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Abstract

Study of anatomy of various flowers and of the often contradictory and controversial literature on floral anatomy have led the writer to a critical review of evolutionary interpretation of floral structure. New theories are not believed to be necessary. Instead, many types of evidence often entertained are considered to be less reliable than often claimed, and misleading. For example, the ways in which patterns of floral vascularization have served as the basis for the most disparate interpretations by various anatomists are examined. Facts of floral ontogeny likewise can be misleading when cited as evidence. Overly literal interpretations are rejected, and the reasons why now-rejected hypotheses were offered are analyzed. Presentation of data on isolated aspects of floral structure (e.g. vascularization) is believed to lead to errors, because floral structures are functioning units, and the pollination systems, dispersal mechanisms, etc., basic to the entirety of a flower or fruit are stressed as more realistic goals or frames of reference for students of plant structure. In order to present a critique involving the totality of floral structure, all topics relative to study of floral anatomy (gross morphology, pollination, dispersal, venation, ontogeny, taxonomy, paleobotany, teratology, etc.) are presented and related to evolutionary theory in the form of a series of 21 commentaries.

Floral anatomists repeatedly issue appeals for use of their data in the study of angiosperm evolution. The continual nature of these appeals leads one to be suspicious: why is there need for such appeals? Does the blame lie with apathetic students of plant evolution or with floral anatomists who promulgate theories and interpretations that do not stand the tests of rigorous scientific examination? Disregarding for the moment more imaginative hypotheses, I find that the more plausible interpretations can contain questionable data and statements. Overly enthusiastic partisans of the better hypotheses propose some lines of evidence which may not, in fact, be valid. If this is true, why has this happened? What truly reliable lines of evidence in interpretation of floral anatomy exist, and which must be abandoned as based on faulty evidence?

1. Received for publication: June 9, 1969. Although the positions taken above are my own, I have naturally gained much by conversations with knowledgeable botanists over the past 15 years or so. Among the many individuals I wish to thank for contributing to my thinking are Professor I. W. Bailey, Professor Katherine Esau, Dr Richard H. Eyde, Dr Verne Grant, Dr G. L. Stebbins Jr. and Dr Robert F. Thome. I have been fortunate in having available to me floral materials of a wide variety of angiosperm families. I am grateful to the botanic gardens mentioned in the legends for figures for such materials. In addition, I have utilized materials collected during travel permitted by a grant from the National Science Foundation, GB-4977x.
The fact that floral anatomy continues to be a controversial field, and that particular interpretations—or a particular interpretation—have not been readily, widely, and uniformly accepted should make us suspect that something is wrong with the nature of the evidence presented. Why have evolutionists readily and uniformly accepted evidence from cytogenetics, while they disregard or avoid, with some exceptions, the literature on interpretive floral anatomy? To be sure, floral anatomy suffers from cumbersome methods of presentations: drawings of sections in long series, indistinct photographs, lengthy and vaguely worded texts mar some papers. However, such disadvantages as these can be overcome, and cannot be blamed for the fact that interpretive floral anatomy has found only a limited audience. I find that invalid lines of evidence have been applied to all of the theories of floral evolution now current, and there seems to be an implicit realization of this, both by floral anatomists (e.g. Puri, 1952a, 1961) and by other botanists.

Theories of origin and evolution of floral structure have proliferated, instead of becoming fewer and clearer. The more imaginative and obviously fantastic of these theories are self-defeating, but others have a degree of plausibility which has slowed their rejection. When Eames (1931) ridiculed Saunders' theory of carpel polymorphism, he was aided not so much by the nature of his own evidence as by the vulnerable extremes presented by Saunders.

Of the theories of floral structure now current, one can be expected to be more nearly correct than the others. However, “supporting” that theory with the wrong evidence not only destroys acceptability of a likely interpretation, it weakens the fabric of science itself. The temptation to find further evidence for a theory one has come to believe is very great. It seems obvious to me that when we restrict ourselves to valid evidence, we can rule out a number of unjustified theories; however, we will also have less solid evidence for the “correct” theory as well, and that will undoubtedly cause many to reject the thoughts I present below. However, retention of invalid lines of evidence will insure continued confusion in floral anatomy. Although some of today's morphologists may not welcome a critical re-evaluation of now-accepted principles, others may find a welcome challenge in trying to construct defensible interpretations, and in demonstrating the adaptive significance of floral structure.

