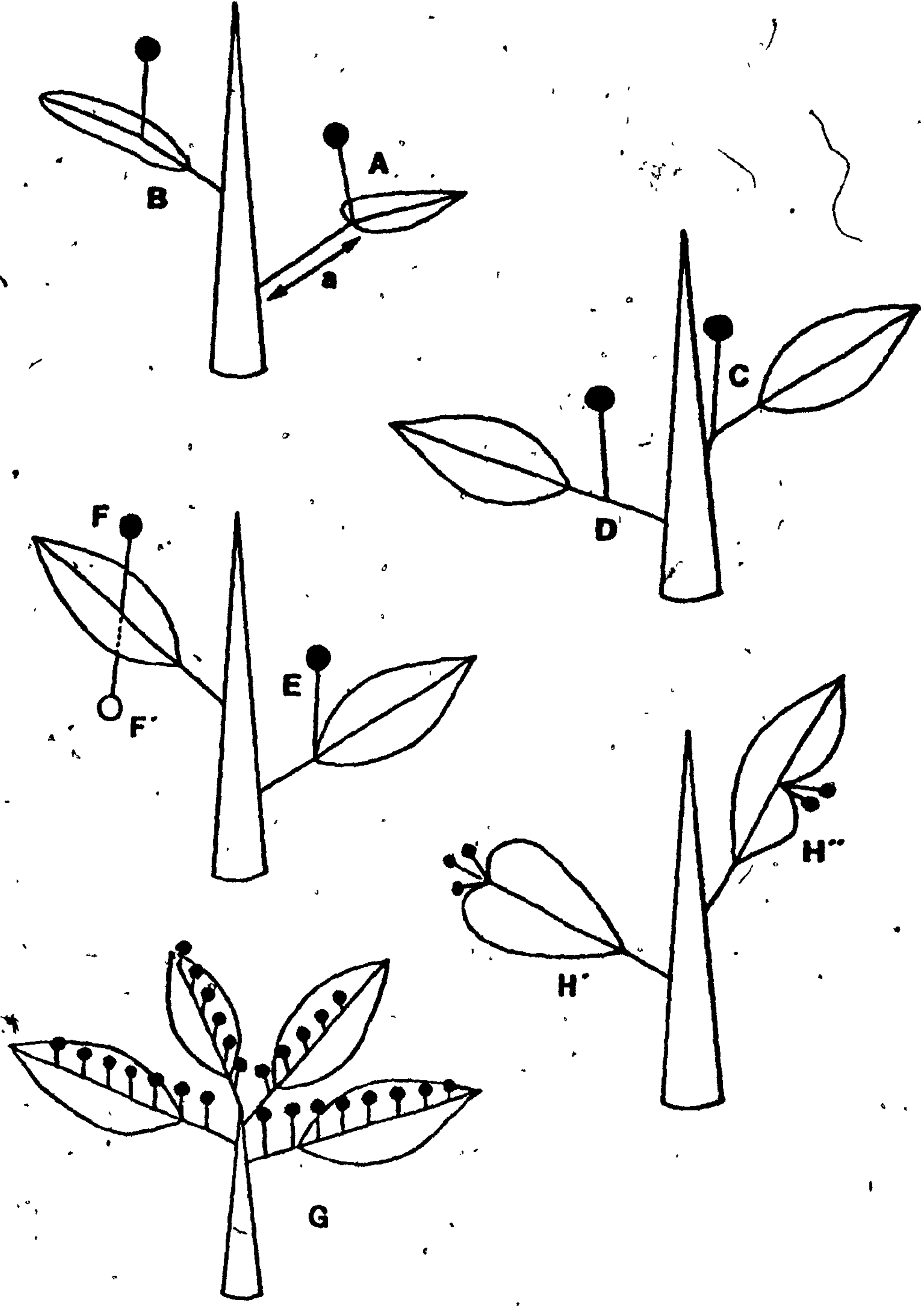


Text _ Figure 1: Positional relationships between leaf and inflorescence.

A.3 MORPHOLOGICAL PATTERNS

a. Epiphyllous Inflorescences

a.1 Text-figure 1 summarizes the variety that occurs in the positional relationships between leaf and inflorescence, and is based in part on the systems used by Harms (1917) and Marchal (1969) to describe epiphylly.

Text - Figure 1 - LEGEND:

A–B Insertion of the infloresence on a bract.

- A) Lamina extends only distally from insertion of inflorescence.
  - a = intercalated segment between stem and insertion of inflorescence.
- B) Lamina extends both proximally and distally around insertion of inflorescence.

C–H Insertion of inflorescence on foliage leaves.

- C) Inflorescence inserted on leaf base.
- D) Epipetiolar inflorescence.
- E) Inflorescence inserted at base of lamina.
- F) Inflorescence inserted in middle of lamina (on adaxial surface)
- F') Inflorescence inserted on abaxial surface of lamina. (cf. *Erythrochiton hypophyllanthus*).
- G) *Phyllobotryum*, *Mocquerisia:* inflorescence arranged along the length of petiole and lamina.
- H') *Polycardia phyllanthoides.*
- H'') *Polycardia lateralis*.

In A-F the large, stalked black circles represent inflorescences. They may equally represent the position of epiphyllous branches or buds. The circles in F', and H represent individual flowers.

The region between the insertion of the leaf on the stem, and of the inflorescence on the leaf (a in A), in each case is the region described by Bugnon (1958) as a "hypophylloclade".

2.2 In the first case (A) an intercalation (a) can be said to exist between the insertion of the bract on the stem and of the inflorescence at the base of the bract lamina. This is the situation found in *Cneorum* L. (Cneoraceae: Harms, 1917); Engler, 1931; Melville, 1962), *Gentiana lutea* L. (Goebel, 1931; Bugnon, 1958), the Saururaceae (Payer, 1857b, Bugnon 1958; Croizat, 1960; Raju, 1961), *Thesium* L. (Santalaceae: Troll, 1937; Thibaut, 1955; Croizat, 1960), *Saintpauliopsis* Staner (= *Staurogyne* Wall), and *Selago* L. (Scrophulariaceae: B.L. Burtt, personal communication). The opposite situation is found in *Roella ciliata* L. (Campanulaceae), where the bracts continue up the outside of the wall of the inferior ovary (B.L. Burtt, personal communication),

2.3 Alternatively, the lamina of the bract may extend below the insertion of the inflorescence (Text-figure 1B); this situation occurs with the female flowers of *Dobinea delavayi*, *D. vulgaris*, and *Camplyopetalum siamense* (Anacardiaceae: Forman, 1954; Melville, 1962), and the flowers of *Neuropeltopsis* van Oostroom (Van Oostroom, 1964), *Bougainvillea* and *Hermidium*, S.Wats, (Nyctaginaceae: Cooper, 1932; Ferris, 1944; Hackett & Sachs, 1968; Menninger, 1970) and *Tilia* L. In varieties of *Hordeum*, a rudimentary floret is formed on the adaxial surface of the lemma (Arber, 1934; Croizat, 1960; see also pp. 69-70).

2.4 In addition, the araceous inflorescence bract or spathe itself bears the entire inflorescence in *Spathantheum* Schott and *Spathicarpa* Hook. (Engler, 1920: 50-57; Troll, 1928; Willis, 1966).

2.5 Foliage leaves also bear inflorescences, anywhere from the base of the leaf and petiole, to its tip (Text - Figure 1 C-H). Fisher (1973) has suggested that 'initiation of an inflorescence bud upon, and continued physical connection with, the leaf base...... may be typical for palms' (cf. Text-figure 1C). In *Chrysalidocarpus* both inflorescences and lateral branches are associated with the leaf base, although by different means (see p. 30). Inflorescences and sterilized inflorescences ("flagellae") are similarly associated with the leaf base in *Calamus* L. and *Daemonorops* Blume ex Schult. (Troll, 1937; Tomlinson, 1961; Corner, 1966).

2.6 In *Turnera* L. (plate II), *Chirita hamosa* R.Br. (Gesneriaceae: Boldt, 1897; Velenovsky, 1907) Dichapetalaceae (Engler & Krause, 1931), the inflorescence is epipetiolar (Text - figure 1D); among these are *Dichapetalum steyermarkii* Prance, *D. mombuttense* Engl., *Stephanopodium* Poepp. & Endl., *Tapura africana* Oliv., *T. amazonica* Poepp. & Endl., *T. capitulifera* Baill., *T. coriacea*, *T. guianensis* Aubl. and *T. le-testui* Pellegrin (Hallé & Heine, 1967; Prance, 1971, 1972). In *D. pedunculatum* (Aubl.) Baill, the inflorescence may be epipetiolar or axillary (Melville, 1962). In *D. glabrum* (Vahl) Prance (Prance, 1971) *D. rudatisii* Engl. and *D. toxicarium* (G.Don) Baill (personal observations) the inflorescence is situated at the summit of the petiole, where it joins the lamina (Text - figure 1E). Finally, in T. peruviana K. Krause and T. juliani Macbride the inflorescence is found on the lamina itself, near its base (Text - figure 1F: Prance, 1972).

2.7. In normally unifoliate and facultatively unifoliate members of the Gesneriaceae (Chirita Buch-Ham., Monophyllaea R-Br., Moultonia Balf. f.& W.W. Smith, and Streptocarpus Lindl.) inflorescences are formed at the base, and along the midrib of the single enlarged cotyledon forming the photosynthetic organ of the plant (Velenovsky, 1907; Balfour & Smith, 1915; Goebel, 1931; Hill, 1938; Jong, 1970). Jong (1970, 1973) however, has suggested that in these cases the classical concept of "leaf" is more usefully replaced by that of the "phyllomorph" in describing the organization of these and related plants. This concept refers to an intermediate organ, which combines characteristics of both leaf and stem. In this way, the patterns of growth of species of Streptocarpus may be understood much better than by using the classical notions of the mutually exclusive categories, "leaf" and "stem". The epipetiolar inflorescence of Epithema tenue C.B. Clarke has also been shown recently (Hallé & Delmotte, 1973) to conform to phyllomorphic organization. Whether or not this concept can be applied successfully to other families still remains to be seen, however.

2.8 Further examples where the inflorescence occurs at the base (Text - figure 1E), or in the middle of the lamina

(Text - figure 1F) are, for the first case: *Begonia paleacea* Kurz., *B. prolifera* A. DC, *B. sinuata* Wall (C.de Candolle, 1890; Goebel, 1902; Irmischer, 1925), and *B. ameliae* Bruant (inflorescences both axillary and epiphyllous: Duchartre, 1886; de Candolle, 1890; Goebel, 1902); *Raphanocarpus* Hook f. (= *Momordica*, Cucurbitaceae: Cogniaux & Harms, 1924); Croizat, 1960); *Nototriche* Turcz. (Malvaceae: Harms, 1917; Burt & Hill, 1948). The second case, that is laminar inflorescences (Text - figure 1F), occur in *Phyllocharis schlechteri* Diels (Campanulaceae: Melville, 1962; Moeliono & Tuyn, 1972), *Polycardia aquifolium* Tul. (Perrier de la Bathie, 1946), *Helwingia* Willd. (Chapter VI), *Phylloclinium* Baill. (Flacourtiaceae: Letouzey, Hallé & Cusset, 1969), and in *Phyllonoma* Willd. (Chapter V). In *Erythrochiton hypophyllanthus* Planch.& Linden (Rutaceae: Planchon, 1853), the inflorescence is attached to the middle of the lower, abaxial surface of the leaf (Text - figure 1F'). In other species of *Polycardia*, the attachment of the inflorescence to the midrib is in a sinus of the lamina, variously lateral (Text- figure 1H"), in *P. lateralis* O. Hoffm., or apical ("acrophylle", Planchon, 1853), in *P. phyllanthoides* (Lamk) DC (Velenovsky, 1907; Harms, 1917; Perrier de la Bathie, 1946).

2.9 In all the cases described above, only a single inflorescence is found in association with a given leaf. Except for isolated examples of double epiphyllous inflorescences in *Tilia* (found on Mount Royal in Montreal on two separate occasions), and in *Helwingia japonica* (on a male plant in the Goteborg Botanical Garden), the only cases in which a series of more than one inflorescence occurs on a single leaf are Phyllobotryum Muell. Arg. and Mocquerisia Hua (Flacourtiaceae: Letouzey et al, 1969; Text - figure 1G). In addition, species of Chisoheton Blume (Meliaceae: Harms, 1917; Melville, 1962; Willis, 1966) may bear inflorescences axillary either to the rhachis or to the leaflets of a pinnately compound leaf (See Page 71).

A.3.b. Epiphyllous Shoots

b.1. In addition to sexual reproduction, epiphyllous shoot systems in intact plants may also be associated with vegetative ramification and propagation. The former case is less common. In the palm Chrysalidocarpus H. Wendl. (Fisher, 1973), it is known, principally from ontogenetic studies (Page 30) that lateral branches are inserted on the abaxial surface of the leaf base - similar situations occur, by way of different ontogenies, in Serenoa repens (Bart.) Small (Fisher & Tomlinson, 1973), and Chamaedorea Willd. (Fisher, 1974).

b.2. In the tuberculate cacti Coryphantha (Engelm.) Lem. and Dolichothele Britton & Rose (= Mammillaria Haw.), a lateral short shoot is found near the summit of a rudimentary leaf (Goebel, 1898; Boke, 1961a,b; Willis, 1966; Kaplan, 1971).

b.3 In Begonia sinuata Wall., up to three or four generations of epiphyllous shoots may occur (Meissner, 1838; quoted by Goebel, 1902). Although they may bloom, the epiphyllous branches apparently do not root, and are presently treated here as a form of ramification.

b.4 While perhaps better treated with other teratological phenomena, the occurrence of similar fertile, epiphyllous branches on leaves of tomato varieties is worth mentioning here because of its long history of occurrence. The phenomenon was first reported by Ducharte (1853) in cherry and pear tomatoes, especially the yellow cherry variety. The branches developed on full-grown leaves, from "mammelons" formed in the axils of leaflets. The condition has subsequently been described by Penzig (1922) and Rozhdestrensky (1958). Fukomoto (1960) produced the condition in the varieties Red Cherry, Jubilee and Yellow Pear, by pinching off the lateral buds, flowers and fruits. Chaudhary (1972) observed similar results in virus-infected plants in which normal growth was halted. In both of the experimentally induced cases, the location of the branches, in the axils of leaflets, was constant. Both Duchartre and Fukomoto reported the occurrence of flowers and fruits on the epiphyllous branches.

b.5 Finally, axillary buds which form lateral branches may occur in epipetiolar positions, as described by Barth (1896) for Tapura pedicellaris Chod., with mention in passing of similar situations in other taxa. Melville (1962) describes two other cases in which a pseudo-axillary bud may occur a leaf, or be vascularized by the leaf trace, in Andersonia R.Br. (Epacridaceae) and Gnetum.

b.6 Vegetative propagules which occur, and may also be formed, on leaves of natural occurring, intact plants exhibit a wide range of behaviour. At one extreme they are discrete, deciduous, dispersible units, often enclosed in one or more layers of protective tissue, and may be observed to play an important part in the distribution of the species beyond the immediate vicinity of a parent plant (see pp. 40-41). At the other extreme, epiphyllous propagules may normally establish new plants while still attached to the parent plant. The best documented examples of the first case are *Malaxis paludosa* Sw. (Orchidaceae : Taylor, 1967), *Drosera* spp. (Droseraceae: Lloyd, 1942), and *Pinguicula vulgaris* L. (Lentibulariaceae: Lloyd, 1942; Raju, 1969). In the latter two examples, bulbils are formed at the end of the growing season and are dispersed and develop the following year. Other examples are *Pinellia ternata* (Thunb.) Breitenbach (= *P. tuberifera* Tenore, Araceae: Braun, 1860; Engler, 1920; Priestley & Swingle, 1929), *Cardamine matthioli* and *C. pratensis* L. (Cruciferae: Braun, 1860; Arnal, 1963; Marchal, 1969; Savile, 1972), *Bryophyllum* spp. (sometimes also referred to *Kalanchoe* Crassulaceae: Braun, 1860; Priestley & Swingle, 1929; Marchal, 1969; Dormer, 1973) and, in the Liliaceae, *Gagea pratensis* (Kerner, 1895; Troll, 1937, Bugnon, 1958), *Ornithogalum* spp. (Braun, 1860; Troll, 1937; Samson & Kerstens, 1971) and *Hyacinthus pouzolsii* Gay (Braun, 1860; Kerner, 1895).

b.7 The other case, in which propagation takes place from the mother plant, occurs in *Haemanthus cinnabarinus* Decaisne (Amaryllidaceae: Hall & Tomlinson, 1973), *Heleniopsis orientalis* (Thunb.) C. Tanaka (Liliaceae : Kato & Kawahara, 1972), *Nymphaea micrantha* Guill.& Perot. and its hybrids (Conard, 1905; Arber, 1950) and *Tolmiea menziesii*, Torr.& Gray (Priestley & Swingle, 1929; Yarborough, 1936).

b.8 Finally, there are a number of cases in which details of the structure and growth of the epiphyllous bud are not available: *Curculigo* (Amaryllifaceae: Kerner, 1895); *Allium*, *Fritillaria*, and *Scilla leddenii* (Liliaceae: Kerner, 1895; Marchal, 1969); *Arabis pumila*, *Brassica oleracea*, *Nasturtium officinale*, and *Rorippa palustris* (Cruciferae: Braun, 1860; Duchartre, 1881; Kerner, 1895; Priestley & Swingle, 1929); *Chirita sinensis* and *Episcia bicolor* (Gesneriaceae: Braun, 1860; Kerner, 1895); and *Chelidonium majus* (Papaveraceae: Braun, 1860).

A. 3.c Epiphyllous Leaves

c.1 Epiphyllous leaf-like structures occur almost exclusively in the genus *Begonia*. Here, laminar stalked, laminar, funnel-shaped and peltate structures occur on the laminas of foliage leaves of *B. hispida* Schott var. *cucillifera* Irmsch. (Thinnes, 1972), *B. manicata* Cels. (Weiss, 1858), *B. phyllomaniaca* Mart. (= *B. manicata* x *B. incarnata* Hooker, 1852; Goebel, 1908) and *B. vitichotoma* Hart (= B. dichotoma Jacq. x *B. vitifolia* Schott : Villiers & Cusset, 1969). Hooker (1852) reported that the epiphyllous structures of *B. phyllomaniaca* were capable of forming new plants when removed and grown as cuttings. Goebel (1908), however, pointed out that these structures did not function as propagules, as they did not fall off, and never formed new plants, unless removed.

In addition, they did not participate in the shoot regeneration of detached whole leaves.

c.2 Schnell (1969) and Villiers & Cusset (1969) have shown that these epiphyllous structures on Begonia leaves are strongly localized along veins, and at the points where veins branch.

c.3 Villiers & Cusset (1969) interpreted the epiphyllous structures of B. vitichotoma as "metamères" or leaflet-homologues. Similar structures on the leaves of B. hispida var. cucillifera, however, were homologized with "emergences" by Thinnes (1972), in order to reconcile their epipyllous position with the classical theory of the shoot in an orthodox way. It has been suggested, however, (Sattler, in press), that it is not necessary to base such an interpretation exclusively on position, and so obscure real similarities between organs, if the shoot model is instead modified to permit the insertion of leaves on leaves.

c.4 In a population of Bergenia ciliata (Royle) A.Br. (Saxifragaceae) in the Royal Botanic Gardens, Edinburgh, small leaf-like structures, laminar and/or peltate, are found at the base of the lamina, where it joins a relatively massive petiole (Jong, personal communication to R. Sattler). Similar structures have been observed on plants of Gunnera chilensis Lam. (as G. tinctoria), in the Montreal Botanical Gardens, and of Iva xanthifolia Nutt. growing wild in Montreal.

(III) A.4. Anatomical patterns in Epiphyllous Inflorescences.

4.1 The examination and interpretation of the anatomy, especially the vascular anatomy, of epiphyllous inflorescences is intimately bound up with the concept of congenital fusion (see pp. 7,33). Certain vascular patterns are allegedly diagnostic of fusion having occurred, "congenitally", or during phylogeny. Other patterns permit the conclusion that an inflorescence may have developed epiphyllously, or that fusion has occurred so completely that it is no longer demonstrable. In fact, it seems that these patterns intergrade and moreover, by themselves alone, without additional ontogenetic information, say very little about how many organs are involved in a given situation, or about what relationships obtain between them.

4.2 Details of the vascular anatomy of the epiphyllous inflorescences of Turnera trioniflora and Begonia ameliae demonstrate the extreme contrasts in internal structure externally similar conditions may present. T. trioniflora (plate II, Figs. 2-7) exhibits all the anatomical requirements for congenital fusion to have occurred. Below the insertion of the flower (Fig.1,3) the leaf and floral traces are distinct, and the floral trace enters the stele directly above the leaf trace (Figs.5-6), much as does that of the axillary bud in Phyllonoma and Helwingia (V. Fig.20, XIV. Fig. 27-28). Lateral branch buds develop in the leaf axil only after flowering is complete. In B. ameliae, on the other hand, Duchartre (1886) has demonstrated that the bundles to the inflorescence split off internally from two lateral groups of petoliar bundles, and extend directly into the peduncle. In default of developmental data, he then takes this as evidence of the epiphyllous origin of the inflorescence, i.e., the inflorescence arose directly from the leaf, rather than having been formed on the apex and "fused" to the petiole.

4.3 The most common occurrence, however, is for a single collateral leaf trace (or group of traces) to depart from the stele, its lateral edges curving together to meet adaxially and forming a closed siphonstelic trace. Within the petiole further up, or within the lamina midrib, this cylinder of vascular tissue becomes partitioned dorsiventrally to form an adaxial and an abaxial component. The adaxial component forms the inflorescence trace, and may once more round up into a siphonostelic configuation. The abaxial component remains as the collateral midrib bundle extending into the remainder of the leaf. This pattern has been demonstrated for both the fertile and sterile leaves of Phyllonoma (de Candolle, 1890, Figs. 20-26; pp. and Figs. 18-27), and the fertile, but not the sterile leaves of Helwingia (de Candolle, 1890, Figs. 1-19; pp. and Figs. 21-29) Polycardia lateralis (as P. hildebrandti; de Candolle, 1890, Figs. 42-47), and Thesium humifusum DC (Thibaut, 1955). In Tilia (Arber 1925, Fig.49), Cneorum pulverulentum Vent., and Erythrochiton hypophyllanthus (Planchon, 1853) there is a similar partioning of vascular tissue within the petiole and midrib, but in these cases the nodal anatomy was not studied. De Candolle (1890, Figs. 38-41) also describes the vascular anatomy of the petiole and leaf Polycardia phyllanthoides;

here the collateral bundle at the base of the petiole becomes closed and siphonostelic and remains so through the midrib to the leaf tip where the inflorescence is borne.

4.4. Similarly, Barth (1896) and Prance (1972) discuss the petiolar and midrib anatomy of members of the Dichapetalaceae. In Dichapetalum cymosum (Hook) Engl. with axillary inflorescences, Barth describes how, in addition to the horseshoe-shaped petiole trace, an additional, opposed trace, is formed adaxially, so that a more or less complete siphonostelic ring of vascular tissue results. In the species studied with epiphyllous inflorescences, this adaxial component leads to the inflorescence (and in T. pedicellaris, to the axillary bud).Barth,als quoted by Prance, made a major point of the fact that these adaxial inflorescence traces remain separate from the base of the petiole, and so provide evidence of "accrescence congénitale" (cf. p. 34). In addition, Prance also cites the presence of "floral" bundles in petioles of the sterile leaves of species with epiphyllous inflorescences in support of the occurrence of "congenital" processes.

4.5 The first point raised simply ignores the possibility that examination of the node in these species might still show that the opposed adaxial bundle, is derived from the lateral edges of the abaxial leaf bundle, as in D. cymosum, apparently, Phyllonoma, and Helwingia.

4.6 In addition, the second point, made by Prance, also ignores the case of <u>D. cymosum</u>, where two opposed vascular bundles, in more or less siphonostelic configuration occur, much as in the epiphyllous species whose anatomy Prance describes, but in this case in conjunction with axillary inflorescences. As Barth himself points out, this is precisely evidence of the vascular anatomical trends in the leaves of the group, independent of epiphylly. Thus it is hard to understand Prance's argument that, "the presence of floral bundles in some sterile petioles and the separate nature ofthe floral bundle demonstrates that the position of the inflorescence has arisen by a gradual fusion of the peduncle with the petiole......"

4.7 Metcalfe and Chalk (1950) have shown in scores of families where epiphylly is unknown, the occurrence of petiolar vascular anatomy similar to that found in the Dichapetalaceae. It seems hard to credit, therefore, that anatomical tendencies are necessarily so closely linked to epiphylly as Prance apparently believes. In addition, Carlquist (1969) and Schmid (1972) have warned of the dangers attendant on interpreting likely vascular bundles as somehow vestiges or forerunners of phylogenetically "gradual" processes.

PLATE II

Figure 1: *Turnera ulmifolia* var. *intermedia*

Figures 2-7: *Turnera trioniflora*. Transverse serial sections of a shoot tip. Vascular connection of the flower to the stele. Stained with safranin and fast green FCF.

Figure 1: Epipetiolar inflorescence.

Figure 2: Section through the base of an unopened flower (F), above its insertion (a, in Fig. 1) on the petiole of leaf L.

Figure 3: 670 nm below the level of Fig. 2, below the insertion of the flower on the petiole.

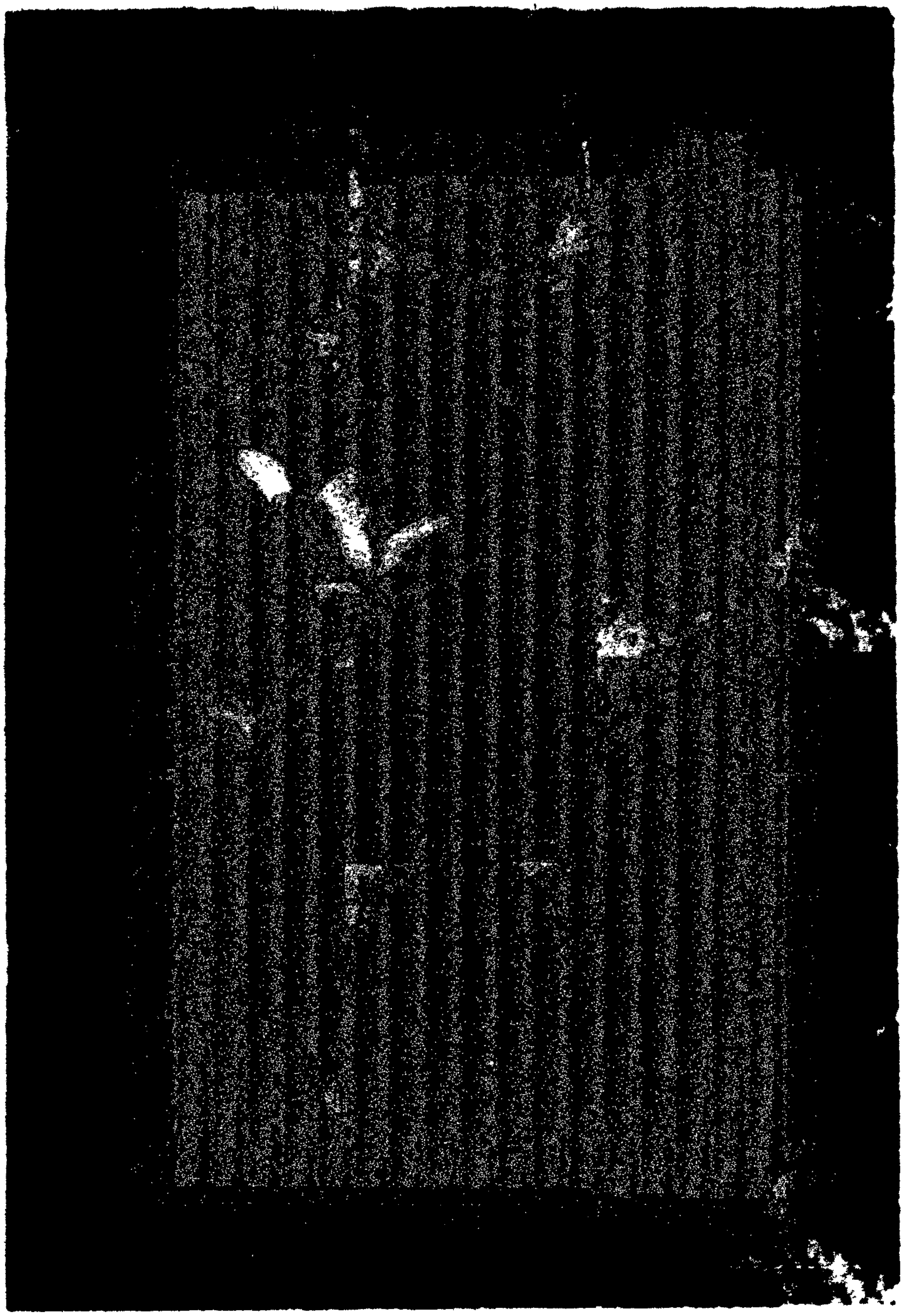
Figure 4: 340 nm below the level of Fig. 3, at the level of the axil of leaf L (b, in Fig. 1).

Figure 5: 60 nm below the level of Fig. 4. The small, densely stained cells in the axil of L (and L-1, in Fig. 4) may indicate axillary bud initiation.

Figure 6: 160 nm below the level of Fig. 5.

Figure 7: 210 nm below the level of Fig. 6.

a, insertion of flower (F); b, axil of leaf (L); L, foliage leaf; B, bract; LT, leaf trace; FT, flower trace; L-1, L-2, the next youngest leaves, with respect to leaf L; L+1, the next oldest leaf.



(III) A.5. Developmental Patterns.

a. Spatial Shifting

a.1. The development of epiphyllous organs, that is, of altered positional relationships between organs may occur by three distinguishable processes: spatial shifts in the position of organ initiation from the stem (axil of a leaf primordium) to the leaf primordium itself; spatial and temporal shifts, from the axil of leaf primordia to the more or less mature leaf; and intercalary or zonal growth, affecting discrete, adjacent primordia at the shoot tip. The first process is that described for <u>Phyllonoma</u>, and discussed in more detail in chapter V, and also, concerning <u>Helwingia</u>, in chapter VI. Comparable situations occur in <u>Hordeum</u> (p. 69), <u>Chrysalidocarpus</u>, and in many ferns.

a.2. In <u>Chrysalidocarpus</u> <u>lutescens</u>, Fisher (1973) has demonstrated a unique instance of the initiation of lateral branch primordia on the abaxial side of leaf primordia, during their first plastochron. Perhaps influenced by the classical model of the shoot, Fisher has suggested that the leaf primordium at the time of branch initiation is not wholly determined as a leaf, but rather, is meristematic throughout, and behaves much like a shoot apex. Thus he describes branch initiation as an unequal bifurcation of the primordium, and as distinct also from the formation of "detached" meristems described by Wardlaw (1952).

a.3. A similar shifting of the site of lateral branch formation occurs in Hymenophyllaceous ferns (<u>Trichomanes</u> spp.: McVeigh, 1937; Bierhorst, 1974). Division of the leaf apical cell leads to formation of one or more sister-apices along the frond, which then give rise to the lateral branches. Similar divisions and branching occur also in <u>Psilotum</u>, Tmesipteris, and Stromatopteris (Bierhorst, 1969, 1971), Actinostachys pennula, A. germania, Gleichenia linearis, G. caudata, and G. breckinridgi (Bierhorst, 1973). In Botrychium, where the axillary bud is sterile, the fertile spike originates by division of the leaf apical cell (Bierhorst, 1971). Sharma and Tripathi (1969) have shown that the proliferation bud at the leaf-tip of Adiantum caudatum L. originates in a similar manner as well.

b. Spatial and Temporal Shifting

b.1. There appears to be a sort of continuum between lateral branch development in Chrysalidocarpus and what is known of the origin of the epiphyllous plantlets on very young leaves of Tolmiea menziesii and Bryophyllum spp., leading to the condition where epiphyllous organ initiation occurs on wholly mature, possibly even senescent, leaves (G. Goebel, 1902: 428).

b.2. In Tolmiea menziesii Yarborough (1936) describes the development of the young plantlet found at the junction of the petiole and lamina from a "residual meristem", a mound of cells visible on leaves over 5 mm long, whose earlier history was not studied. It develops continuously, and mature leaves bear miniature plants consisting of entire rosettes of leaves.

b.3. Thinnes (1972, cited by Sattler, in press) has studied the ontogeny of the leaflike structures which form on foliage leaves of Begonia hispida var. cucullifera, and showed that they are initiated in the second layer of cells, develop like leaves, and are anatomically similar to leaves. Perhaps in order to conform to the dicta of the classical shoot model forbidding insertion of phyllomes on other phyllomes, as well as the fact that these structures never develop to a size comparable to that of the leaf bearing them, their lamina rarely exceeding 2 - 3 cm. in length, Thinnes interpreted these structures as "emergences".

b.4. The development of the epiphyllous leaf-like structures of B. vitichotoma, interpreted as "metamères" (leaflet-homologues) by Villiers and Cusset (1969) and Cusset (1970), has been reported by Villiers (1972). The surface of the leaf is covered with relatively large pointed multicellular trichomes; at the base of some of these growth occurs, leading to formation of a cup-shaped structure. On veins, and especially at the branch-points of the major veins (Villiers and Cusset, 1969) these trichome outgrowths become enlarged and stalked, much as in B. hispida var. cucullifera. These are "metamères"; the others, not located on veins, are described by Villiers as "emergences". The anatomy of the principal vein of the metamère is shown to be similar to that of the leaf midrib. However, Villiers provides no clear indication on the mode of initiation of these structures, nor on the meristematic activity by which they develop.

b.5. Development of branches, buds, and "foliar embryos" by localized remeristematization of differentiated, subepidermal leaf tissue has been shown to occur in Tomato (Fukumoto, 1960; p. 22), Cardamine pratensis (Marchal, 1968), and Malaxis paludosa (Taylor, 1967), respectively. However, in none of these cases has the actual initiation of this development been demonstrated. Marchal herself suggests that in fact a residual "detached meristem" is present, that the subepidermal cells throughout the adaxial surface of the mature leaf remain meristematic, although her illustration alluded to (II B) does not appear to bear this out. As in Tomato, there is in C. pratensis a strong localization of the epiphyllous buds in the axils of leaflets, and, like Begonia vitichotoma, in the angles of major vein branchings.

b.6. A study of the ontogeny of the buds developing from the midrib on the underside of intact, attached leaves of Haemanthus cinnabarinus (Hall and Tomlinson, 1973) suggests that here, proliferation is associated with leaf senescence, proceeding by way of parenchyma hypertrophy, which results in formation of callus-like tissue. Subsequently, within this callus isolated vascular differentiation occurs, and growth centers appear. Leaf primordia form on a shoot apex, and burst through the epidermis. Roots then form, and vascular connection with the midrib is established. In Heleniopsis orientalis a similar development of epiphyllous buds by internal callus-like tissue formation beneath the adaxial surface of the leaf has been reported by Kato and Kawahara (1972). In neither case does there seem to be any evidence of pre-existing "residual" meristematic tissue responsible for bud formation.

c. Zonal Growth

c.1. The concept of "intercalary" or "zonal" growth developed first (Payer, 1857b) as a description of the ontogeny of organs, e.g. in calyx and corolla tubes, joined "congenitally", i.e. organs whose independance was only conceptual, based on homologization with similar but independant organs in related taxa. Thus, Payer (1857a: 114) describes the inflorescence of Tilia as follows (quoted in Bugnon, 1958): "... le groupe de fleurs adhère par la partie inférieure de son pédoncule commun avec la base de la bractée... Cette union du groupe de fleurs à la bractée... ne se produit pas postérieurement à leur naissance; elle est congénitale. La partie inférieure de la bractée ou de la feuille qui adhère avec la base du groupe de fleurs est contemporaine de cette base; elles sont nées toutes deux en mêmes temps et réunies. Voila pourquoi nous avons souvent employé l'expression de conné (connatus) pour indiquer une adhérence congénitale entre deux organes..." and this situation is clearly illustrated by him (1857b: plate 4). In this way, adjacent organs are initiated separately, and these free primordia are then supposed to be carried up by an intercalation (cf. (a) in Text - figure 1) developing beneath them. A modern advocate of this point of view is Kaplan (1971).

c.2. Depending on whether this intercalation maintains the characteristics of the organs whose primordia it carries up, or not (and appears sui generis, i.e. stem-like, where no stem "should be") van Tieghem (1891) describes such a result of intercalary growth as, respectively, either "concrescence" of the organs involved (as in Helwingia, Phyllonoma, and Tilia), or "accrescence" of the stem, which grows out from the node, beneath them (cf. Text - figure 1A).

c.3. Goebel (1933: 1672) however apparently recognized that such an intercalation could assume characteristics of any, all or none of the organs involved, and avoided such distinctions which retained the notion of distinct, separable organs. Similarly, other workers (Schumann, 1890; Schinz 1894; Coulter, Barnes, and Cowles, 1910; McLean Thompson, 1934; Schaffner, 1937; Sattler, 1974, and in press) have also used the idea of intercalary, zonal, or toral growth to describe the ontogeny of phenomena such as epiphylly, syncarpy, etc., wholly dissociating it from, and rejecting, the concept of congenital fusion it was originally designed to support.

c.4. Bugnon (1958) has developed the concept of the "hypophylloclade" to describe nodal deformations arising through intercalary growth which incorporate the primordia of leaves, as well as those of other organs (e.g. inflorescences, axillary buds). Thus, epiphyllous situations ascribed by van Tieghem to "accrescence" are understood by Bugnon as hypophylloclades. These intergrade with "hypophylloclades complexes", as Bugnon describes the epiphyllous inflorescences, etc. in which the intercalation (a) in Text - figure 1 becomes invested with lamina (Text - figure 1B, 1F). In van Tieghem's terminology, this would be the result of "concrescence".

c.5. Leins, Merxmüller, and Sattler (1972) have recently proposed a terminology for floral structure arising by intercalary growth, in which they also seek to dissociate the products from the notion of fused individual organs.

c.6. Intercalary growth has been described as being associated with the incomplete individualization of the primordia involved (Stebbins, 1950; Cusick, 1966; van Heel, 1969; Croizat, 1973), or due to "meristem fusion" (Hagemann, 1970) in the sense of "interprimordial growth" (Sattler, 1973) or "zonal growth" (Sattler, 1974). These processes may not always be readily distinguished from each other in descriptions, or from growth occurring at well defined "intercalary meristems". Such meristems may appear as very localized, highly meristematic regions between regions of differentiated, vacuolated tissue (Cutter, 1971) in the phyllomorphs of Streptocarpus and the gynophore of the peanut (Jong, 1970, as well as in the growth of many monocots (Fisher, 1970, 1971, 1973, 1974) and dicots (Cutter, 1971).

c.7. However, in other situations whose external morphology and morphogenesis suggest "intercalary" or "zonal" growth, a much more diffuse pattern of growth has been described. As in some leaves (Stebbins and Yagil, 1966; Thomasson, 1970) and internodes (Wetmore and Garrison, 1966;

Cutter, 1971; Steeves and Sussex, 1972) longitudinally oriented cell division and expansion appears to occur in a rather large zone, i.e. the common insertion of the associated primordia, e.g. Ornithogalum caudatum (Troll, 1937; Samson and Kerstens, 1971), and Spathicarpa sagittafolia (Troll, 1928). A similar occurrence has been described in the internodal expansion which results in the "concaulescent" position of the inflorescence of Solanum melongena (Shah and Patel, 1970).

c.8. In Helwingia japonica, however, it is possible to describe a pattern of "basal" (Clowes, 1961) or "intercalary" growth responsible for the upgrowth of the "intercalated zone" or "hypophylloclade complexe" of the fertile leaf. In conjunction with initiation of the inflorescence on the base of the leaf primordium, basal growth beneath the two primordia can account for the observed anatomical and developmental data independant of specific processes by which primordia have been described to coalesce, or fail to individualize, such as extension of the apical growth of adjacent primordia ("meristem fusion", Hagemann, op. cit.; "Interprimordial growth", Sattler, 1973).