Floral anatomy has featured not only proliferation of theories, it has shown a tendency for authors of these theories to reiterate them in paper after paper. This tactic has never proved a successful one in science, but the emotional attachment that authors develop for their theories seems to dictate this consequence. So plastic and varied in structure are angiosperms that proponents of any theory can find examples to fit it, and describe these in a series of papers. Thus, we find that carpel polymorphism, stachyospory—phyllospory, “durian theory”, gonophyll theory, etc., reiterared but not really enhanced as page numbers allotted to them mount. Interpretation also intrudes into what should be purely descriptive work. For example, Kasapligil's (1951) description of Umbellularia (see Fig. 17) is non-committal in interpretation of anthers. However, when Eames (1961) reproduces Kasapligil's drawings, his legend states, “stamen fascicles of Umbellularia showing lateral members transformed into carpals and ectomes...”, and thereby several unwarranted evolutionary assumptions are made.

We do not need any more “new” floral morphology. We need instead a reliable floral morphology. We can no longer afford to adhere to any theory simply because it is widely accepted, its author is famous, or because the printed page impresses us. Unjustified hypotheses in floral anatomy would perhaps most effectively be countered by sheer disuse, by refusal to cite them. When one cites them, even while ridiculing them, they are given a currency which suggests a degree of credence. However, passive erosion of an unsupported theory is probably not sufficient. Even though some may be offended by my critique
below, I find that so much work in interpretive floral anatomy fails tests of critical thinking that a more active demolition is required. My rationalization for this demolition is that I can demonstrate the basic reasons why and whereby particular interpretations have erred. However, space does not permit a critique of all recent papers which seem erroneous in various respects. Such a compilation ought to be unnecessary. In my view, skepticism has been insufficient where interpretation of floral anatomy is concerned. Puri (1951) still finds that vascular bundles are “fairly reliable if used judiciously”, and Moseley (1967) also urges “judicious consideration” of floral vasculature. I feel that a view even more critical than those is required at present, if only because neither Puri nor Moseley nor others spell out clearly what evidence must be rejected, and “used judiciously” is the sort of phrase under which any worker, regardless of his interpretation, could justify his theories. While disallowing certain lines of evidence, I have attempted to account for the evolutionary phenomena that seem to be involved. For convenience, this critique is organized as a series of headings or principles.

Commentary

1. Anatomy of flowers can be studied meaningfully only in relation to adaptations for particular modes of pollination, dispersal, and allied functions. Structures in flowers are, with very few exceptions, not functionless relics but positive adaptations. Angiosperms are an exceptionally plastic and rapidly-evolving group of plants, and may be expected to lose non-functional structures rapidly. Venation relates, with virtually no exceptions, to contemporary functions.

Floral morphology has, historically, become divorced from gross morphology, systematics, and other fields of inquiry dealing with flowers. This explains why vein systems (and other structures) of flowers have been studied in isolation, and these structures regarded as evolving in isolation, without relation to function. This tendency has not been intentional, it has developed by default, an occurrence perhaps inevitable in, typical of, the diversification of science. Perhaps in the twentieth century one can no longer expect those who study floral anatomy to be conversant with the pollination and dispersal systems of the species they study. If so, this situation is lamentable, and the more isolated that anatomical studies become, the more suspicious we should be of interpretations offered.

One byproduct of the tendency to study structure independently from function is the designation of particular structures or parts as typologically defined. For example, the telome theory yielded its least credible interpretations precisely when vein endings were regarded independently of the structures in which they were enclosed. In Wilson’s (1950) study of stamens of Melastomataceae, the rather numerous vein endings in stamens are interpreted literally as vestiges of telomes or telome-like units. Melastomataceae have peculiar pollen-presentation mechanisms to which these stamens are related, but this is not taken into account.