(III) A.6. Functional Considerations.

a. Epiphyllous Inflorescences

a.1. The functional and/or adaptative significance of "epiphylliflory", i.e. epiphyllous inflorescences, is not at all clear, as it has not yet been the object of direct field study. It is, however, clear that no one explanation will serve for more than a limited number of cases. One of the first conjectures which comes to mind is the possible implication of plant-pollinator relationships. Certainly only a very small number of epiphylliflorous plants are wind pollinated. But the array of combinations of leaf and flower sizes, position, bract showiness, and breeding system makes it difficult to see any obvious pattern.

a.2. Stone (personal communication) has suggested that it may be advantageous for a plant not to have to depend on determinate locations for flowering. However, in practically all of the cases reviewed (III.A.3.), there is little or no indeterminacy in flower or inflorescence position. The variation which occurs is between epiphyllous and axillary positions, as for example, in <u>Chisoheton pohlianus</u> (Harms, 1917), <u>Raphanocarpus kirkii</u> (the female flower; Hooker, 1870), and in <u>Dichapetalum toxicarium</u> (Engler and Krause, 1931), <u>Saururus cernuus</u> (Baillon, 1874), and <u>Thesium</u> (Thibaut, 1955). In the latter three cases, this variation is associated with position of the flower or flower cluster within the inflorescence as a whole. In <u>Saururus</u> and <u>Thesium</u> there is an acropetal transition from sessile, axillary flowers, to those carried up and epibracteous, as in Text - figure 1A.

a.3. Epiphylliflory may be seen as one strategy for flower presentation. In forms whose stems do not branch, or branch only rarely ("Modèle de

Corner"), Hallé and Oldemann, 1970), where axillary structures are not formed, such as in Phyllobotryum and the other Phyllobotryeae (Richards, 1966; Letouzey et al., 1969; Hallé and Oldemann, 1970; Letouzey, personal communication), the flowers are displayed along the length of the petiole and midrib.

a.4. Analogously, in Begonia paleacea and B. prolifera the inflorescence occurs on the single, sessile, palmate leaf formed on the rhizome (Irmischer, 1925). Such a unifoliate habit, and the concommitant adjustment in growth pattern (to "phyllomorph" organization, cf. p. 19) in Streptocarpus (Burtt, 1970), Epithema tenue (Hallé and Delmotte, 1973), and Chirita (Hill, 1938) appears to be associated at least in part with the ability to take advantage of vertical and overhanging substrates.

a.5. Faegri and van der Pijl (1971, pp. 18-27) and van der Pijl (1972, p. 3) mention, by way of rejection, the "antiteleological" and "anti-adaptation" arguments of Goebel, Troll and others, and can point to the increasing number of studies in the literature which support their approach and testify to the intricacy of co-evolutionary relationships between plants and the agents of their pollination and dispersal. Still, it seems foolish to overlook the possibility that some morphological variations, such as instances of epiphylly may be adaptively neutral consequences of the morphogenetic potential of a plant, which may or may not be "utilized" (sensu Goebel, van der Pijl, 1972, p. 3) by it. In the absence of strong evidence to the contrary, this possibility must be considered, in every case. The distribution of epiphyllous and axillary inflorescences among congeneric species (e.g. of Erythrochiton, Chisocheton, Dichapetalum, Peperomia, Polycardia) and closely related genera (Raphanocarpus/

Momordica, *Phyllocaris* / *Lobelia*) suggest a possible means of approaching the problem (cf. also *Neuropeltopsis* and *Neuropeltis*, below).

b. Epiphyllous Fruits

b.1. In addition to the foregoing, one of the most significant aspects of epiphylliflory is that it can lead to "epiphyllicarpy", i.e. the epiphyllous position of the resulting fruit. The most obvious adaptive significance of this is for the dispersal of the fruit. In his study of plant dispersal, Ridley (1930) points out, "In a number of plants the fruits... are dispersed by the aid of bracts, or by persistent, and usually accrescent, leaves below the flower. To act as flying organs, the detachment of the fruit must be below these modified leaves.". As examples, Ridley cites *Bougainvillea* and *Tilia*, describing flight records of the fruits of *T. dasystyla* of upwards of 18 yards, from a twenty foot tree. In *Tilia*, the configuration of bract and fruit also leads to rotation of the unit as it falls, and to its being blown further along the ground after it lands. Nevertheless, in his monograph of the American species of *Tilia*, Jones (1968) deprecates the role of the bract in dispersal, pointing to the tendency in *T. americana* and *T. heterophylla* for the fruits to readily become detached from their pedicels. Thus, van der Pijl (1972) suggests the bract may serve instead to shake the fruit loose in the wind. In addition to these examples, epiphyllicarpy likely plays a part in the dispersal of *Dobinea* and *Camplyopetalum* (Forman, 1954), and of *Neuropeltopsis* (van Oostroom, 1964).

b.2. In the related genus *Neuropeltis* Wall., a similar morphological and functional effect is produced by an alternative ontogenetic strategy. Two small and inconspicuous floral bracts after fertilization form a single large wing which bears the fruit (Ridley, 1930). Dispersal is similarly aided in Engleh̲a̲r̲d̲t̲i̲a̲ (Ridley, 1930) and species of Carpinus (Ridley, 1930), where a bract and two bracteoles unite and grow into a large fruit-bearing three-lobed wing following fertilization (Willis, 1966).

c. Vegetative Epiphyllous Organs

c.1. The integrated, regular and natural occurrence of branches or their homologues on leaves of Chrysalidocarpus, Dolichothele, and Coryphantha seems to be a prime example of adaptively neutral morphological variation proceeding from the epigenetic and morphogenetic propensities of the plant where it occurs (cf. "laws of growth", pp. 70-72), an example in any case where "need" and "adaptation" perform a chicken and egg routine (which came first....?). However, as is seen in many ferns (Troop and Mickel, 1968; Bierhorst, 1971) the ability to produce epiphyllous branches may allow exploitation of a prostrate, straggling growth habit which spreads the plant over a large area.

c.2. The epiphyllous occurrence of vegetative propagules, on the other hand, is merely one form of vegetative propagation, examined here because of its particular location. The functional advantages of vegetative propagation in any manner are well known, and are recorded for some of the examples cited here. It appears that the deciduous, epiphyllous plantlets of Cardamine pratensis, dispersed by running water, are at least in part responsible for its distribution in the Arctic, where it is not known to set seed (Savile, 1972; cf. Ridley, 1930). Hall and Tomlinson (1973) point out that Haemanthus cinnabarinus appears to be similar to several other herbaceous species of the West African forest floor in reproducing almost exclusively by vegetative means. Field data compiled by Yarborough (1936) suggest that *Tolmiea menziesii* behaves similarly, although in this case abundant seed is produced. Stoudt (1938) has suggested there is a phylogenetic sequence of increasing specialization in propagation from leaves in the Crassulaceae, from *Sedum* (and *Crassula*; Dormer, 1972), where there is relatively little specialization for the establishment of new plants ~~from~~ detached leaves, through *Byrnesia* and *Kalanchoe rotundifolia*, where one basal meristem is present on each leaf. The most advanced condition would be in *Bryophyllum*, where multiple marginal meristems are present, and where the production of entire, deciduous plantlets, capable of rapid establishment (van der Pijl, 1972) may occur.

(III) A.7. Teratological and Related Instances of Epiphylly.

7.1. In addition to the epiphyllous formation of supernumerary florets in strains of barley (Takahashi et al., 1953; pp. 69-70), of branches in tomato varieties (Duchartre, 1853; Fukomoto, 1960; p. 22), and of leaflets in Bergenia, Iva, and Gunnera (p. 25), which appear to be more or less repetitive, and/or constant, within the populations involved, Caspary (1874) recorded three teratological instances of epiphylly, in single plants of Rheum undulatum, Cucumis sativus, and Urtica urens. While in the first two cases the condition was observed during one season only, a second plant of Urtica was found which showed the condition and had set seed, which appeared to produce, in the following year, normal plants.

7.2. There are also two remarkable cases where galls greatly resembling shoots are produced on leaves by insect larvae. Larvae of Oligotrophus oleariae become enclosed "by annular upgrowth of the stem, or more rarely, of the leaf surface", of Olearia species (Philipson, 1964). The apical meristem induced by the larvae which produces this upgrowth also produces a rosette of miniature leaves resembling the foliage leaves of the Olearia species involved, in the phyllotactic sequence normal for the plant. On leaves of Shorea pauciflora king, larvae of Gallococcus anthonyae embedded within the leaf induce the formation on the leaf surface of a conelike structure, bearing upwards of two dozen "leaves" (Anthony, 1972). These "leaves" have been described as resembling cataphylls, in which the "Oberblatt" is almost totally inhibited (Cusset, cited by Anthony, 1972), and are arranged in the phyllotaxy normal to S. pauciflora. This situation is apparently unique for two reasons: the insect emerges and re-encysts again twice in the new growth of the shoot-like gall, as it develops; and the gall itself develops from an apparently normal apical meristem.

(III) B. Occurrence of Epiphylly.

B.1 Generalizations concerning the Occurrence of Epiphylly.

1.1 Table I (B.2., below) lists the genera and species in which epiphyllous organs and organ systems occur, according to Engler's system, as used by Willis (1966). Epiphyllous formations are subdivided into five types: inflorescences, branches, attached propagules, deciduous propagules, and leaf-like structures. The middle three categories follow the breakdown of "epiphyllous shoots" made in the discussion of their morphological patterns (pp. 16-25) that correlates with their function (pp. 37-41) probably, but not with their ontogeny (pp. 30-36). The capital letters A-H which indicate the occurrence of one of the five epiphyllous structures refer to Text - figure 1, and specify the position of the structure in question. Asterisks indicate situations in which the position is not known, or in which it cannot adequately be described in terms of Text - figure 1. Similarly, situations in which the nature of the epiphyllous structure is not known are indicated to the right of column (5). The references given are not the only ones cited in the text, but rather the most informative ones for the taxon concerned, with respect to the ontogeny or anatomy of the epiphyllous condition, where available. Often, however, they refer to articles which simply describe the epiphyllous condition, and/or the systematic position, habit, or habitat of the plant involved.

B.1.2 Epiphylliflory does appear very generally to be a tropical phenomenon. Only a few genera (e.g. <u>Helwingia</u>, <u>Hermidium</u>, <u>Hordeum</u>, <u>Thesium</u>, <u>Tilia</u>) are restricted to the north temperate zone, while the remainder are typically tropical (Willis, 1966). Vegetative epiphyllous ramification appears to occur only in Begonia sinuata, Coryphantha, Dolichothele, and the palms. However, vegetative propagation from leaves as indicated above, serves from the tropical forest to the arctic. The preponderant occurrence of epiphylly (other than as a means of vegetative propagation) in the tropics is especially interesting because of the great age and complexity of the tropical rain forest ecosystem (cf. Spome, 1973). Ashton (1969) has suggested that the presence of a variety of "apparently non-adaptive" characters, such as epiphylly (see below, and elsewhere, pp. 71-72), in tree families of the tropical rain forest may "have arisen when the early angiosperms invaded and diversified... in what was to them a vacant humid tropical environment occupied by gymnospermous forest". It may be that similar considerations could apply as well to the species of the substory layers of the tropical rain forest, among which are many of the epiphylliflorous species.

B.1.3 It is evident from Table I (below) that epiphylly is widespread among the families of the flowering plants. Its occurrence is distinguished by its apparent randomness, with respect to systematic or phylogenetic relationships. Using the dendrogram of phylogenetic relationships proposed by Takhtajan (1969), epiphylly is found to occur in all of the major groupings but three, the subclasses Hamamelididae, Ranunculidae (except for the probably teratological occurrence in Papaver, cf. Braun, 1860), and Alismadae. However, most of the occurrences are in the Dilleniidae and Rosidae. Other concepts of the relationships between the families represented in Table I, such as those of Hutchinson (in Lawrence, 1951) or Croizat (1960), although the former shows some of the same clumps of groups as Takhtajan's, do not distribute epiphylly any less widely, within the angiosperms as a whole, or any less so between supposedly advanced and primitive groups.

B.1.4 This sort of analysis however does not take into account the relative rareness of epiphylly in general. The taxa in which it occurs seem to be quite isolated, among others of equal or higher rank in the same assemblage, as for example, Bougainvillea, Hermidium, Coryphantha, and Dolichothele, among the remainder of the Caryophyllidae (16 families), the Dichapetalaceae, within the Euphorbiales (7 families), or Helwingia or Phyllonoma, within their respective families (sensu lato; Cornaceae, 12 genera; Saxifragaceae, 80 genera: Engler, 1966).

B.1.5 Similarly, plants with epiphyllous inflorescences appear also to constitute only very small proportions of the total angiosperm flora, with respect to the total number of species, in the regions where they occur. Nor do they constitute any great proportion of the biomass there.

Thus, epiphylliflory and epiphyllous branching are distributed widely among diverse groups of angiosperms. It is an infrequent condition, and does not appear from present information to be a character which confers any disadvantage or unique advantage on plants possessing it. Instead, these are further reasons to think of epiphylly, other than its involvement in vegetative propagation, as a condition which occurs primarily as a result of the plant's potential for a variety of growth patterns (cf. pp.19,30-36) and which may duplicate adaptations obtained more commonly by more "orthodox" ontogenies.

III. B. 2.

TABLE I. NORMALLY-OCCURRING EPIPHYLLOUS ORGANS IN ANGIOSPERMS

	Inflorescence (1)	Branch (2)	non-deciduous propagule (3)	deciduous propagule (4)	Leaf-like structure (5)
MONOCOTYLEDONEAE					
GLUMIFLORAE					
Gramineae					
Hordeum vulgare (varieties)	B (Croizat, 1960; Stebbins, 1965)				
PRINCIPES					
Palmae					
Calamus spp.	C (Corner, 1966)				
Chrysolidocarpus lutescens H. Wendl.	C	C (Fisher, 1973)			
Daemonorops spp.	C (Corner, 1966)				
SPATHIFLORAE					
Araceae					
Pinellia tuberifera Tenore				D (Engler, 1920; Troll, 1939).	
Spathantheum Schott	F cf.	G (Troll, 1928)			
Spathicarpa Hook.	F cf.	G (Troll, 1928)			
Amorphophallus bulbifer Blume					* (Troll, 1939)

Table 1

	(1)	(2)	(3)	(4)	(5)
LILIIFLORAE					
Liliaceae					
Allium sp.				* (Kerner, 1895; Troll, 1937)	
Frittilaria sp.				* (Kerner, 1895)	
Gagea pratensis				* (Bugnon, 1958)	
Heleniopsis orientalis (Thunb.) C. Tanaka				F' (Kato & Kawahara, 1972)	
Hyacinthus pouzolsii Gay (= H. fastigiatus Bertol.)				G (Braun, 1860)	
Ornithogalum spp.				F' (Braun, 1860; Samson & Kerstens, 1971)	
Scilla ledienii Engl.			F cf. H' (acrophylle) (Marchal, 1969)		
Amaryllidaceae					
Curculigo sp.					* (Kerner, 1895)
Haemanthus cinnabarinus Decaisne			F' (Hall & Tomlinson, 1973)		
MICROSPERMAE					
Orchidaceae					
Malaxis paludosa Sw.				F cf. H' (Taylor, 1967)	
DICOTYLEDONEAE					
ARCHICHLAMYDEAE					
PIPERALES					
Saururaceae					
Anemopsis Hook. & Arn.	A (Payer, 1857b; Raju, 1961)				
Houttuynia Thunb.	A (Raju, 1961)				
Saururus L.	A (Payer, 1857b; Raju, 1961)				

Accession No.	Date	Sex	Condition	Fixation	Collector
	YAMAGATA CITY, JAPAN				
TAD 42	6.10.71	male/ female	dormant	FAA	Prof. Yamazaki
	NIKKO, JAPAN				
TAD 44	10.71	male/ female	dormant	FAA	Dr. R. Sattler
	ROYAL BOTANIC GARDENS, KEW				
TAD 156	7.8.71	Female	dormant	FAA	Dr. R. Sattler
	ROYAL BOTANIC GARDENS, EDINBURGH				
TAD 157	23.8.71	Female	dormant	FAA	Dr. R. Sattler

Table I.3

	(1)	(2)	(3)	(4)	(5)
SARRACENIALES					
Droseraceae					
Drosera spp.				* (Troll, 1939; Lloyd, 1942)	
ROSALES					
Crassulaceae					
Bryophyllum (or as Kalanchoe) spp.				F (Vardar & Acarer, 1957; Dormer, 1972)	
Saxifragaceae					
Phyllonoma Willd. ex Schultes	F (de Candolle, 1890; Stork, 1956)				
Tolmiea menziesii Torr. & Gray			E (Yarborough, 1936)		
GERANIALES					
Cneoraceae					
Cneorum pulverulentum Vent.	A (Harms, 1917)				
Rutaceae					
Erythrochiton hypophyllanthus Planch. & Linden	F' (Planchon, 1853)				
Meliaceae					
Chisocheton pohlianus Harms	(F) (Harms, 1917)				
C. sp. nov.	(F) (Melville, 1962)				

Table I.4

	(1) (2) (3) (4) (5)
Dichapetalaceae	
Dichapetalum spp.	DEF
Stephanopodium Poepp. & Endl.	D (de Candolle, 1890; Barth, 1896;
Tapura Aubl.	EF Melville, 1962; Prance, 1972)
SAPINDALES	
Anacardiaceae	
Camplyopetalum siamense Forman	B (Forman, 1954)
Dobinea delavayi Baill.	B (Melville, 1962)
D. vulgaris Buch.-Ham.	B (Melville, 1962)
Celastraceae	
Polycardium quifolium Tul.	F (Perrier de la Bathie, 1946)
P. lateralis O. Hoffm.	H'' (de Candolle, 1890; Perrier de la Bathie, 1946)
P. phyllanthoides (Lamk.) DC	H' (de Candolle, 1890; Perrier de la Bathie, 1946)
MALVALES	
Tiliaceae	
Tilia L.	B (Arber, 1925)
Malvaceae	
Nototriche Turcz.	E (Harms, 1917; Burtt & Hill, 1948)

Table I. 6

	(1)	(2)	(3)	(4)	(5)
PARIETALES					
Flacourtiaceae					
Mocquerisia multiflora Hua	G				
Phyllobotryum lebrunii Staner	G				
P. spathulatum Muell. Arg.	G (Letouzey et al, 1969)				
Phylloclinium bracteatum Lecomte	F				
P. paradoxum Baill.	F				
Turneraceae					
Turnera spp.	D				
Begoniaceae					
B. sinuata Wall.	E	E (Goebel, 1902)			
B. paleacea Kurz.	E (Goebel, 1902)				
B. prolifera A. DC	E (Goebel, 1902)				
B. ameliae Bruant	E (Duchartre, 1886)				
B. hispida Schott var. cucullifera Irmsch.					F (Thinnes, 1972)
B. manicata Cels.					F (Weiss, 1858)
B. phyllomaniaca		F			F (Goebel, 1908)
B. vitichotoma Hort.					F (Villiers, 1972)
OPUNTIALES					
Cactaceae					
Coryphantha (Engelm.) Lem.		H' (Boke, 1967b)			
Dolichothele Britton & Rose		H' (Boke, 1967a)			

	(1)	(2)	(3)	(4)	(5)
UMBELLIFLORAE					
Cornaceae					
Helwingia Willd.	F (Payer, 1857; de Candolle, 1890)				
SYMPETALAE					
CONTORTAE					
Gentianaceae					
Gentiana lutea L.	A (Goebel, 1931)				
TUBIFLORAE					
Convolvulaceae					
Neuropeltopsis van Ooststroom	B (van Ooststroom, 1964)				
Scrophulariaceae					
Selago sp.	A (Burtt, personal communication)				
Gesneriaceae					
Chirita sinensis			* (Braun, 1860)		
Chirita spp.	* (Velenovsky, 1907; Hill, 1938)				
Episcia bicolor					* (Kerner, 1895)
Monophyllaea	* (Balfour & Smith, 1915)				
Moultonia Balf. f. & W.W. Smith	* (Balfour & Smith, 1915)				
Streptocarpus Lindl.	* (Jong, 1970)				

	(1)	(2)	(3)	(4)	(5)
Lentibulariaceae					
Pinguicula vulgaris L.				* (Raju, 1969)	
Acanthaceae					
Saintpauliopsis sp.	A (Burtt, personal communication)				
CUCURBITALES					
Cucurbitaceae					
Raphanocarpus Hook. f. (= Momordica)	E (Cogniaux & Harms, 1924)				
CAMPANULATAE					
Campanulaceae					
Phyllocharis schlechteri Diels	F (Moeliono & Tuyn, 1972)				

IV MATERIALS AND METHODS

A. *Phyllonoma* Material

1. A large (1m) branch of *Phyllonoma integgerima* (Turcz.) Loes., Stone 3278, was collected for me by Dr. D.E. Stone of Duke University, near Muñeco, Costa Rica, in June 1972, and preserved in FAA. This branch and associated twigs bore a large number of leaves, the majority of which were fertile, in all stages of development. These leaves had completely entire margins, and bore inflorescences at the base of the acuminate leaf tip. It is on the basis of these characters that I identified my material, following Engler's (1930) account of the genus.

2. Voucher specimens of the material examined are on deposit in the McGill College Herbarium, at MacDonald College, Ste. Anne de Bellevue, Quebec, (No. 82707) and in the herbarium of Duke University (Stone 3278).

B. *Helwingia* material

1. Material for this project, i.e. shoot tips and associated fertile and sterile leaves, was obtained from several localities, the principal ones being represented by several collections, made at different times during the growing season. Collection data for this material is summarized in Table II.

2. In Table II, "Post-flowering" refers to male branches which still bore fertile leaves (inflorescence scars on their adaxial surfaces) near their tips. The corresponding female branches would bear fertile leaves with fruits ("Fruiting"). "Sterile" indicates male branches which bore exclusively sterile leaves at their tip, the older fertile ones having not been collected. "Dormant" refers to the presence of bud scales enclosing the apex and leaf primordia, in the absence of any other information about the condition of the shoot when collected. In the October collections, this refers principally to branches which were almost entirely leafless at the time. In earlier collections, from July on, however, except for the most vigorous ones, the branches tended to have already ended in a bud at their tip.

TABLE II. HELWINGIA COLLECTIONS USED IN THIS STUDY

Accession No.	Date	Sex	Condition	Fixation	Collector
ARNOLD ARBORETUM, JAMAICA PLAIN, MASS, U.S.A.					
TAD 61,62	15.6.72	male	flowering	Acrolein	TAD
TAD 65	26.4.72	male	vernation	EtoH	Dr. Gordon DeWolf
TAD 66	1.5.72	male	vernation	EtoH	Dr. Gordon DeWolf
TAD 170	21.7.72	male	post-flowering	EtoH	Dr. Gordon DeWolf
TAD 195	14.5.73	male	flowering	Acrolein	TAD
TAD 197	12.6.73	male	post-flowering	EtoH	Dr. Gordon DeWolf
TAD 198	22.6.73	male	post-flowering	Acrolein	TAD
KURAMA, near KIBUNE, KYOTO CITY, JAPAN					
TAD 43	11.10.71	male/female	dormant	FAA	Dr. R. Sattler
TAD 78-81	2.5.72	female	unopened flowers	FAA	Mr. H. Takahashi
TAD 117-120	10.6.72	female	fruiting	FAA	Mr. H. Takahashi
TAD 167-168	2.7.72	female	fruiting	FAA	Mr. H. Takahashi
TAD 169	18.7.72	female	sterile	FAA	Mr. H. Takahashi
TAD 171	18.8.72	female	sterile	FAA	Mr. H. Takahashi
TAD 172	4.10.72	female	sterile	FAA	Mr. H. Takahashi

Table II.2

Accession No.	Date	Sex	Condition	Fixation	Collector
			GOTEBORGS BOTANISKA TRADGARD, GOTEBORG, SWEDEN		
TAD 178	18.5.72	male	unopened flowers	FAA	MM. E. Sahlin & Prof. P. Wendelbo
TAD 179	18.5.72	female	unopened flowers	FAA	"
TAD 180	18.5.72	female	unopened flowers	FAA	"
TAD 181	3.6.72	male	flowers (open)	FAA	"
TAD 182	3.6.72	female	flowers (open)	FAA	"
TAD 183	3.6.72	female	flowers (open)	FAA	"
TAD 184	31.7.72	male	post-flowering	FAA	"
TAD 185	31.7.72	female	fruiting	FAA	"
TAD 186	31.7.72	female	fruiting	FAA	"
TAD 187	1.10.72	male	sterile	FAA	"
TAD 188	1.10.72	female	fruiting	FAA	"
TAD 189	1.10.72	female	fruiting	FAA	"

N.B. For each date from the same three separate plants as collected.
N.B. For each date above, the same three plants were collected from.

Accession No.	Date	Sex	Condition	Fixation	Collector
YAMAGATA CITY, JAPAN					
TAD 42	6.10.71	male/ female	dormant	FAA	Prof. Yamazaki
NIKKO, JAPAN					
TAD 44	10.71	male/ female	dormant	FAA	Dr. R. Sattler
ROYAL BOTANIC GARDENS, KEW					
TAD 156	7.8.71	Female	dormant	FAA	Dr. R. Sattler
ROYAL BOTANIC GARDENS, EDINBURGH					
TAD 157	23.8.71	Female	dormant	FAA	Dr. R. Sattler

Table II.3

C. Additional Material Examined

1. For comparison, material of Turnera trioniflora, collected by Dr. R. Sattler in the Botanic Garden, Singapore, 13 November, 1971, was sectioned to demonstrate the vascular anatomy of the fertile leaf and its node. Additional material of T. ulmifolia var. intermedia was grown in the greenhouse, from seed sent from Caracas, Venezuala, by Dr. Leon Croizat.

2. Fruits of Cneorum pulverulentum Vent. were obtained through the courtesy of Dr. Gunther Kunkel, Tafira Alta, Canary Islands. Hand sections were made and examined to determine the vascular relationships between the bract, hypoclade and peduncle.

3. In addition, Dr. J.J. Bos, of the Laboratory of Plant Taxonomy and Plant Geography, Wageningen, Netherlands, kindly sent me alcoholic specimens of Dichapetalum mombuttense Engl. and D. rudatisii Engl., from Cameroun, D. toxicarium (G.Don.) Baill., from Côte d'Ivoire, and Tapura guianensis Aubl., from French Guiana. This material is the basis of the descriptions of these species in Section III, A.3.2.

D. Methods

1.1. Fixation. The materials used in this study were fixed mainly with standard botanical fixatives, FAA, and 70% ethanol (EtOH). In addition, however, acrolein (CH_2CHCHO; from BDH), 10% in water, at 0°C, was used, when it was possible to make the collections myself. The excellence of acrolein as a histological, as well as ultrastructural, fixative is described by Feder and O'Brien (1968); this is primarily due to its high degree of chemical reactivity with a wide range of biological molecules, resulting in formation of stabilizing cross-links throughout the cytoplasm, rather than precipitation. In addition, acrolein penetrates relatively large blocks of tissue very rapidly, making it especially valuable in studies at the level of groups of organs, such as apical meristems, often too large for effective application of fixatives such as glutaraldehyde and osmium tetroxide. For the same reason, it is also possible to use acrolein - with caution, as it is a tear gas - as a routine fixative in the field. Additional information on its chemical and physical properties, and on its safe handling, can be found in Shell Chemical Company publications SC:59-66 ("Acrolein, its chemistry and its applications") and IC:69-7 (Industrial Hygiene Bulletin - Acrolein).

2.1. Staging of the Material: Because living material of neither P. integerrima nor H. japonica was available in Montreal during the course of this study, it was not possible to stage the leaf primordia of an apex sequentially with an quantitative plastochron time scale, as has been done in some recent studies (Lyndon, 1968; Maksymowych 1973). Instead, the description of leaf development has been based on observations of relative size, differentiation, and position in the phyllotactic sequence. Thus a series of primordia is recognized, beginning with L_1, the smallest leaf primordium visible on the shoot apex, and continuing with increasingly larger and more histologically differentiated primordia L_2, L_3, L_4 etc., in 2/5 phyllotaxy in both genera.

2.2. In the case of <u>Helwingia</u>, where collections span the growing season, it is possible also to describe the sequence (sensu Bierhorst, 1960 p.275) of organogenetic activities taking place at the shoot apex during one season of growth (Text figure 2). Again, however, this must necessarily be based on inference from observations of the patterns of growth visible in whole plants, and comparisons between apices of different plants, either between or within localities and seasons of collection.

3.1. <u>Dissections</u>. Shoot-tips, from unexpanded axillary buds, as well as the tips of branches, were dissected and examined, and photographed directly, after staining in 0.5% Acid Fuchsin in 95% EtOH, according to the technique of Sattler (1968), using a Leitz epi-illuminator with dipping cone objectives (see Ernst Leitz, GMBH publication 513-90/Engl., "Leitz Ultropak Instructions," 1968).

4.1. Paraffin embedding and sectioning. Material prepared for sectioning in paraffin was dehydrated in a tertiary butanol series and infiltrated and embedded in Tissuemat (Fisher), m.p. 61°C. Apices were sectioned at 7-8 nm, while mature leaves and nodes were sectioned at 10 nm.

4.2. In addition, in a few preparations of acrolein-fixed material, a modification of the dehydration schedule of Zirkle (1930) was used to bring specimens from 100% ethanol to paraffin via 10, 20, 35, 55, 75 and 100% n-butanol. The results obtained, however, did not appear significantly better than those of the routine tertiary butanol technique, since the cytoplasm shrank away from the cell walls, although its structural preservation appeared good.

5.1. Glycol Methacrylate embedding and sectioning. Glycol methacrylate(2-Hydroxyethyl Methacrylate; (GMA) monomer mixture was prepared according to the method of Feder (1967) and Feder and O'Brien (1968). GMA, 94% was obtained from Rohm and Haas Co. and treated with Amberlyst A-27 anion exchange resin (Rohm and Haas) and activated charcoal (Nuchar C-190N, Fisher), in order to remove, respectively, contaminant methacrylic acid, and polymerization inhibitors added by the manufacturer. The purified GMA was then stored at -10°C until needed

5.2. The monomer mixture was prepared for infiltrating tissue and embedding by addition of the polymerization catalyst, 2,2'-azobis (2-methylproprionitrile) (Eastman), and the plasticizer, polyethylene glycol 400 (Fisher). The proportions used in the work presented here were 0.5% (w/v) and 7.5% (v/v) respectively. In practice, the blocks this produced were on the hard side, but completely usable.

5.3. Embedding and sectioning were done according to the suggestions of Feder & O'Brien (1968), and Dr. M. McCully (personal communication). Acrolein-fixed material, following dehydration in an anhydrous series of 2-methoxyethanol, 24h (two changes); ethanol, 24h; n-propanol, 24h; and n-butanol, 24h, all at 0-4°C. Material was commonly stored at 0-4°C in 100% ethanol. Before transferring to GMA monomer mixture, the material in n-butanol was allowed to come to room temperature, taking care not to open the specimen vial until then, to avoid condensation of atmospheric water vapor on the jar and surface of the liquid.

5.4. The material was infiltrated over several days, in two changes of GMA monomer mixture, and finally embedded flat, between two aluminum foil weighing dishes (to exclude O_2, an inhibitor of polymerization) in a third change of the monomer, about 2 mm deep. Polymerization was effected at 37-38°C for 24h. Higher temperatures were found to produce cracks in the plastic in and around the specimen. For greater visibility in the hardened block, specimens were often stained with safranin, 5.5 For sectioning, the specimens were cut from the flat plate with a fine coping saw, and the small blocks glued with a two-part epoxy cement to discarded BEEM capsules of spurr or other embedding media. The blocks were trimmed with a fine file and sectioned at 2-4 nm on a Sorvall MT-1 Porter-Blum ultramicrotome, using a dry glass knife. Sections were mounted on glass slides by transferring them to a drop of distilled water there and then evaporating the water by placing the slide on a hot (60-80°C) warming table.

6.1 Staining. Paraffin sections were routinely stained by standard techniques with Johansen's safranin and fast green FCF (Gray, 1958) and Delafield's Hematoxylin, with (Jong, 1970) or without dilute safranin as a counterstain. In addition, Toluidine Blue O was employed according to Sakai (1973), using a standard aqueous staining solution, 0.05% in 0.1M phosphate buffer, pH 6.8 (O'Brien, Feder & McCully, 1964) to stain mounted sections in the ribbon, before deparaffinization. This method has the advantage that by avoiding ethanol, air-drying the slides instead, and then transferring them directly to xylene, the polychromatic staining of Toluidine Blue is retained. This is especially useful in sections of mature structures containing lignified elements (Plates VIII and XIV)

6.2 Following Feder & O'Brien (1968), and McCully (personal communication), GMA sections were stained routinely with the standard Toluidine Blue solution given above, with or without prestaining with Acid Fuchsin, 1% aqu. In addition, some material was stained with the Periodic Acid -Schiff (PAS) reaction (Feder & O'Brien, 1968), and then counterstained with

Toluidine Blue. For this, aldehyde blockage with Dimedone (24h) was found more useful than other agents.

7.1 Clearings. Rodin & Davis (1967) present a method for clearing FAA - preserved material using a Papain NaOH - chloral hydrate treatment. Lignified elements can be stained with a dilute aqueous Safranin solution and the material then mounted via xylene in Bioplastic (Wards; Dr. D. Bierhorst, personal communication), or observed directly in xylene. This technique was used successfully with material of both Phyllonoma and Helwingia, following slightly modified schedules suggested by Dr. F. Pauzé (personal communication).

8.1 Photography. Sections were photographed using a Zeiss photomicroscope, and Kodak Pan-X or Plus-X (new forumalation) film. Safranin and Fast Green stained sections were photographed using a green filter for contrast, while with Toluidine Blue stained material, a yellow filter was used. These same films were also used for close-up photography with a 35 mm reflex camera and bellows attachment. In either case, they were developed for maximum fineness of grain with diluted Kodak Microdol-X developer. Dissections were photographed with the Leitz system on Agfa high contrast Copex film, developed with Kodak D-19 developer. Prints were made on Agfa Brovira paper, and on Kodak polycontrast Rapid RC paper.

V. DEVELOPMENT OF THE EPIPHYLLOUS INFLORESCENCE OF *PHYLLONOMA INTEGERRIMA* (Turcz.) Loes.

(7.)

A. INTRODUCTION

1. The natural occurrence of leaves, shoots, and in particular, flowers or whole infloresences upon leaves (epiphylly) appears to be unusual, in terms of our commonest experience of the higher plants. Yet there are, in fact, many species of angiosperms which exhibit this condition. These include several entire genera, such as, for example, Phyllonoma Willdenow ex Schultes (1821) (Dulongia H.B.K., 1825: Fig.28), assigned to the Saxifragaceae (Bentham & Hooker, 1865, I:648), Escalloniaceae (Metcalfe & Chalk, 1950), or to its own family, the Dulongiaceae (Willis, 1966). This genus occurs as small trees and shrubs in the mountains of Central and South America. According to Engler (1930), the genus divides into six species, with one (P. laticuspis (Turcz.) Engler) in Mexico, and the remainder, including P. integerrima (Turcz.) Loes. occurring in Costa Rica and Panama, and south into Colombia, Bolivia, and Peru. Phyllonoma in Costa Rica occurs as isolated trees in the substory of premontane rain forest (Stork, 1956; Holdridge et al, 1971; Stone, personal communication).