The tremendous quantity of literature devoted to anatomy of the crucifer gynoecium is an excellent example of misinterpretations caused by belief in usability of anatomical data in isolation. A wide variety of interpretations—now abandoned—was offered by numerous workers: Arber (1931a, 1931b), Eames & Wilson (1928, 1930), Eggors (1935), Klein (1894), Puri (1941), Saunders (1923), and Spratt (1932). The fact that so many theories could be invented about a single structure, and that rather unlikely theories could be seriously entertained, gives us a hint as to what supposed sources of evidence about floral evolution should now be regarded as unacceptable. Eames & Wilson (1930) and Puri (1941) gave series of diagrams to show intermediate steps by which the crucifer gynoecium, in their interpretations, was derived. These diagrams propose such things as carpels which are retained in a sterile, functionless form, and then conveniently amalgamated so as to produce
the contemporary crucifer configuration. Such a series poses far more problems than it solves, for production of functionless carpels, and thereby presumed development of fruits with what must be difficult dispersal mechanisms (not described by the authors, of course) is required. Although the crucifer gynoecium has a few peculiarities, there is nothing in it not consonant with interpretation as a parietal placentation in a bicarpellate gynoecium. Puri (1952b) finally came to this conclusion, but Eames (1961) did not change or withdrew his complicated and curious interpretation. The gynoecium of Capparaceae is identical to that of Brassicaceae, merely lacking the septum. The inverted bundle of the placentas can be explained by phylesis (change from axile to parietal placentation) and physiological considerations (phloem supplying nutrients to ovules—a correlation noted by Eggers, 1935).

The divorce of floral anatomy from other aspects of floral structure explains why some floral features are not satisfactorily explained by floral anatomists. For example, floral anatomists offer lengthy venation analyses and interpretations of the inferior ovary, but do they explain or take into account why inferior ovaries evolve in angiosperms? Apparently not. In this regard, one notes that the review by Douglas (1957) does not mention the single most important contribution to understanding of this evolutionary feature, the paper by Grant (1950a). The tendency toward syncarpy needs satisfactory evolutionary interpretations; the ideas of Carr & Carr (1961), who relate syncarpy to patterns of pollen-tube growth, are worth attention in this regard.

Likewise, everyone is familiar with the fact that some ovules which mature into large seeds are richly veined (e.g., *Mangifera*), but size correlations seem not to be sought by floral anatomists. Relationship of veins to dispersal mechanisms is rarely if ever taken into account. Shouldn’t one expect a richer venation in a large fleshy drupe, as in *Prunus*, than in a small dry fruit, such as that of *Spiraea*? Studies on anatomy of these have not invoked pivotal considerations of fruit type (Sterling, 1953, 1964, 1966). The elongate receptacle of Magnoliaceae (Figs. 13-16) should not be regarded as a primitive characteristic, but as a specialization related to dispersal mechanisms.

Numerous other examples could be cited in this regard. However, one could say that floral anatomy would have been served better if those who are primarily students of pollination mechanisms and dispersal types were the ones to perform studies on floral anatomy. Unfortunately, this has rarely if ever been true.

2. Supposed conservatism of the vascular system of the flower is the insufficient and fallacious framework on which most phylogenetic interpretations of floral anatomy still rest. In fact, with certain exceptions (see section 3 below), there is no reason for believing that the vascular system lags behind external form to any appreciable degree:

The principle of vascular conservatism has been used, if only implicitly, by most students of floral anatomy, and is the basis of the most disparate interpretations. The fact that it has produced or enabled such diverse and conflicting theories ought to make one suspicious about its value as a phylogenetic tool.

Here is one typical statement of the principle of vascular conservatism by an adherent of that principle: “The vascular system is nearly always more conservative than the organs it supplies. Changes in the vascular patterns tend to lag behind morphological alterations; hence, the nature of the changes, often not discernible by gross morphological studies, may be revealed by an examination of the internal characters of the vascular anatomy, such as: nodal lacunae, bundle orientation, vestigial traces. A corollary [of this] is that the pattern of the vascular system of a flower 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.” This statement, by Moseley (1967); (italics his) is typical of the view basic to the work of many floral anatomists, and is quoted because it clearly shows the assumption underlying the interpretations
of these workers. One notes the reservations of various workers concerning the application of vascular conservatism, but those who employ veins as vestige-indicators must, in fact, employ a form of intuition to discriminate between cases where conservatism applies and cases where it does not. This seems a perilous method in scientific work.

Why has the vascular system of the flower been supposed to be conservative? Is it not because of some suggestive examples (which, in part, are probably correctly interpreted)? Has an appealing but mistaken analogy between the vascular system of plants and bones and teeth of vertebrates played a part? The complexity of animal structure, the closed system of growth in animals, the different modes of evolution of teeth as compared to any structure in plants force rejection of this analogy, yet undoubtedly some botanists are motivated to discover conservative features in plants, and vascular strands have had an inordinate appeal.

Adherents of the classical theory must concede that once vascular conservatism is accepted, patterns of vascular strands can be cited as evidence for entirely opposed theories, and no objective criterion can be uniformly employed to make vascular patterns support the classical theory only. If conservatism of traces is basic to envisioning of laminar structure of carpels (e.g. Eames, 1961), it is also the basis for interpreting carpels as compound structures (Melville, 1962, 1963), or for viewing gynoecia as products of stachyspory, or even carpel polymorphism. Once veins are conceded to be vestiges, they can logically be said to be vestiges of anything desired by any theorist. Attempts to restrict theoretical use of supposedly relictual veins (e.g. Eames, 1931) to one interpretation rather than another are ingenious, but untenable and futile. There is nothing to prevent overly literal interpretation of bundle vestiges, and this is very likely to happen. Little wonder that Puri (1952a), after completing study leading to the most thorough review of floral anatomy ever published (Puri, 1951), states that "the anatomical method in general is of little use in solving the problem of the inferior ovary". This quotation is interesting to me, because Puri perceptively attacks not particular interpretations, but the nature of evidence used.

3. With very few exceptions, the majority of flowers can be expected to show evolution of vascular system at approximately the same rate as other anatomical and morphological features of the flower. "Conservatism" can be expected where function and total amount of venation remain roughly the same during phylogensis, but degree of union between adjacent bundles does change. Lagging in degree of union of bundles (really not conservatism at all, strictly speaking) is the only clear exception to evolution of vascular bundles contemporaneously with evolution of other floral features. This single class of "exception" probably formed, for Eames and others, a precedent after which numerous other types of conservatism were claimed:

When Eames (1931) cited a series in Ericaceae in which bundles lagged in fusion as compared to fusion of organs, he produced a believable interpretation. The fact that within a single genus (Vaccinium) different degrees of union can be found seems compelling. Similarly, his citation (Eames & MacDaniels, 1947; Eames, 1961) of a series in union of bundles between a pair of flowers in Lonicera, the work of Wilkinson was a logical interpretation. Other cases might be cited: for example, bundles of adjacent carpels that remain separate after syncarpy has occurred. However, all of these examples agree in the following features: (a) the amount of vascular tissue remains approximately the same—the same number of conducting elements is involved, in general; (b) the functions to which vascular bundles are related remain the same—the organs supplied in the final member of a series are the same as the organs in the first member of the series, there are no vestigial bundles, and all perform the same function as in the ancestral type; (c) the series forms the basis for interpretation, and the series is within a natural taxonomic group; and (d) factors other than
veins make union rather than separation the likely explanation. Because, in these examples, function and amount of vascular tissue remain unchanged, there is relatively little selective value for fusion of vascular bundles. Ontogeny is a process in which efficiency will prevail, and fusions eventually might be expected to occur, at least in some instances.

Much has been made of differential rates of evolution within various organs of a plant, and some acceptable examples of this have been cited. However, can differential rates of evolution be evoked to explain all phenomena? For example, adherents of vascular conservatism in flowers tell us that stamens of zingiberalean families (Musaceae; see Fig. 18; Zingiberaceae; Strelitziaceae) are primitive (Eames, 1961). Why should we believe that primitive staminal structure has been retained within families specialized in so many respects? The credibility of such primitiveness is weakened not only by that consideration, but by the fact that zingiberalean pollination mechanisms are different from those in other families claimed to have primitive staminal structure. Should we not expect that deviation among evolutionary rates is usually relatively little (with exceptions, of course), and re-examine our concepts of primitive and advanced accordingly? The reasons for differential rates of evolution ought to be examined in any given case by those who propose this as an explanation. One type of evolutionary lag is illustrated by xylem, which is most frequently claimed to be more primitive than other organs of a particular plant. This is conceivable, because xylem is not directly exposed to the environment, whereas leaves are.