2. Although a number of earlier workers have investigated Phyllonoma (C. de Candolle, 1890; Schumann, 1890; Velenovsky, 1907; Goebel, 1898, 1933; Stork, 1956), none of them have fully demonstrated the initiation of the inflorescence and development of the fertile leaf, i.e. the foliage leaf that

bears the infloresence. The present study was undertaken in order to clarify these events, and as part of an attempt to arrive at an understanding of epiphylly in general. So as to be able to make comparisons with interpretations of epiphylly based on the mature foliar anatomy, I have also studied the vascular anatomy of mature fertile and sterile leaves, and their connection with the vascular system of the branch.

(V.) B. OBSERVATIONS

Organography

1.1. The leaves of *P. intergerrima* are alternate, in 2/5 phyllotaxy (Fig.1). Stipules are present, bearing on their inner surface numerous glandular hairs, and enclosing the unexpanded, apparently sylleptic (sensu Tomlinson & Gill, 1973), axillary shoot (Fig.21) before falling off as the leaf matures. In the material examined (as in Fig.28), many of the younger leaves of the main leader axillated young unexpanded scale-less shoots, and many of the twigs were still associated with their axillating leaves. It also appeared, from the leaves of lateral twigs, that the first one or two leaves formed on such an axillary shoot may be sterile.

1.2. In the axillary buds which were sectioned, such sterile leaves were not detected. The shoot apices used in the study of fertile leaf ontogeny had already formed a number of fertile leaves, so that it can be reasonably assumed that the youngest leaf primordia that have not yet initiated epiphyllous infloresences in figures 7-10 represent leaves which would have formed infloresences. There is no indication, in our material, or in the literature, that alternating flushes of fertile and sterile leaves occur along the same shoot axis in Phyllonoma.

1.3. The infloresence is borne at the base of the elongate leaf tip, or acumen (Fig.17). It is organized into a longitudinal series of variously erect or prostrate, expanded or unexpanded axes and associated bracts. There are no appendages formed laterally. Although Stork (1956) reports the infloresence as cymose, the material examined exhibited a great deal of variation in the extent of development and branching within the mature infloresence and infrutescence.

1.4. The organs referred to as leaves here are recognized as such since they are dorsiventral, and there are no organs present which are in an axillant position with respect to them, and since they are associated with stipule-like structures, and themselves axillate lateral shoots.

Organogenesis

2.a.1. Leaf Development - The shoot apex is organized into a two-layered tunica, and a corpus, of which the outermost cell layer may resemble a third tunica layer (Fig. 5,6). Leaf primordia arise as centres of growth on the periphery of the apical dome (Fig.9). At first, enlargement occurs due to meristematic activity throughout the leaf primordium (L_2, Fig.1,4 & 5) with stipules arising as lateral growth centres (L_2, Fig.1; L_1, Fig.8-9). With further growth the primordium, originally elliptical, becomes semicircular in cross-section the adaxial surface flattened or slightly concave (L_3, Fig. 1; L_2, Fig. 8-9). This remains the overall configuration of the midrib, and of the petiole, which develops later. Meanwhile, the lamina develops from the flanks of the leaf primordium. As the dorsiventrality of the primordium becomes more pronounced, cellular differentiation occurs within the leaf primordium. The apical and abaxial cells become relatively more enlarged and vacuolated (Fig. 5,10). The apex of vacuolated cells at this stage (Fig. 5,10) represents the entire mature acumen, into which it develops precociously (Fig. 14-16).

2.a.2. Like the acumen, the stipules also develop precociously, becoming greatly enlarged early in the course of leaf development (Fig.1). Except for the development of multicellular hairs on their inner surface, the cells of the stipules become completely non-meristematic, and much more enlarged and vacuolated than those of the young petiole and lamina.

2.a.3. Elongation is accompanied by elaboration of the lamina (Fig.14-16) from meristematic activity developing on the flanks of the primordium (L_3, L_5, L_6; Fig. 1). The two halves of the lamina remain adpressed until late in development; proportionally, the greater part of the width of the lamina is produced before the leaf matures and opens out.

2.b.1. Initiation of the Infloresence - The infloresence arises on the adaxial surface of the developing leaf, when the latter is about 300 nm long, measured from the axil (Fig. 5,11). The initium of the infloresence, that is, the primordium at the time of its inception, when it first becomes distinguishable from the surrounding cells (see also p. 76 ff.), is produced more than 50 nm above the axil of the leaf (Fig.5), between the young lamina-halves (Fig.14-16), by periclinal divisions in the third cell layer (Fig.6). The cells involved become highly meristematic, more so than the other cells of the adaxial side of the leaf, closer to the shoot apex (Fig.6,11,12), and form a vigorous reproductive apex, or infloresence primordium (Fig.12,14,16). Following initiation of the infloresence, the fertile leaf elongates greatly, principally through continuation of the intercalary, basal growth of the primordium below the acumen and insertion of the infloresence (Fig.7,14). In this way, the infloresence remains inserted at the base of the acumen, where it is enclosed by the adpressed halves of the lamina until the leaf matures and opens.

2.c.1. Initiation of the Axillary Bud - The axillary bud subtended by the fertile leaf is formed in a manner similar to that of the infloresence, and at approximately the same time, or slightly after. Prior to infloresence initiation (Fig.4,9,10), there is no indication of any axillary initium. At a stage of leaf development when the infloresence primordium is well established (Fig.7,12), however, the presence of a group of cells more meristematic than their surroundings is observed in the axil, on the base of the leaf primordium (Fig.13). These cells subsequently form a shoot apex, which grows out as a lateral branch, or not, apparently in some relation to the position, or vigor, of the axis on which it is formed.

2.d.1. Procambial Development of the Midrib of the Fertile Leaf -

Early in leaf development, before initiation of the inflorescence (Fig.10), a single median procambial strand is laid down acropetally (Fig.4) as a block of tissue within the leaf primordium, relatively close to its adaxial surface (L_2, L_3; Fig.1). This block of procambial tissue, however, is laid down progressively, in an abaxial-adaxial direction, the earliest-formed, abaxial portion of the strand leading into the acumen, and forming protoxylem first(L_4, Fig.3, Fig.10-12). Differentiation of the adaxial portion of this strand apparently accompanies inflorescence initiation (L_4, Fig.1,2; and L_5, Fig.1-3), and occurs into the new primordium and between it and the axil of the leaf (Fig.11). In this way, a complete unitary ring of vascular tissue is eventually formed (L_6, Fig.1), the central procambial cells differentiating as parenchyma, while the abaxial arc of elements is continuous with that in the acumen, and the adaxial arc supplies the inflorescence.

3.1. Vascular Anatomy of the Mature Fertile Leaf

The node is unilacunar, giving off one trace to the leaf, and two to the axillary bud, laterally (Fig.19-20). There are no vascular traces to the stipules (Fig.21). The vascular bundle to the leaf, between the base of the petiole (Fig.21) and the insertion of the inflorescence is similar in structure to the whole stele of the stem, which is an ectophloic siphonostele (Fig.18,21-24). However, the ring of vascular tissue may be more or less discontinuous laterally (Fig.23). In the lamina, the midrib of the leaf is enclosed by a fibre sheath (Fig.22-24). Clearings and sections show that the median, adaxial portion of the leaf bundle, which supplies the infloresence (Fig.24-27), is continuous proximally with the lateral portions of the leaf trace (Fig.20-21). The abaxial arc, which gives rise to the lateral veins of the lamina, is left to continue as a collateral bundle into the acumen (Fig.24-27).

3.2. Sterile leaves show the same midrib vascular anatomy in transverse sections as fertile leaves (Fig.22-24, Fig.27). This confirms de Candolle's (1890) observation that the vascular anatomy of the fertile leaf is independent of the presence of the infloresence.

C. DISCUSSION

1. One of the first surveys of epiphyllous inflorescences, C. de Candolle's 'Recherches sur les Inflorescences Epiphylles' (1890) included the results of developmental and anatomical studies of the fertile and sterile leaves of both Helwingia japonica Dietr. and Phyllonoma laticuspis Turcz. In both cases the anatomy of the midrib of both sterile and fertile leaves was found to be identical, subject to some interpretation in the case of Helwingia. Similarly, dissections of shoot tips of both surfaces showed the association of the youngest inflorescence promordia with already well-developed leaf primordia. Furthermore, the identification of the organs in question as leaves, was confirmed by the presence of stipules and axillary buds in their normal positions. Consequently,

de Candolle concluded that in both cases the inflorescence is form by the leaf, rather than the shoot apex, and that the fertile and sterile leaves are completely homologous with each other. In this way, he saw epiphylly as an example of heterophylly.

2. This view was challenged by Schumann (1890), who suggested that intercalary growth was responsible for most epiphyllous inflorescence, Schinz (1894) concurred, and argued that de Candolle's anatomical data could be used equally well to support Schumann's interpretation. Both authors, with de Candolle, rejected the hypothesis that congenital fusion was in any way implicated in the condition.

3. Gravis (1891) dismissed de Candolle's work, simply considering all such leaf productions as adventitious. However, Velenovsky (1907: 610, 1913: 117-118), also disagreeing strongly with de Candolle's interpretations of *Helwingia* and *Phyllonoma*, felt that if their epiphyllous inflorescences were interpreted (as de Candolle did) as leaf-products, they must be reduced to the status of adventitious buds. Instead, he argued that there probably existed in the inflorescence of *Phyllonoma* lateral appendages, similar to those he found in *Helwingia*. These proved to him the homology between the *Helwingia* inflorescence and an axillary bud. Thus the inflorescence of *Phyllonoma* would be a fertile axillary bud "carried up" (verschoben) onto the leaf, and both de Candolle's anatomical and ontogenetic evidence completely discounted, in the light of this morphological "fact".

4. Goebel (1898 fn. p.609) also dismissed de Candolle's use of anatomical evidence to settle morphological questions. However, his account of the inflorescence of *P. ruscifolia* Willd. (as *Dulongia acuminata* H.B.K.) and its development (1898, 1933) does not differ markedly from de Candolle's, insofar as he also reported the epiphyllous origin of the inflorescence, although he suggests that the remainder of the fertile leaf, below the acumen and inflorescence insertion (in this case, the entire leaf blade, although this would not be true for *P. laticuspis*, *P. tenuidens*, and *P. triflora*) results from an intercalation.

5. Stork (1956) investigated *P. integerrima* (as *P. ruscifolia*) from Costa Rica, and concluded also that the inflorescence arose epiphyllously. However, this conclusion was apparently based only on the observation of the inflorescence primordia of fairly well-developed leaves, 4 mm. long.

6. Our present results lead us to concur with the interpretations of C. de Candolle, Goebel and Stork, with respect to the epiphyllous initiation of the inflorescence in *Phyllonoma*, and the acceptance of this situation for what it is, the insertion of an inflorescence upon a leaf.

7. This interpretation, however, does not agree with the classical theory of the shoot, which requires that inflorescences (shoot-homologues) be inserted upon stems (caulomes) and never on their lateral appendages (phyllomes). To conform with the dicta of the classical theory, the observed, prohibited insertion

of an inflorescence or other shoot homologue on a leaf has been reinterpreted, in a number of ways:

(1) It could be due to a developmentally unobservable "congenital or "phylogenetic" fusion (concrescence, adnation, connation). The separate organs would be revealed within their union by their adjacent but separate vascular supplies (Duchartre, 1886; Velenovsky, 1913; 117-118). According to Payer (1857b) this situation arises in ontogeny by intercalary growth beneath the separate primordia of the fused organs initiated in the required sires, and is described by van Tieghem (1891: 74-75, 352) as "concrescence".

(2) The condition could be dismissed as accidental, or "adventitious" much as new shoots are produced from cuttings of leaves (Gravis, 1891).

(3) Finally, it could be denied that the leaf in question is in fact a leaf, as in <u>Ruscus</u> (several authors, cited by Duval-Jouve, 1877), redefining it as a leaf-like shoot, or phylloclade (cf. Stork, 1956). It might be noted that the first specific epithet applied to <u>Phyllonoma</u> was ruscifolia, by Willdenow, however it may be that he interpreted the case.

8. Concerning the first interpretation, Stebbins (1950), Cusick (1966), van Heel (1969), and Croizat (1973), interpret congenital fusion as the result, in ontogeny, of incomplete individualization of separate primordia, so that they are

carried up by a common intercalation, in the same way as Payer (1857b), for Helwingia, and Schumann (1890), van Tieghem (1891), and Schinz (1894) for Phyllonoma, described the axillary origin of the epiphyllous inflorescences. We have shown, however, that this is not the case in Phyllonoma, where the inflorescence is initiated on a well-developed leaf primordium.

9. Anatomical evidence of fusion having taken place congenitally is based on the principle of vascular conservatism, whereby the vasculature 'may reveal the former boundaries, relative positions, numbers, and categories of organs, or their parts, which may now be obscured by reduction, connation and adnation' (Moseley, 1967, quoted in an analysis of vascular conservatism by Schmid, 1972). Thus, Planchon and Linden (1853), Duchartre (1886), Velenovsky (1907, 1913), and Prance (1972) can describe epiphyllous inflorescences of other taxa as phylogenetic, or congenital, fusion products because below the inflorescence insertion they find evidence of separate vascular traces to the inflorescence and leaf. Melville (1962) points out, however, that the more or less unitary siphonostelic vascular bundle present in both fertile and sterile leaves of Phyllonoma is not consistent with such an interpretation. Our observations of procambial development in fertile leaves of P. integerrima support this argument. In addition, the anatomy of sterile leaves suggests that the structure of the vasculature is not necessarily related to the presence of the inflorescence. A similar situation occurs in sterile leaves of members of the Dichapetalaceae with epiphyllous inflorescences (Barth, 1896; Melville, 1962; Prance, 1972).

10. In the second interpretation, the use of the term "adventitious" to describe the appearance of the inflorescence primordium on the developing leaf of Phyllonoma is of questionable value. As originally defined by Du Petit-Thouars (1809), the term describes all buds which are not either terminal or axillary (Priestley & Swingle, 1929). Such a broad definition, although a convenient catch-all for situations (e.g. epiphylly) otherwise difficult to classify, is unfortunate since the term has the pejorative connotation of "accidental", and of meaning simply, "out-of-place" and so it directs away serious consideration from such situations (Arber, 1934; Croizat, 1960; Jong, 1970).

11. Alternatively, "adventitious" buds may be defined strictly, as Priestly and Swingle : 28-29 (1929) have done, emphasizing the abnormal conditions under which the bud appears, to denote apical meristems arising in "tissues which whether meristematic or permanent, were not previously organized as meristematic shoot apices". Broertjes et al (1968), instead based their definition on the origin of the adventitious bud, from "re-embryonalised cells at points where no primordia or resting meristems were pre-existing."

12. There may, in fact, be a continuum between the strictest form of adventitious axis formation, described by Broertjes et al, and the "normal" formation of lateral axes at apical meristems, by means of "detached" meristems, in view of the evidence of Koch (1893, cited in Priestly & Swingle, 1929), Champagnat (1961), and Esau (1965) that,

especially in woody plants, lateral axes (organs) may normally arise from tissues no longer meristematic (e.g. undergoing internodal development). The growth centres associated with the development of the fertile leaf of P. integerrima (inflorescence and axillary bud initia) seem to occupy middle ground in such a continuum, originating neither from fully differentiated, nor from fully meristematic groups of cells, on the leaf primordium and shoot apex.

13. Thus it might be convenient that "adventitious" be used only in the narrow sense of Broertjes et al (1968), in order to limit its pejorative connotations, and to refer to it only in the extreme case, of organs arising by "re-embryonalisation" of differentiated cells (see e.g. Kato & Kawahara, 1972; Hall & Tomlinson, 1973) rather than those derived from a localized increase in mitotic frequency among only partially differentiated cells (Esau, 1965; Stebbins, 1965), as occurs on the inflorescence of Phyllonoma, or the epiphyllous floret in barley (see below). It might be preferable, instead to use a still more limited definition of "adventitious" as has been proposed by Jong (1970), restricting the term to ".......structures not conforming to the regular pattern or relative position usual for the plant or species". Finally, it might even be best to do away with the term altogether since it has been used so loosely, and since, in all its uses, it obscures the real organogenetic potential of a tissue.

14. Concerning the third interpretation of epiphylly, there can be no question that the fertile leaf here is, in fact, a leaf, or at least much more homologous to a leaf than any other category, in terms of a semi-quantitative homology concept (Sattler, 1966). It looks like a leaf, that is, it grows, and apparently functions like a leaf; it has stipules, and axillates a lateral shoot bud; finally, it is not itself axillated in any way by any other structures. The stem-like siphonostelic structure of the petiole and midrib of both fertile and sterile leaves represents a variation in leaf anatomy widespread among dicots (Skutch, 1946; Metcalfe & Chalk, 1950: 1337-1338; Esau, 1965).

15. These observations, like those of Fisher (1973) on the epiphyllous initiation of lateral branches in the palm (Chrysalidocarpus, cannot adequately be incorporated into the rigidly formulated classical theory of the shoot without distortion of the observations themselves, or of our understanding of them. However, a revision of the shoot concept, such as Sattler (1971, and in press) has presented can accommodate these observations by simply accepting changes in the positional relationships between organs as such.

16. It is interesting to compare the observations here with those of Stebbins and Yagil in a series of papers on a hooded genotype of barley. This genotype, which appears as natural populations in Central Asia (Takahaski et al, 1953; Croizat 1960: 1524-1534), results in the formation of a hood, or inverted rudimentary floret, on the adaxial surface of the

developing lemma. It has been shown that a single gene locus is responsible for the new pattern which is associated with a localized increase in peroxidase activity (Yagil & Stebbins, 1968), and in mitotic activity (Stebbins, 1965; Stebbins & Yagil, 1966) on the adaxial side of the lemma primordium. A meristematic cushion results from the ensuing changeover from divisions in one plane, perpendicular to the long axis of the primordium, to divisions in many planes, and this cushion then follows the normal developmental sequence of a reproductive apex, in inverted polarity with respect to that of the lemma on which it is borne. Excepting the polarity reversal in the epiphyllous floret, our observations of the development of the fertile leaf of _Phyllonoma_ resemble in outline those of Stebbins and Yagil. A change in the relationship between cell division and elongation appears to occur in the leaf or lemma primordium at a site specified either directly or indirectly by the genome, such that the frequency of divisions, and their orientation changes to form a new reproductive apex.

17. The findings of Stebbins & Yagil, as well as the work of Bugnon and his associates (for references, see Bugnon 1959), Jong (1970) and of Fisher (1973), and the evidence presented here, suggest that evolutionary changes in the positional relationships between organs of higher plants ("phylogenetic shifting", Zimmerman, 1961; c.f. Leavitt, 1909) can be more satisfactorily related to "Laws of Growth" (Darwin, 1872; Croizat, 1962: 426, fn. p.531, 1973 (fn.90, p.144) involving genetically controlled, but developmentally and environmentally

adjustable changes in cell division and elongation. These result in phenomena such as changes in the site of primordium initiation, otherwise interpreted as products of metaphysical processes such as congenital fusion, as required by classical morphology.

18. The value of atypical situations like epiphylly is that they point out aspects of the real morphogenetic potential of plants in nature corresponding to these "Laws of Growth" that we often overlook. As an example, Chisoheton pohlianus Harms may exemplify a shift of inflorescence initiation, where inflorescences may be formed either in the axil of a pinnately compound leaf-like appendage, or in the axils of the leaflet-like appendages; these latter appendages are formed successively from a bud at the tip of the rhachis-like axis (Harms, 1917; Corner, 1964).

19. Faegri and van der Pijl (1971) and van der Pijl (1969) review pollination and dispersal ecology and the role of morphological adaptations. Modifications such as cauliflory can play a role in displaying flowers upon otherwise naked branches to pollinators (Faegri & van der Pijl, 1971: 156, re Durio; cf., in temperate regions, Cercis and Forsythia), and in supporting massive fruits (Artocarpus, Couroupita, Durio; see Corner, 1964). However, there does not yet seem to be very much corresponding information on the related question of the selective advantage epiphyllous infloresences may confer upon the plants that bear them. It may be likely that given the morphogenetic opportunity to display flowers and fruits upon leaves, rather than on stems, a plant may do

so, as long as this does not adversely affect it's reproductive functioning (Croizat, 1962, 1973). Such an event could occur directly as the product of a mutation leading only to epiphylly, or it could be the "adaptively neutral by-product" of the effect of natural selection on an unknown aspect of the plant's reproductive biology (Stebbins, 1968). Finally, epiphylly could have been selected for, as an alternate strategy for the optimal presentation of flowers to pollinators (Ganong, 1901; Stebbins, 1972) transferring and display function to an organ already "present" (Corner, 1958).

20. Such scenarios would make it unnecessary, as seems to be unlikely anyway (Jong, 1970), that the tropical rain forest, in which a great many species with epiphyllous inflorescences occur, offers "the lowest competition intensity" which van Steenis (1969) believes is necessary for the survival of nearly teratological "hopeful monsters", as he describes some epiphyllous species.

PLATE III

Figures 1–3: Transverse serial sections of a shoot tip. Inflorescence initiation. Stained with Delafield's Hematoxylin and dilute Safranin.

Figure 1: 90 nm above the apex.

Figure 2: 240 nm above the level of Figure 1, at the level of the inflorescence primordium of L_4 (approximately the same stage as L_5, Fig.7).

Figure 3: 290 nm above the level of Figure 2, at the level of the infloresence primordium of L_5 (approximately the same stage as Fig. 14-16). L_4 is sectioned through the acumen; note the arc of procambium present at this level, which is continuous with abaxial arc in Figures 1 and 2.

L_2, second youngest leaf primordium; L_3, L_4....., succeeding leaf primordia; S, stipule; H, stipular hair; Infl, inflorescence primordium.

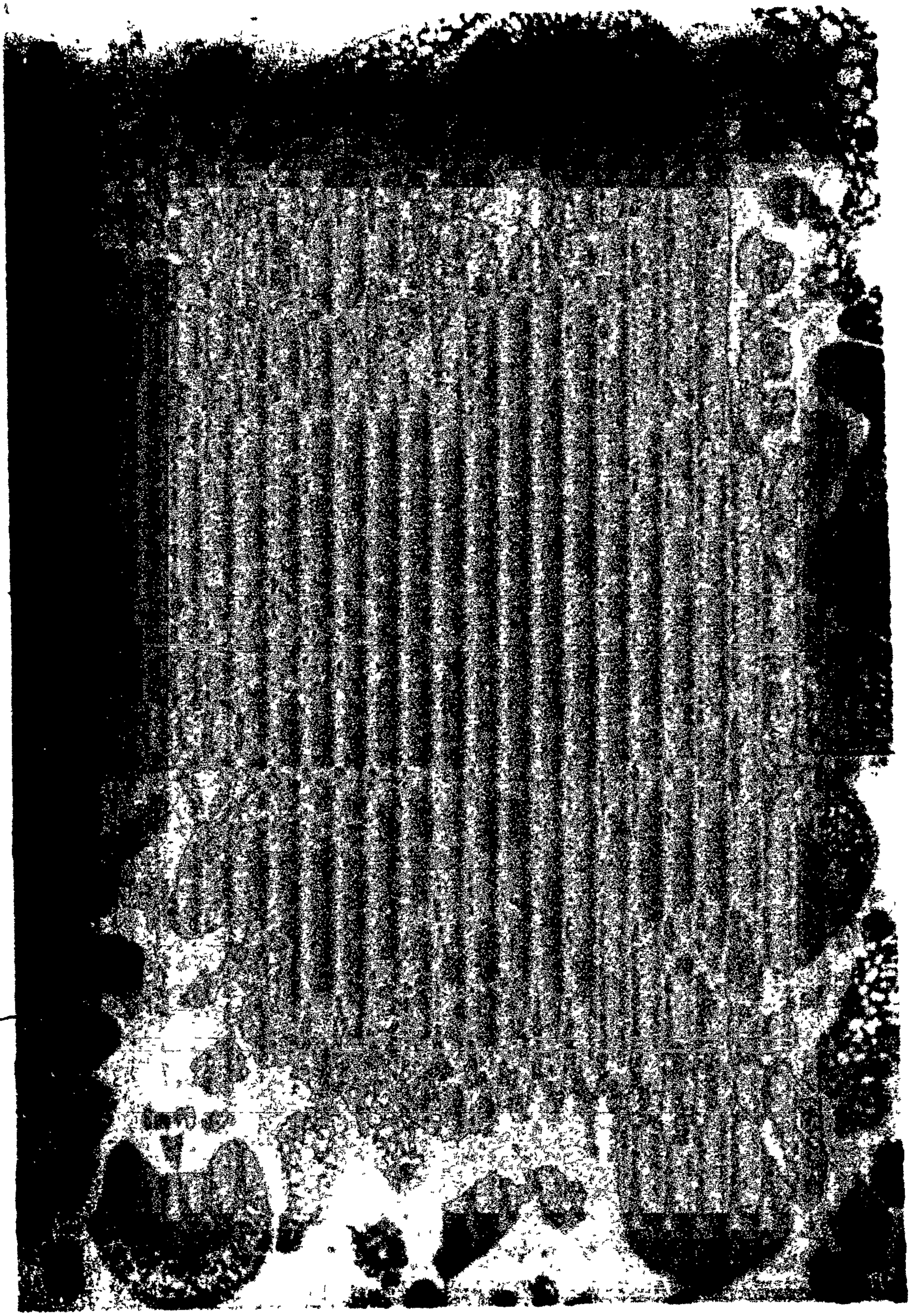


PLATE IV

Figs. 4-7, 10-13 Longitudinal sections through different shoot tips. Initiation of the infloresence and axillary bud. Stained with Safranin and Fast Green FCF.

Figs. 8-9 A shoot tip, dissected out and stained with Acid Fuchsin.

Fig.4. L_2 in near median section. The apical and abaxial cells of the primordium already appear larger and more vacuolated than those of the shoot apex and adaxial side of the leaf primordium. Acropetal procambial differentiation is visible.

Fig.5. The same apex as that of Fig. 4, 15 nm beyond L_3 in near median section, showing inflorescence initiation 50-75 nm above the apex. Note the region of small cells abaxially, at the base of the primordium (Arrowhead), and the size and degree of vacuolation of the cells of the acumen and abaxial side of the primordium.

Fig.6. The infloresence initium of L_3 in Fig.5, at the same magnification as Fig.4.

Fig.7. L_5 in near median section; a later stage of inflorescence development. The flank of L_1, of a stipule of L_2, and, at S,

of a portion of a stipule of L_5 are present also. Note a similar region of small cells (Arrowhead), here further removed from the apex.

Fig.8. View of the adaxial surface of L_2. Approximately the same stage as L_2, Fig.4. L_1 has formed stipules already.

Fig.9. View of the axil of L_2, and of the surface of the shoot apex, where L_0 will appear (SA).


7.


4


8

PLATE V

Fig. 10. Near median section of L_3, prior to inflorescence initiation. However, the dark staining cells (Arrow) may indicate the incipient inflorescence initium. Note the procambial strand continuing into the acumen.

Fig. 11. L_4, the same apex as that of Fig. 7, in oblique vertical section. The inflorescence primordium is at a slightly later stage of development than the one in Fig. 5. Note the adaxial procambial differentiation, below the inflorescence and continuous with the abaxial procambium.

Fig. 12. The inflorescence primordium of Fig. 7, at higher magnification. Note the protoxylem elements abaxial to the inflorescence primordium.

Fig. 13. The same leaf, L_5, as that of Figs. 7 and 12, 21 nm before that section. The axillary bud has been initiated at the base of the leaf primordium.

Ac, acumen; AB, axillary bud; SA, shoot apex; rS, rL, removed stipule and leaf.

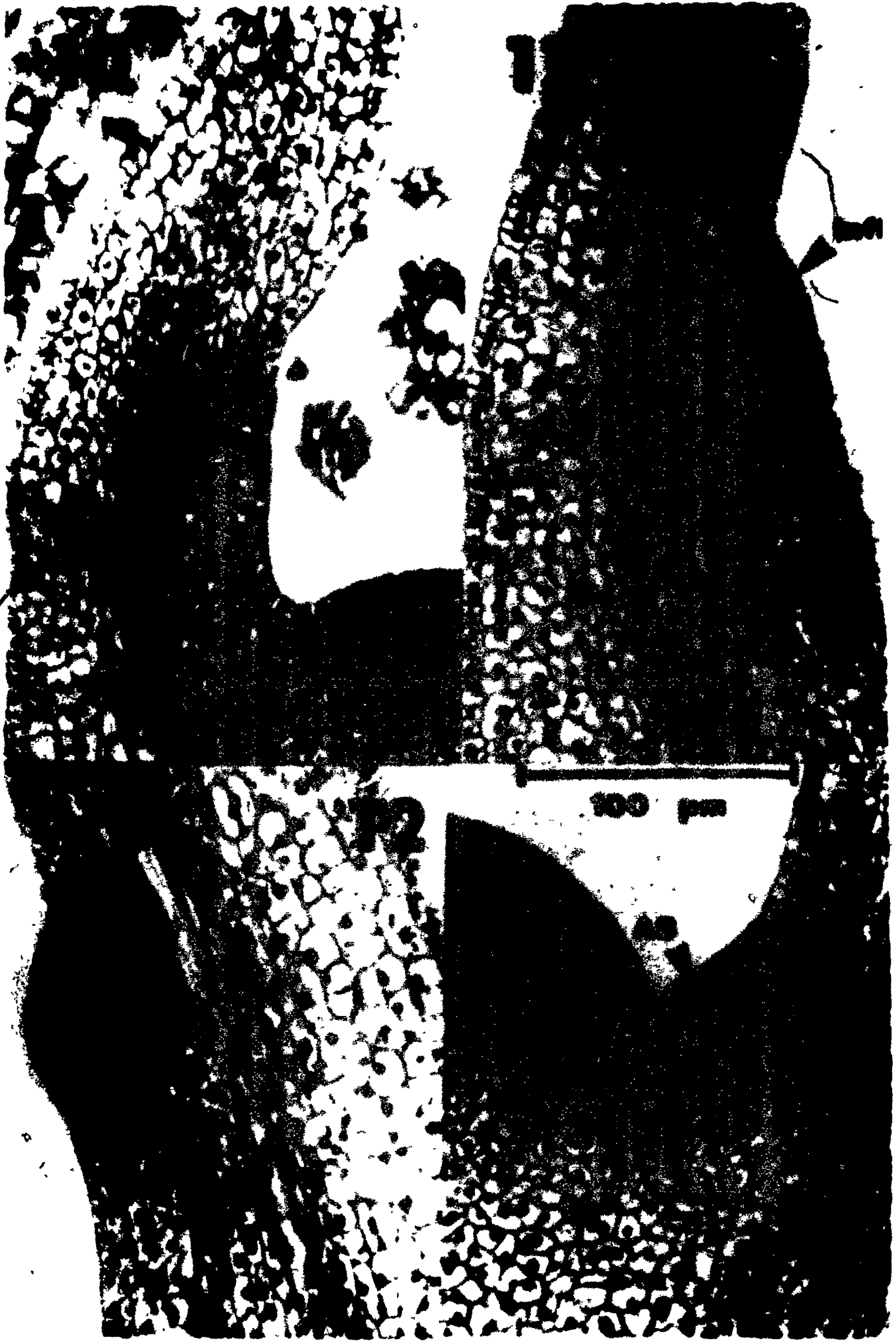

1
2
100 µm

PLATE VI

Figs. 14-17: Leaf development.

Fig.14 Frontal section of L_4, from same apex as Figs. 4-6. Stained with Safranin and Fast Green FCF.

Fig.15 L_4, as removed from apex (similar to that in Figs. 8-9), coated with muciligenous substance in the vicinity of the inflorescence primordium. Stained with Acid Fuchsin.

Fig.16 The same leaf primordium, partially dissected, and the mucilage removed, to show inflorescence primordium, at a stage comparable to, or slightly older than that in Figs. 7 and 14.

Fig.17 An unstained, mature leaf, bearing an infrutescence (Infr) at the base of the acumen. A, B, and C are the levels at which the sections in Figs. 22-24 were taken.

Infr, infrutescence

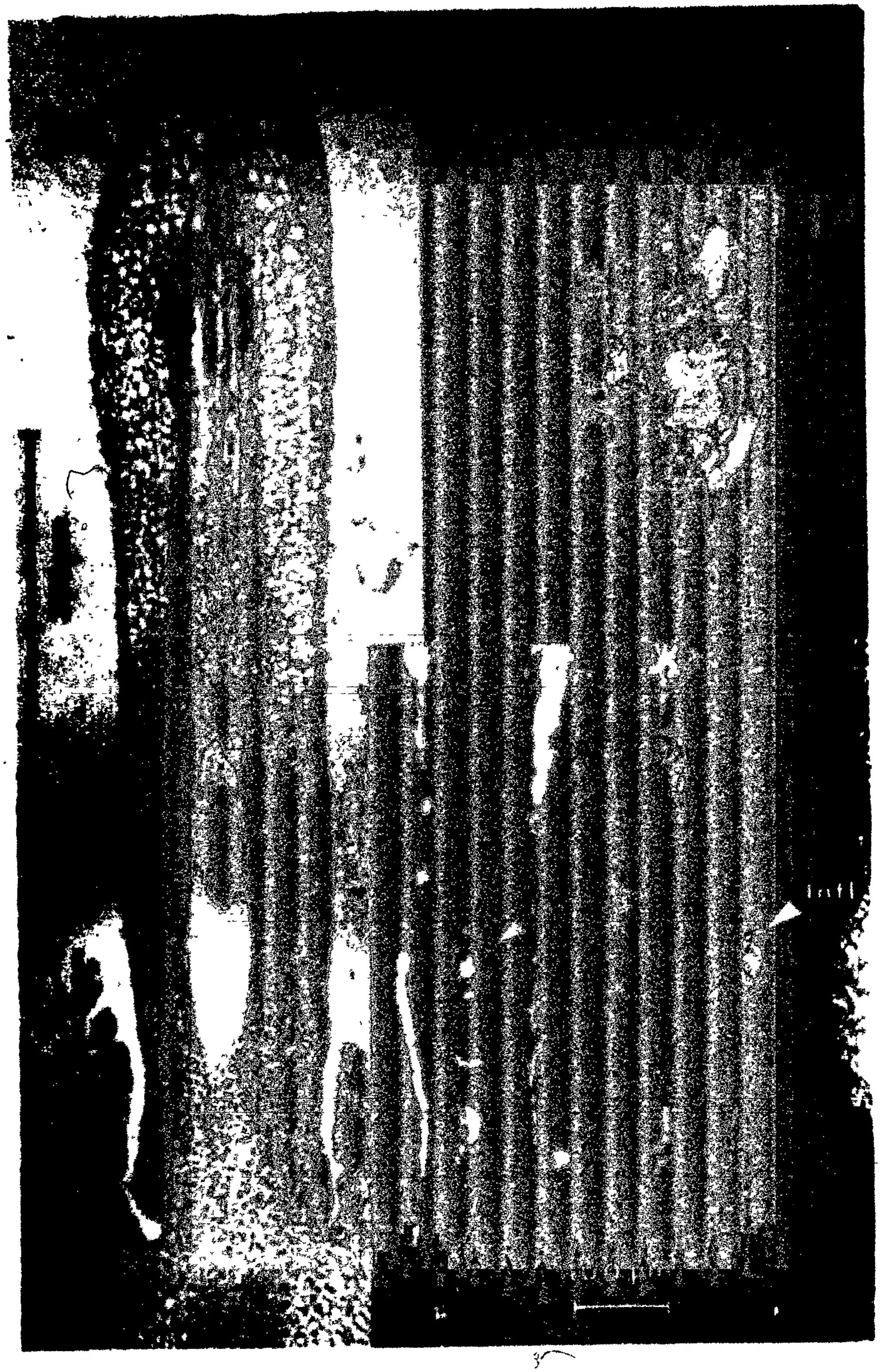


PLATE VII

Figs. 18-21: Nodal anatomy. Stained with Safranin and Fast Green FCF.

Fig.18	Base of the leaf
Fig.19	90 nm above the level of Fig.18.
Fig.20	280 nm above the level of Fig.19.
Fig.21	290 nm above the level of Fig.20.

C, cortex; Ph, phloem; X, xylem; P, parenchyma; AB, vascular supply to the axillary bud.

PLATE VIII

Figs. 22-27: Transverse sections through an infrutescence-bearing leaf. Vascular anatomy of the mature fertile leaf. In each case, the orientation is the same as in Figs. 18-21, with the adaxial direction toward the top of the page. Figs. 22-24 are stained with Toluidine Blue O by Sakai's method (1973); Figs. 25-26 with Delafield's Hematoxylin, and Fig.27 with Safranin and Fast Green FCF.

Fig.22 Section of the petiole (level A in Fig.17).

Fig.23 Section of the midrib, at level B. Note the presence of a sheath of fibres surrounding the bundle.

Fig.24 Section of the midrib, at level C, immediately below the insertion of the inflorescence, at the base of the acumen. Note departure of lateral vein (LV) from the abaxial bundle.

F, fibres; LV, lateral vein.

PLATE IX

Fig.25	Base of the infrutescence insertion
Fig.26	320 nm above the level of Fig.25
Fig.27	690 nm above the level of Fig.26

L, abaxial collateral vascular bundle continuing into the acumen of the leaf; IB, adaxial vascular bundle supplying the inflorescence region, providing two traces, of which the one closest to the leaf axil (IB_1) supplies the infrutescence visible in Fig.17, while the upper one (IB_2) supplies an unexpanded axis bearing unopened flowers.

25

27

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PLATE X

Fig.28 Dulongia acuminata H.B.K.
(= Phyllonoma ruscifolia Willd.)