The so-called "ranalean" families have been regarded, in recent years, as primitive to the exclusion of mention of specialized characters. One author (Moseley, 1961) gives a typical statement of such a view: "the widely claimed thesis that Ranales are primitive angiosperms has been substantiated during recent decades. As a corollary to this thesis, it is thought that Ranales should reveal many primitive angiospermous features which, if discovered and evaluated, could be of value in solving the riddle of angiospermous origin." This statement is, in its present wording, incorrect: because only characteristics, not particular living plants, can be primitive or specialized, one can only claim that "Ranales" contain more numerous primitive characteristics than do other living groups of plants. Even conceding that to be true, they must also contain a number of specialized characteristics—in fact, if they were not adapted to contemporary conditions, and thereby specialized, in a number of respects, they would not be alive today. Moreover, the "ranalean" families are exceptionally different from each other in floral characteristics. Where so many different floral types are present, they cannot all be primitive. Any given feature in a "ranalean" plant might be either primitive or specialized. If five characters are primitive, there is no reason to believe that the sixth will be primitive in a given plant. We must assess each character on its own merits, and present solid evidence for such interpretations.

In fact, there is probably more synchronization of characteristics than some workers have been willing to recognize. Magnoliaceae is a family often cited as being rich in primitive characteristics. Let us hope that it is cited because it is grown in the north temperate zone, and is thus a convenient plant for many botanists. Magnoliaceae, and the allied families Himantandraceae and Degeneriacae are, in fact, not strongly primitive in wood structure (Canright, 1955); there are many families with more primitive woods, such as the woody Saxifragaceae ("Hydrangeaceae", etc.) and Theaceae. Why, then, should botanists so frequently select Magnoliaceae, Himantandraceae, and Degeneriacae as examples of primitive structure? Indeed, there is considerable irony in doing so. If numerous, spirally-arranged carpels are primitive, then Degeneria with its single carpel (Figs. 6, 8) must be counted out—on that characteristic. If we must count that out as a primitive characteristic, why should we be sure that any other
given feature of Degeneriaceae is primitive—or, for that matter, specialized? If a roughly synchronous rate of evolution among characters within a plant is to be expected, and if correlations are supposed, we would do better to look in plants with more primitive xylem. Trends of xylem evolution are unidirectional according to Bailey and others, for reasons cited by Carlquist (1961). In that case, Winteraceae (Figs. 1-4) might be expected to have more numerous primitive floral characteristics than Magnoliaceae, Himantandraceae, or Degeneriaceae.

4. Increase in vascularization of flowers should be expected as often as reduction—although virtually no papers, at present, claim the former. The uniformity with which workers always choose to hypothesize a reduction series is little short of hilarious. If reduction of venation system is so much more frequent than expansion, then there ought to be huge numbers of minute flowers with minute appendages and virtually no large flowers. In fact, flowers tend to follow something of a normal distribution curve in size and therefore of richness of venation, which is related to size. Size of flowers is related to pollinating agents (excepting for anemophily), and there is no reason to believe that a unidirectional evolution toward smaller and smaller pollinating agents occurs:

Why are plant anatomists so unwilling to concede or mention cases of increase in vascularization? Probably one reason is the tendency of workers to think that reduction of venation takes place in an orderly fashion, whereas increase would result in disorderly patterns. This tendency might result from observation of certain cultivated plants in which selection for increase in parts (over short periods of time) produces disorderly arrangement of veins in bizarre or gigantized parts. An example of this can be seen in the cultivated sunflower (Carlquist, 1961).