Plate 623 in Humboldt, Bonpland and Kunth's Nova Genera et Species Plantarum Vol.7, 1825, by P.J.F. Turpin.

The original illustration measures 23 x 30 cm.

Copied from the volume held by the Gray Herbarium, Harvard University.

DULONGIA [illegible].

[illegible]

[illegible]

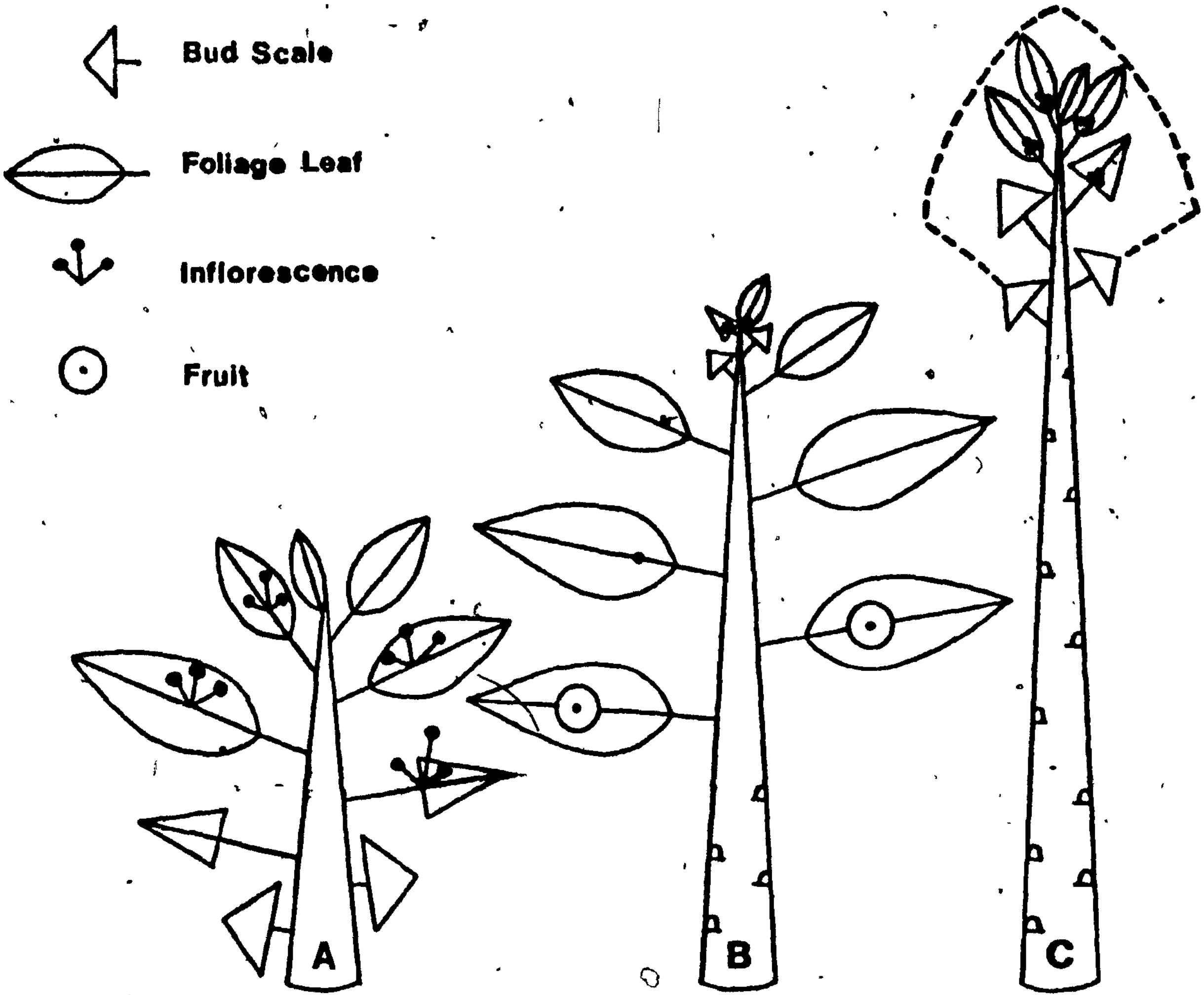
VI. Development of the Epiphyllous Inflorescence of <u>Helwingia japonica</u> (Thunb.) Dietr.

A. Introduction

1. The genus *Helwingia* Willd. (Willdenow, 1806) is a dioecious shrub, with two species (*H. himalaica* Hook. f. & Thoms. and *H. chinensis* Batalin) in China, and a high polyploid species, *H. japonica* (Thunb.) Dietr. in Japan (Hara, 1972). Originally placed in the Santalaceae (as *Osyris japonica*) by Thunberg (1784), the genus is presently assigned to the Cornaceae (Wangerin, 1910), or to its own family, the Helwingiaceae (Decaisne, 1836; Willis, 1966), and is distinguished by the epiphyllous position of the inflorescences of both sexes.

2. The development of the male inflorescence of *H. japonica* was studied by Payer (1857b; as *H. rusciflora* Willd.), Schumann (1890), and C. de Candolle (1890). Velenovsky (1907; Plate V, Fig. 9-11) describes and figures in detail the morphology of an epiphylliflorous male shoot of *H. japonica* (as *H. rusciflora*). Subsequent descriptions of epiphylliflory in *Helwingia* (e.g. van Tieghem, 1891; Schinz, 1894; Troll, 1937; McLean & Ivimey-Cook, 1951; Bugnon, 1958; Croizat, 1960; and Melville, 1962) are based on these studies, as no other work has been done on its development or morphology.

3. This study has been undertaken in order to obtain more information about the origin of the epiphyllous inflorescence, and about the development of the intercalation which develops beneath the primordia of the inflorescence and leaf, resulting in the epiphyllous position of the inflorescence. As



Text - figure 2: Seasonal Succession of Appendicular Organs.

A: Spring; vernation, and flowering. B: Early summer; initiation of fertile leaves, and fruit development, in female plants. C: Late summer-autumn; formation of the overwintering buds. Note: Foliage leaves, as indicated, may be either fertile, bearing inflorescences, or sterile, without them. The dotted lines in C indicate the enclosure of the structures within by the scales of the overwintering bud. Axillary buds are indicated in B and C, associated with the scars of leaves fallen off.

with Phyllonoma, the vascular anatomy of mature fertile and sterile leaves has also been examined, to provide a basis for comparison with other cases of epiphylliflory, especially Phyllonoma, and so as to be able to better assess interpretations of epiphylly based on its vascular anatomy.

B. Results

B.1 Organography.

1.1 Text - figure 2 and Fig. 19 illustrate diagramatically and directly the morphology of a fertile branch at the time of flowering. The stipulate leaves are arranged alternately in 2/5 phyllotaxy (Fig. 5) and form an acropetal, i.e. chronological, with respect to initiation, transition from bud scales through fertile leaves to sterile leaves. Inflorescences are borne on the adaxial surface of leaves transitional in form between bud scales and foliage leaves (Fig. 19), as well as on foliage leaves. In female plants, fruits ripen on the leaf (Fig. 20). Male flowers, and female ones which do not develop into fruit, fall off, following anthesis, leaving behind a small scar (dot, in Text - figure 2B).

1.2 As indicated in Text - figure 2, during the growing season the shoot apex produces a sequence of leaf types. Following vernation (Text - figure 2A; Fig. 1) it produces sterile leaves which expand later the same year. Subsequently (Text - figure 2B), there is a changeover to the formation of bud scales which will enclose the overwintering bud (Fig. 2), followed by the next year's foliage leaves (Fig. 3-15). At the same time, approximately, there is a transition to inflorescence initiation and development (Fig. 2-15). Thus the fertile leaves which expand in Spring are initiated and develop the previous summer, passing the winter enclosed by bud scales (Text - figure 2C).

1.3 In the axils of foliage leaves are formed the buds of sylleptic (sensu Tomlinson & Gill, 1973) lateral branches. These are initiated the same year as their subtending leaves (Fig. 3) but do not develop appreciably until the subtending leaves expand (Fig. 17-18). Thus the axillary buds of sterile leaves are formed in the same year they are initiated, and those of fertile leaves do so in the following year. Their morphology is constant. Two bud scales form laterally (Fig. 17-18), and enclose a third, abaxial scale (Fig. 26). Subsequently, leaf primordia are formed adaxial to this scale, slightly off-center, so as to begin the phyllotactic spiral.

1.4 The organs referred to here as "leaves" are so designated because of their dorsiventrality, because they are not axillated by any structures, and because they are associated with stipule-like structures and themselves axillate the buds of lateral shoots.

B.2 Organogenesis.

a. Early Development of the Fertile Leaf.

a.1 At the time of fertile leaf production, the shoot apex is nearly flat, and is organized into a tunica of a single cell-layer, and a corpus (Fig. 1-4, 6, 7, 14). The subjacent rib meristem, more active earlier (i.e. during the production and expansion of that year's sterile leaves and their internodes - Fig. 1), is less active, the nuclei there relatively more condensed (Fig. 2-4). Leaf primordia arise on the shoot apex in a 2/5 phyllotactic sequence (Fig. 5, 9). Initially, enlargement of the primordium is due to meristematic activity throughout the primordium. Within the first plastochron, however, the cells of the abaxial portion of the primordium become enlarged and more vacuolated than those of the adaxial portion (Fig. 4, 14), with the result that the primordium begins to arch slightly over the shoot apex. During its second plastochron, the primordium elongates, the apex remaining meristematic, and vacuolation occurring adaxially as well as abaxially (Fig. 6). During this time it has also become more markedly dorsiventral in cross-section (Fig. 9, 10).

b. Initiation of the Inflorescence and Subsequent Development of the Fertile Leaf.

b.1 During the second plastochron, vacuolation and nuclear condensation in the cells of the adaxial portion of the leaf primordium proceeds so as to differentiate a region of still meristematic cells, at least three cell layers deep, at the base of the primordium (Fig. 6). These cells constitute the initium of the inflorescence. This region also appears to be separated from the cells of the shoot apical meristem by a layer of narrow cells resembling a shell zone (Clowes, 1961), which remains distinguishable through the third plastochron (Fig. 7), while the inflorescence primordium is still adjacent to the shoot apex.

b.2 In the third plastochron, the cells throughout the leaf primordium have become vacuolated to a degree, except those of the enlarging inflorescence primordium (Fig. 7). This vacuolation is more pronounced abaxially (Fig. 5), but most of the nuclei appear to remain as uncondensed as those of the shoot apex and inflorescence primordium (Fig. 7). Also during the third plastochron the leaf primordium becomes semi-circular in cross-section (Fig. 5).

b.3 Following the third plastochron, development of the fertile leaf is characterized by basal growth of the leaf primordium, subjacent to the insertion of the inflorescence primordium on the leaf primordium. This results in the formation of an intercalated zone of tissue, homogenous with the remainder of the leaf, beneath the inflorescence primordium (Fig. 10-13). This growth appears to proceed primarily by cell divisions and enlargement in the base of the leaf primordium. By the fifth plastochron considerable vacuolation has occurred immediately above, in the base of the developing inflorescence, and the adjacent leaf (Fig. 3, 14).

b.4 Development of the individual flowers occurs on the apex of the inflorescence primordium to which meristematic activity is restricted (Fig. 3, 11-14). During the third plastochron, the lamina begins to develop, from the adaxial, lateral flanks of the leaf primordium, which remain relatively more meristematic (Fig. 5). The development of the stipules was not observed, but they appear to arise adjacent to the edges of the developing leaf base, after the fourth or fifth plastochron.

b.5 The onset of inflorescence initiation in the late spring and early summer appears not to coincide with beginning of production of the following year's foliage leaves. Thus, repeatedly in dissections basipetal transition series of foliar members were obtained, from young fertile foliage leaves through the older bud scales enclosing them. With increasing developmental age, the inflorescences were inserted higher and higher on the adaxial surface of the fertile leaves (Fig. 10-13). Finally, reduced inflorescence primordia were also found high up on the adaxial surface of the inmost scale-leaves. Inflorescence production thus appears tobe at least partially independent of the exact stage of the annual developmental cycle of the shoot apex. What are probably inflorescence initia have also been observed on the primordia of developing bud scales (Fig. 2). Similarly, in vernating shoots it can be regularly observed that morphologically intermediate foliar members occur among the inmost bud scales which bear normal flowers (Fig. 19).

c. Initiation of the Axillary Bud.

c.1 The axillary bud subtended by the fertile leaf does not appear to be initiated until the fourth or fifth plastochron, after development of the intercalated zone beneath the inflorescence primordium has begun (Fig. 3). If, as in the case of fertile leaves, the axillant leaf remains dormant first, before expanding, the axillary bud meristem remains at a stage comparable to that shown in Fig. 3 regardless of the plastochron age of the axillant leaf. The following spring, as the bud opens, development resumes (Fig. 17-18), and a new shoot apex is organized (Fig. 26).

d. Procambial Development.

d.1 Early in the first plastochron a procambial strand differentiates acropetally into the leaf primordium (Fig. 4, 14), and extends the length of the leaf primordium as it develops (Fig. 6, 7). The inflorescence initium (Fig. 6) and primordium (Fig. 7) when they develop are separated from this leaf procambial strand by one or two layers of vacuolated cells. Thus, the procambial strand to the inflorescence appears to arise from the base of the leaf strand, beginning after the third plastochron, when development of the intercalated zone occurs (Fig. 14-15), rather than as soon as the inflorescence is initiated.

B.3 Vascular Anatomy of Mature Fertile and Sterile Leaves.

3.1 The node is unilacunar, giving off one trace to the leaf, and two, laterally, to the axillary bud (Fig. 28-29). The leaf trace as it departs from the stele is an ectophloic collateral bundle (Fig. 28-29) whose lateral edges curve together to meet adaxially (Fig. 25-27), at the same time as they disengage from the abaxial portion (Fig. 25), within the base of the petiole. In this way the vascular configuration of the remainder of the petiole is established (Fig. 24), with an abaxial collateral bundle curving around and opposed to an adaxial bundle (also collateral and ectophloic). In some cases the parenchyma separating the edges of these two bundles may be insignificant, resulting in a siphonostelic configuration as in Phyllonoma and other examples (pp. III.A.4.3; cf. de Candolle, 1890, plate I: Fig. 5).

3.2 Within the midrib of the fertile leaf the adaxial component becomes more and more dissociated from the abaxial one (Fig. 22-24), and leads to the inflorescence (Fig. 3, 8, 14, 15). Meanwhile, the abaxial component continues as the small midrib vascular bundle to the leaf tip (Fig. 20-21).

3.3 Mature sterile leaves have the identical vascular anatomy, but absolutely no adaxial bundle is present. A single collateral bundle departs from the stele and continues to the leaf tip. These observations on the anatomy of mature fertile and sterile leaves corroborate those made by de Candolle (1890).

C. Discussion

C.1. Earlier interpretations.

1.1. Decaisne (1836), in establishing the family Helwingiaceae, points out that the position of the inflorescence is, 'le résultat de la soudure du pédoncule avec cette nervure (moyenne), comme il est facile de s'en assurer d'après le diametre qu'elle présente jusqu'à la place occupée par les fleurs'. Similarly, on the basis of the vascular anatomy of mature fertile leaves Planchon (1853) and Duchartre (1886) also described the epiphyllous inflorescence of Helwingia as the product of congenital fusion.

1.2. As indicated earlier (pp. 33-34), the results of his ontogenetic study of the inflorescence of Helwingia led Payer (1857b: Plate 109, Fig. 21-24) to describe its position as the result of congenital fusion in the same manner as described for Tilia (1857a) Essentially the same views were subsequently held by Kerner (1895) and Troll (1937), who, like Decaisne, Planchon, and Duchartre based their conclusions on the evidence of the vascular anatomy, as well as the developmental data. Van Tieghem's (1891) interpretation followed that of Payer, essentially.

1.3. Schumann (1890) however vigorously abstained from ascribing the ontogeny of epiphyllous inflorescences to congenital fusion. Referring to his own studies, he described how the position of the inflorescence in Helwingia and practically every other case arose by development of an intercalation which carried the inflorescence up from the axil. This was seen as an ontogenetic explanation of exceptions to the rule that all flowers arise in leaf axils, and nothing more.

1.4. Casimir de Candolle (1890) also described the displacement of the inflorescence from the axil by upgrowth with the leaf, in the manner described by Payer and Schumann. However, on the basis of morphology of the fertile leaf primordia on the apex, and of the procambial development and anatomy observed in limited sectioned material (Plate I: Fig. 16; cf. Fig. 71) he claimed that the inflorescence arose on the leaf base, and that leaf plus inflorescence constituted a single phyllome, as such directly homologous to a sterile leaf.

1.5. Even subsequent authors who also rejected congenital fusion failed to accept de Candolle's views on the origin of the inflorescence. Schinz (1894) simply agreed with Schumann, suggesting that de Candolle's anatomical findings were in fact compatible with this view. Goebel (1898, 1933) similarly described the inflorescence as arising in the axil. Its epiphyllous position was supposed to result from an elongation of the common region beneath it and the axillant leaf primordium ('gemeinsamen unteren Teil stark gestreckt, und nur als Blatt ausgebildet'), much as he also described the development of the blade of the fertile leaf of Phyllonoma.

1.6. Velenovsky (1907) totally rejected de Candolle's use of anatomical and developmental data to resolve morphological problems. For him, the homology of the inflorescence with an axillary bud was proved by the presence, on a fertile bud-scale, of two small scales on either side of the single flower. These supposedly corresponded to the two lateral bud-scales of a vegetative axillary bud (Fig. 17, 18, 26). Thus, he described the epiphyllous inflorescence as the result of an exclusively conceptual, morphological process of "Verschiebung" ("displacement") of a reproductive axillary bud, defined in such a way (1913) as to admit neither anatomical nor ontogenetic description.

1.7. More recently, McLean and Ivimey-Cook (1951) have described the position of the inflorescence of Helwingia as the result of one of a series of two axillary buds "coalescing" with the leaf and being carried up by its growth. Bugnon (1958: 54-55) has described the portion of the fertile leaf of Helwingia between the axil and the insertion of the inflorescence as a "hypophylloclade complexe", the result of intercalary growth beneath the primordia of inflorescence and axillant leaf. Croizat (1960, 1973) has described the same situation in the same way, but has instead emphasized the way in which the primordia involved apparently fail to completely individualize. Melville (1962, and personal communication) has included Helwingia with other examples of epiphylly which he believes manifest a primitive gonophyll-like structure.

C.2. Development of the Intercalated Zone.

2.1. The development of the region of the fertile leaf of Helwingia between the leaf-axil and the insertion of the inflorescence (cf. "intercalation": Schumann, 1890; Schinz, 1894; Goebel, 1898, 1933; "hypophylloclade": Bugnon, 1958; "intercalated zone"; this study) is of considerable interest because the growth which occurs there, and in analogous regions of other structures, has often been referred to ("intercalary growth": Bugnon, 1958; Leins, et al, 1972; "Zonal Growth": Coulter, et al, 1910; Stebbins, 1950; Sattler, 1974) but seldom described in detail. Jong (1970) has described the behavior of very distinct intercalary meristems in Streptocarpus, but the extreme localization and behavior of meristematic activity in this case appears to be exceptional.