There is, however, no reason to believe that evolution under natural circumstances will show disorderly venation in parts which have increased in size. For example, evolution in nodal anatomy from 2-trace unilacunar to trilacunar to multilacunar is generally accepted, yet multilacunar is not regarded as a disorderly condition. Angiosperms are sufficiently efficient in evolution of structure and ontogeny that the simplest and most orderly form of a vein system can be expected to be achieved within a few generations. Gigantisms and teratological formations are not representative cases, and there is no reason to believe in consistent decrease in size of flower parts and their venation.

I can cite, from my own observations, a number of instances of probable increases in size and venation in flowers. In Fitchia (Asteraceae), species with more than three veins per corolla lobes, F. rapensis and F. mangarevensis, clearly show increase in venation (Carlquist, 1957; Carlquist & Grant, 1963). The achene walls in all species of Fitchia contain large numbers of veins, corresponding to the exceptionally large size of achenes of Fitchia when compared with the probable ancestors of this group, plants like Bidens and Coreopsis. Evolutionary increase in size of flowers and fruits of Fitchia is very likely related to ornithophily in this genus and also to loss of dispersibility (Carlquist, 1966).

Eames (1961) states that most monocotyledons have three veins per stamen. This statement is probably false, but those he specifically cites (Musaaceae, Zingiberaceae, Marantaceae) probably have larger, more richly-veined stamens as a result of increase in size. The flowers in Musa (Fig. 18) and other members of these families show adaptation to ornithophily. Ornithophily is accompanied by increase in size of flowers and flower parts as an accommodation to large size of birds as compared to insects. The large stamens in Musa seem related to the impreciseness with which birds visit flowers: large unavoidable displays of pollen must be available to bird visitors. Likewise, large, richly-veined stamens in Fremontodendron and Cheirostemon seem related to evolution toward particular modes of pollination (Figs. 19, 20; see section 12 below for further descriptions of these).

Rich venation in carpels, as in Degeneria (Fig. 8), Prunus, etc., seem instances
Figs. 1-4 — Floral details of Winteraceae. Fig. 1. *Drimys winteri*, flower and bud at right, immature fruit carpels at left. From a specimen cultivated in the Botanic Garden, University of California, Los Angeles. × 5. Fig. 2. *Drimys lanceolata*, nearly mature fruits; only one carpel is present in each flower. The prominent stigmatic crest is evident. From a specimen cultivated in the Christchurch Botanic Garden, New Zealand. × 1. Fig. 3. *Drimys winteri*, longisection of carpel, showing stigmatic crest at upper right, mound of floral axis terminus at lower right. × 30. Fig. 4. *Drimys winteri*, portion of transection of flower, showing one carpel and portions of two others, and one stamen. No evidence of laminar stamen structure or conduplicate carpel structure is visible. × 30.
of increase in venation related to pollina-
tion and dispersal mechanisms. Flowers
of Magnolia are probably all examples of
increase in size phyletically, and the
venation of all parts may be suspected
of having increased with this gigantism.
The size of flowers in Winteraceae
(Fig. 1), Illiciaceae (Fig. 5), and Trocho-
dendraceae seems much more likely closer
to the size of flowers in ancient angio-
sperms. Flowers in Nymphaeaceae very
likely represent gigantisms over ancestral
sizes, and venation seems to me corre-
spondingly increased. Obviously many
more examples could be cited. Nectaries
seem excellent examples of increase in
venation in many cases. Nectaries occur
in a wide variety of positions on the
flower, and seem mostly to be structures
evolved as adaptations to pollination, not
vestiges of former structures; their vena-
tation patterns (Frei, 1955) certainly give
no aid to those who believe in vascular
conservatism in flowers.

Examples can also be cited of struc-
tures in which vascular bundles have
been entirely lost phyletically. Arber
(1933) cites some, and others, such as
female flowers of Balanophoraceae,
anthers of small-flowered Asteraceae,
pappus structures of most Asteraceae,
etc., could be cited. That vascular
strands can be lost before organs are,
and thus run counter to the principle of
vascular conservatism, is not new to
students of floral anatomy. Significant
in these examples, however, is that the
non-vascularized structures tend to be
of an almost predictable size or thickness
in number of cell layers. This suggests
that vascular tissue bears a certain rela-
tion to size of an organ.

5. Presence of vascular bundles should
be interpreted as functional structures
related to actual physiological activity, not
as vestiges that do not function yet have
not yet been lost. Vascular bundles differen-
tiate according to principles of morp-
ogenesis, and not in response to non-existent
organs or to past events in the phylesis of a
group. The efficiency of angiosperms is
such that vascular bundles retained as in an
historical archive are not to be expected:

Although vascular strands in flowers
may not bear a perfect relationship to
physiological functions, and bundles may
vary from flower to flower in a species, a
close correlation to actual functions
should be expected. In fact, much of
the interesting challenge now awaiting
floral anatomists consists of correlation
function with vascular structure in
flowers. Nectaries are a good example
of this, because their function is an
obvious one. They are probably struc-
tures mostly formed de novo on various
organs of a plant. Indeed, simple necta-
ries are difficult to identify anatomically,
for they show only slight staining differ-
ces in microtomed material whereby
such regions might be differentiated
from ordinary parenchyma. Of course
there must be stomata for exudation
of nectar, but these are present on
many floral organs anyway. Venation
of nectaries suggests origin de novo in
most cases. Appropriate to secretion of
sugars, phloem is usually much more
developed than xylem in nectaries, and
sometimes is present to the exclusion of
xylem as in Asteraceae (Frei, 1955).

Another good example of venation in
relation to function is the search for so-
called supracarpellary venation, also
called “residual stelar tissue” (Moseley,
1961). Eames (1931) thought that if
vascular tissue extended beyond the last
carpsels into the axis tip, this was evidence
of retention of a primitive condi-
tion wherein the determinate-shoot nature
of the flower still retained relics of an
indeterminate condition. The drawings
by Eames of floral vascularization in
Aquilegia suggest far more vascular tissue
than is, in fact, present in that example.
The flower he figures may have been
exceptional, for Tepfer’s (1953) studies
on Aquilegia flowers failed to confirm
presence of supracarpellary bundles.
Apparently, the example studied by
Eames had a relatively large conical
receptacle terminating the axis, so not
surprisingly a small amount of vasculari-
ization was present there. However,
very few flowers have supracarpellary
vascularization of any appreciable degree
— nor would they be expected to have
any, for vascular bundles form with
relation to actual organs, not non-
existent ones. If supracarpellary vascular
Figs. 5-8 — Fig. 5. *Illicium floridanum*, flower photographed in the National Arboretum, Washington, D.C. The stamens are short, intermediate between latrorse and introrse. x 2.

Figs. 6-8. *Degeneria vitensis*. Fig. 6. Immature fruits from specimens collected in Fiji by the writer in 1962. Fruit at left shows stigmatic crest; fruit at right seen in lateral view. x 0.75. Fig. 7. Portion of transection of flower: stigmatic crests paired at lower left; other structures shown are stamens: the ones at left are sectioned below the level of the anther sacs — corresponding to the wider nature of bases, 5 veins can be seen; 3 veins occur in stamen sections at level of anther sacs, which are extrorse. x 30. Fig. 8. Carpel, from longisection of flower. The stigmatic crests, above, are not vascularized; veins supplying the ovules are, in this particular flower, the uppermost and no "supernumerary" veins are present. x 30.
tissue were relictual, one might expect it in flowers of Winteraceae, but it does not exist there (Tucker & Gifford, 1966a; see also Fig. 3). The presence of supracarpellary vascularization in the few instances where it occurs merely indicates presence of supracarpellary structures.

Other "stubs" of tissue in various groups of angiosperms are credited with significance (viz. Puri, 1951, p. 482). However, I have analyzed the cases cited by Puri, and find the bundles in question probably have other explanations, related to actual functions or irregularity in vascularization. There are too many instances where "expected" vestigial bundles are not, in fact, present to credit usefulness of a "stub" here or there in flowering plants.

The corollas of Asteraceae provide a good example of correlation between veins and structures. One would expect median veins running to the tips of the corolla lobes in disk flowers. However, disk flowers typically have lateral veins only—these usually fused in pairs or apparently so, so that a single vein extends downward from each sinus (Carlquist, 1957). The reason for this configuration is obvious when one takes into account the stamens in these flowers. The stamens are opposite the sinuses, so that veins that supply stamens are directly in line with the fused lateral corolla-lobe veins. Thus an efficient configuration is attained.