2.2. In Helwingia japonica this intercalated zone consists of a basal, intercalary meristem, and an increasing number of its derivatives above. Its development proceeds from cell divisions in the intercalary meristem, a narrow band of cells smaller, and with less condensed nuclei, than those in the subjacent shoot. These divisions are accompanied by cell enlargement and vacuolation in the derivatives of the intercalary meristem above, which form the remainder of the intercalated zone (Fig. 3, 8, 14, 15). Given the initiation of the inflorescence from a "detached" meristem (detached, however, from the eumeristematic leaf primordium, rather than the shoot apex. cf. Chrysalidocarpus, p. 30) on the base of the leaf primordium, and the development of the intercalary meristem beneath both primordia, the early development of the fertile leaf can be seen to be independent of any process of meristem "fusion", in the sense of "interprimordial growth".

C.3. Interpretation of the Vascular Anatomy of Mature Fertile and Sterile Leaves.

3.1. The account of fertile leaf development above is useful for understanding the mature vascular anatomy, and the extent to which that can be a guide to the morphological of situations such as epiphylly, involving as they do shifts in the position of initiation of structures, and intercalary growth. Prior to the onset of intercalary growth, during the third plastochron, the procambial strand of the leaf primordium forms an arc, abaxial to the inflorescence primordium (Fig. 5, 7). As intercalary growth occurs, procambial differentiation to the inflorescence takes place acropetally, from the leaf strand, mainly below the intercalary meristem. This differentiation would appear to be continuous with the intercalary growth, so that procambial continuity is maintained.

3.2. The single collateral leaf trace which departs from the stele (Fig. 28) corresponds to the base of the leaf procambial strand, below the leaf primordium (Fig. 7). The formation of the opposed inflorescence trace within the petiole base (Fig. 25-27) corresponds to the differentiation of the inflorescence strand from the leaf strand. The opposed traces which then continue through the greater part of the petiole and midrib (Fig. 24) result from the continued procambial differentiation by the two opposed strands in the region of the intercalary meristem, as the intercalated zone elongates (compare L_3, L_5, L_7, and Figs. 9-13). The structure of the inflorescence trace, immediately below the inflorescence, and its departure there from the leaf trace appears to be the result of acropetal differentiation of the inflorescence strand away from the leaf strand and toward the inflorescence apex (Fig. 3, 14, 15).

3.3. The activity of the intercalary meristem appears to precede the appearance of mature vascular elements. These do not seem to develop until after the fifth or sixth plastochron, and then, in the midrib above the intercalary meristem first.*

3.4. Thus, the mature vascular anatomy of the fertile leaf of <u>H. japonica</u> can be seen to be related to specific ontogenetic processes affecting the organs involved. Comparison of fertile leaf anatomy with that of sterile leaves suggests that, in the case of <u>Helwingia</u>, the presence of the inflorescence primordium is a significant factor in inducing additional vascular development. However, as pointed out earlier with regard to the Dichapetalaceae (pp. 26-29), the same vascular anatomy which is associated with development of the epiphyllous inflorescence in Helwingia may also arise in related species without such inflorescences (e.g. Cynoxylon nuttallii (Audub.) Schafer, Cornaceae; Metcalfe and Chalk, 1950) or within the same species, even, as in the fertile and sterile leaves of Phyllonoma.

3.5. The present results do not by themselves, however, exclude the anatomically or developmentally based interpretations of epiphylliflory in Helwingia which invoke congenital or phylogenetic fusion. However, the resort to such processes as explanations of present phenomena, especially as the somehow "fundamental" explanation seems beside the point, unless actual evolutionary mechanisms could be proposed. A "purely" morphological interpretation such as Velenovsky's seems completely unreal. However, the demonstration here of the epiphyllous initiation of the inflorescence is in agreement with de Candolle's findings. His proposed homology of fertile and sterile leaves in toto is made acceptable, in view of the periodicity of fertile leaf production at the shoot apex.

3.6. In addition, the development of the fertile leaf found here also agrees in part with the suggestions of Schumann, Schinz, Goebel, and Bugnon. However, the description of the fertile leaf as, in part, an intercalation, or hypophylloclade complexe raises the question of whether these structures are to be thought of as completely homologous with leaves which do not necessarily involve intercalations, or bear inflorescences. In view of these questions, it seems as if de Candolle's suggestion is best as well as simplest: the structures in question are leaves, with or without flowers.

Plate XI

Figures 1-4: Near median longitudinal sections of shoot tips showing transition from formation of sterile leaf primordia to formation of fertile leaf primordia. GMA sections. Fig. 1, 2 stained with Acid Fuchsin and Toluidine Blue. Fig. 3, 4 stained with Toluidine Blue.

Fig. 1. (TAD 61) Sterile leaf formation in a young, expanding shoot. At the right, the leaf base of a young, only partially expanded leaf. Note the relative narrowness of the shoot apex, and in the rib meristem, the very thin transverse walls and uncondensed nuclei.

Fig. 2. (TAD 198) Bud-scale formation and transition to inflorescence initiation. Note the broader shoot apex, and the region of meristematic cells (arrowhead) on the adaxial surface of the base of the scale primordium.

Fig. 3. (TAD 198) Fertile leaf formation. L_5 shows development of the initium of a lateral branch in its axil (white arrowhead). Note the acropetal increase in cell size and vacuolation from the base of L_5.

Fig. 4. (TAD 198) The same apex as in Fig. 3, but to show L_1 in median section. Note the acropetal procambial differentiation.

Figure 5: (TAD 156) Transverse section through a shoot tip producing fertile leaves, approximately 65 nm above the surface of the apex. X indicates the position of L_1, covered by the base of the inflorescence of L_4. Procambial cells (small compact nuclei) visible abaxially in L_2 and, in an arc, in L_3, with vacuolated cells between them and the inflorescence primordium on the adaxial side of the leaf primordium. L_2 sectioned through its tip. L_4 and L_5 sectioned below the apex of their inflorescence primordia through relatively non-meristematic regions. L_{6-8} show distinct adaxial procambial strands to the inflorescence. Note the presence of stipules at the flanks of L_6. Stained with Safranin and Fast Green.

L_1: the youngest leaf primordium visible on the shoot apex; L_2, L_3, L_4 etc.: the succeeding leaf primordia, which have developed for two, three, and four plastochrons respectively.


100nm

Plate XII

Figures 6-13: Development of the fertile leaf. Fig. 6 stained with Safranin and Fast Green. Fig. 7-8, GMA sections, stained with Toluidine Blue. Fig. 9-13 stained with Acid Fuchsin. Fig. 9, 11-13 are all at the same scale.

Fig. 6. (TAD 189) Near median longitudinal section through L_2. The arrowhead indicates the inflorescence initium, a region of meristematic cells on the adaxial surface of the base of the leaf primordium.

Fig. 7. (TAD 198) Near median longitudinal section through L_3. Inflorescence primordium (Infl) developing at the base of the leaf primordium. Note the narrow shell zone-like cells between apical meristem and the inflorescence primordium, here and in the previous figure. Also note the absence at this stage of procambial development to the inflorescence primordium.

Fig. 8. (TAD 198) Near median longitudinal section through L_7, to show development of the intercalated zone beneath the insertion of the inflorescence primordium on the leaf primordium. L_2 sectioned tangentially. The same apex as in Fig. 3-4. Note the development of the procambial strand to the inflorescence, and the acropetal increase in cell size and vacuolation from the base of L_7.

Fig. 9. (TAD 156) View of a shoot apex producing fertile leaves. Note the absence of organogenetic activity in the axil of L_2.

Fig. 10. (TAD 157) Adaxial view of L_3, to show the inflorescence primordium (Infl) at its base.

Fig. 11. (TAD 156) Adaxial view of L_4 from the same apex as in Fig. 9, to show the inflorescence primordium at the summit of a short intercalated zone.

Fig. 12-13. (TAD 157) Adaxial views of L_5 and L_6, to show further growth of the intercalated zone. Note that in these leaves from a female plant the inflorescence consists only of a single flower.

Infl: Inflorescence; rL: indicates the site of a removed leaf primordium.

Plate XIII

Figures 14-15: GMA sections from the same apex as Fig. 3, 4, 8, showing the development of the intercalated zone. Fig. 14, section blocked with Dimedone and stained with PAS and Toluidine Blue. Fig. 15 stained with Toluidine Blue.

Fig. 14. (TAD 198) Near median section of the intercalated zone between the apex of the inflorescence primordium and the insertion of L_5. Note development of the procambial strand to the inflorescence primordium. Note also the distribution of the PAS-positive granules, their relative absence in meristematic cells, and presence in more vacuolated ones, e.g. the rib meristem. L_1 is at the right.

Fig. 15. (TAD 198) Detail of the intercalated zone of L_7 as shown in Fig. 8. Note the departure of the inflorescence procambial strand from the leaf strand at the base of the primordium. Note also the acropetal increase in cell size and vacuolation from the base of L_7.

Figures 16-18: Development of the axillary bud. Fig. 16, GMA section stained with Toluidine Blue and Acid Fuchsin.

Fig. 17-18. Stained with Acid Fuchsin.

Fig. 16. (TAD 61) Detail of the lateral branch initium in the axil of the young leaf base shown in Fig. 1. At the same scale as Fig. 14-15.

Fig. 17-18. (TAD 80) Views of the adaxial surface of the petioles of young leaves which expanded the year of collection, showing the primordia of the two bud scales, at two stages of development. At the same scale as Fig. 10.

Figures 19-20: Mature fertile leaves. Unstained.

Fig. 19. (TAD 61) Vernating male shoot. Note the clusters of unopened flowers on the adaxial surface of the foliage leaves, and of the expanded bud scale.

Fig. 20. (TAD 186) Female fertile leaf, bearing infrutescence. A third fruit is present but hidden by the larger of the two fruits. A-D are the levels at which the sections in Fig. 21-24 are taken.

1

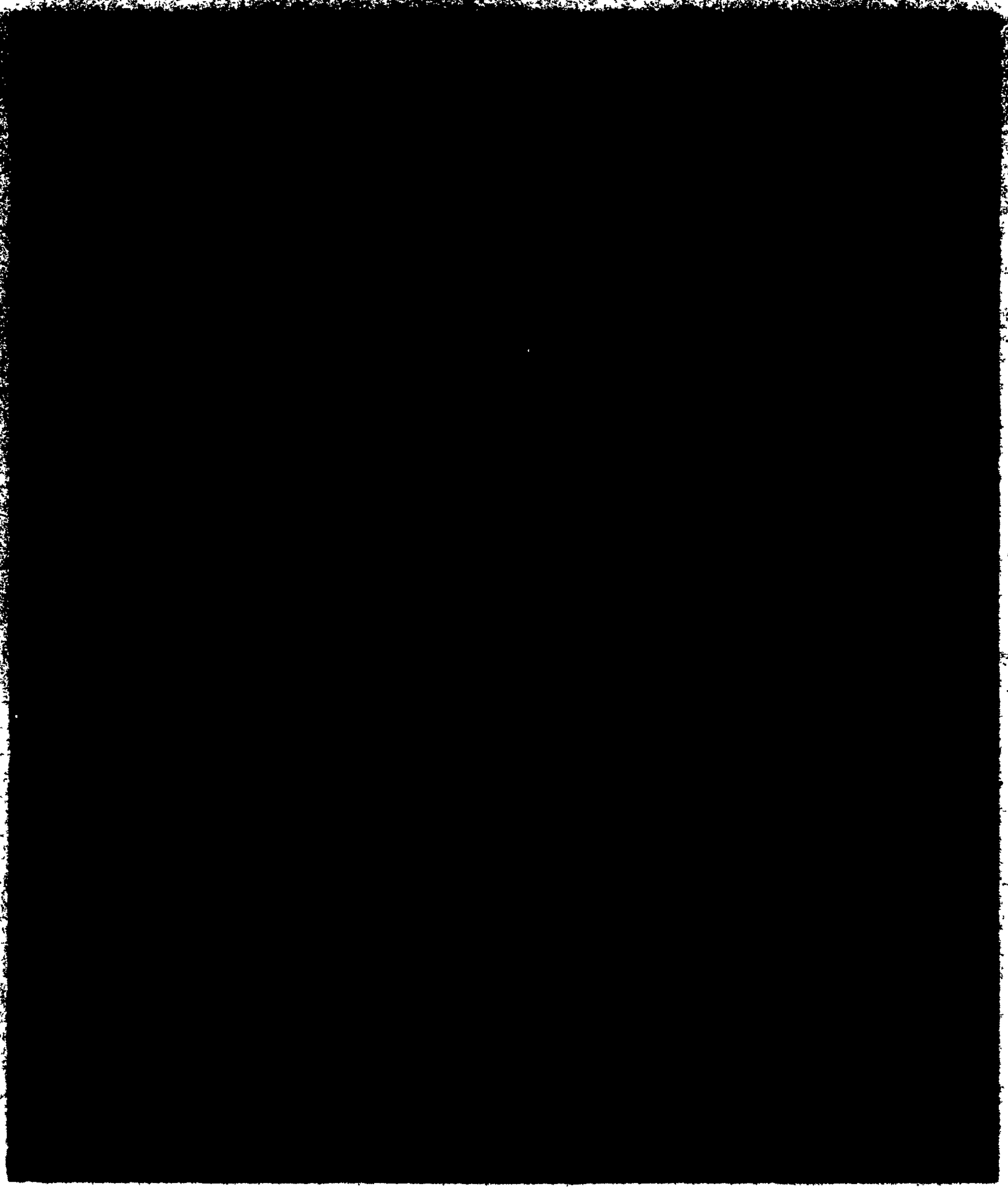


Plate XIV

Figures 21-24: (TAD 167) Vascular anatomy of the midrib of a fertile leaf. Transverse sections through the midrib of an infrutescence-bearing leaf.

Figures 25-29: (TAD 189) Nodal anatomy. Transverse sections through a stem, to show the vascular connection of a fertile leaf to the stele.

Fig. 21, 22, 24, 26-29 stained with Toluidine Blue by Sakai's (1973) method. Fig. 23, 25 stained with Safranin and Fast Green.

In all the figures, the orientation with respect to the leaf is the same, the adaxial surface toward the top of the page.

Fig. 21. Section of the midrib above the insertion of the infrutescence (level A in Fig. 20).

Fig. 22. Section of the midrib immediately below the infrutescence insertion (level B in Fig. 20). Note the almost closed-circular, adaxial inflorescence trace.

Fig. 23. Section of the midrib at level C.

Fig. 24. Section of the midrib at level D, at the summit of the petiole.

Fig. 25. Section of the stem and petiole of a fertile leaf.

Fig. 26. 270 nm below the level of Fig. 25. Note presence of the axillary bud.

Fig. 27. 220 nm below the level of Fig. 26.

Fig. 28. 250 nm below the level of Fig. 27.

Fig. 29. 300 nm below the level of Fig. 28.

VII. CONCLUSIONS

In conclusion, epiphylly in and of itself is not a rare or unusual phenomenon. Plants displaying it are themselves somewhat uncommon, as a rule, but the condition is only one of several which appear to be derived from the way plants grow. Comparative developmental investigations of other conditions, such as, e.g. cauliflory would show a similar array of growth patterns, as already work on Swartzia pinnata (McLean Thompson, 1951), Couroupita guianensis (McLean Thompson, 1953), Theobroma cacao (Lent, 1966) and the Solanaceae (Delosme, 1955; Shah and Patel, 1970) has shown.

Likewise, outside the angiosperms the condition also occurs repeatedly - Gingko (Bierhorst, 1971), Cephalotaxus (Nozeran and Grauvogel-Stamm, 1971) as well as in the ferns, where it has been studied extensively (Goebel, 1902, 1908; McVeigh, 1937; Bierhorst, 1969, 1971, 1973; Troop and Mickel, 1968), and is more likely also to be, in some respects, a primitive condition (Mickel, personal communication).

In this study, in reviewing different aspects of epiphylly in general and in particular, the following points have stood out:

1) as understood, epiphylly ranges from the minute association of buds and flowers with leaves and bracts, to the macroscopic, unquestionable occurrence of whole inflorescences or branches on foliage leaves. Given this vast range of scale, it is likely, as Burtt (personal communication) has suggested, that the list, as presented, of occurrences could be extended considerably. In large part the list given here is the cumulative product of several generations of more or less classically-oriented western

morphologists remarking on "unusual" situations.

2) However, it appears that the anatomical characteristics, and developmental processes associated with epiphylly are in fact not unusual, but rather, the same old morphogenetic processes that are perhaps too readily pigeon-holed as to their "typical" occurrence.

2.a. Processes such as intercalary or zonal growth, discussed concerning *H. japonica*, clearly affect the external morphology and internal differentiation of a wide range of situations. The occurrence of as defined intercalary meristems as Jong has demonstrated in *Streptocarpus*, and the associated radical reorganization of the plant's growth habit is probably exceptional. The discussion of the unifoliate Gesneriaceae here proceeds principally from tradition, as well as from interest in the remarkable information available for some of them now (Jong, 1970; cf. Hallé and Delmotte, 1973). In fact, Jong's development of the phyllomorph concept suggests very strongly that here "leaves" in the commonly accepted sense, as used in this study, are not involved, and that the plant has instead evolved new organs (i.e. old organs for which we must develop new concepts) which combine characteristics of "shoot" and "leaf".

2.b. The shifting of the site of inflorescence or lateral branch initiation onto the primordia of leaves perhaps is less common but doubtless occurs more widely than is known yet.

3) Besides as a subclass of vegetative reproduction, epiphylly does not appear to be able to be understood yet as occurring as a response to natural selection. Instead, it seems probable that the condition, where it occurs, reproduces adaptations or functions found elsewhere as the result of more common developmental patterns. St. Hilaire's (1840) classification of epiphylly as a type of pedunculation seems quite reasonable.

4) Finally, epiphylly is instructive of the tendency in classical comparative morphology decried by Schumann (1890): 'Ist irgend ein Prozess heute reell nicht vorstellbar, so wird er doch dadurch der Wirklichkeit nicht näher gebracht, dass er in phylogenetischem Sinne aufgefasst wird, d.h. dass sein Verlauf in irgend eine Vergangenheit zurückversetzt wird. Sind die Verschiebungen heute nicht möglich, so haben sie früher auch nicht stattfinden können'. In view of the continuing ontogenetic research carried on in plants, and the analyses of congenital fusion such as that of Jardine (1969), it is hard to understand why such a process continues to be invoked, other than to supply metaphysical seasoning. Reinterpretation of concepts of the shoot, like Sattler's, as well as work like that of Jong, is needed to lessen the need for such "congenital" processes (but cf. Kaplan, 1971), as well as terms like "adventitious", etc. (see pp. 67-68) and make it possible to appreciate leaves as well as other organs, as they are, "fertile" in the Goethean sense, or not.

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