Of greater theoretical importance to some workers is the occurrence of placent-supplying veins that appear to form a series additional to those of the remainder of the carpel. This situation can be found in occasional flowers (Sterling, 1953, 1964) and has been claimed by some authors, such as Melville (1962, 1963) as evidence that the carpel is a compound structure. One is piqued that in such situations, the nature of the fruit with respect to such venation patterns is not described or considered. Does the carpel form two distinct regions — inner and outer — which therefore are related to two systems of veins? Does a thick, fleshy fruit type correlate with richer venation? Such questions must be answered before we can interpret venation patterns. Data on venation of carpels should be expected to be relevant first to fruit morphology and the dispersal mechanisms that relate to this morphology.

Floral anatomists typically omit the nature of the fruit when considering venation: for example, Keng (1965) claims that carpels of *Illicium* show reductions when compared to the more richly-veined carpels of Magnoliaceae. The reverse hypothesis could equally well have been entertained instead. However, what one wishes at least is consideration of the fact that *Illicium* fruits consist of thin, dry follicles at maturity, whereas the carpels of Magnoliaceae are thick and complex at maturity (Figs. 13, 16), and that in each case venation correlates in pattern and abundance with the volume of the fruit.

The 3-veined condition thought to be basic in carpels is based on physiological correlations: the two ventral veins typically are related to supply of ovules, the dorsal vein typically supplies the stigma. Deviations from this pattern are usually related to greater number of ovules, different morphology of the stigma, nature of the fruit, etc. At any rate, there is nothing "sacred" about the 3-veined condition.

Other examples of how veins can be interpreted in terms of function existing in the contemporary form of flowers rather than in the past history of a group of plants can be found in sections below describing calyx, corolla, stamens, and carpels.

6. **External morphology of the flower and fruit** are probably the most reliable criteria for understanding of phylogeny of flowers and fruits. This principle derives from the fact that externally visible organs function in pollination and dispersal. The veins supplying these organs are simply components of, and therefore morphologically secondary to, the organs themselves.

Quite often, one suspects, morphologists do, in fact, interpret form from external morphology, and go to anatomy in the hope of finding, on another level, justification for the interpretation. Misinterpretation is possible on either level, of course, but studying both gross
morphology and anatomy does not insure a greater degree of reliability in interpretation. Swamy's (1953) chart of the various interpretations offered for flowers and flower parts in Scyphostegia is a good example of this.

The case of the inferior ovary is interesting in this regard. Anatomy is often alleged to provide considerable evidence concerning the nature of the inferior ovary in angiosperms (e.g., Douglas, 1944, 1957). As mentioned above, Puri (1952a) disagreed. Flowers of Cactaceae and Calycanthaceae are claimed to show invagination, and thus a cauline mode of structure, as opposed to appendicular fusion resulting in an inferior ovary. There are many recent studies in anatomy of flowers of Cactaceae (Tiagi 1955, 1957, 1960a, 1960b, 1963a, 1963b; Boke, 1964) and Calycanthaceae (Tiagi, 1963c). If one viewed these flowers only from the standpoint of gross morphology, the same conclusions would doubtless have been reached. The areoles on ovaries of Cactaceae, and the spiral of tepals on the outer surface of the Calycanthus flower could hardly be explained in any other way. Dispassionate reading of interpretive papers in floral anatomy reveals that the problematic flowers are not "solved" by data from floral vasculature with any more certainty than they were by data from gross morphology.

Inferior ovaries claimed to have originated by means of appendicular fusion reveal this nature at least as clearly in external morphology as in anatomy, especially where a series within a natural taxonomic group is assembled. The gross morphology illustrates, in arrangement and appearance of parts, relationship to bird or beetle pollination, factors which have been cited as selective factors (Grant, 1950a). The anatomy of the flower does not give any direct information concerning selective factors producing the ovary, or how a pollinator or dispersing agent acts on any of the components of the flower.

7. Changes in ontogeny are required for phylogenetic changes in external form of flowers. In the case of floral parts, relatively small changes in ontogeny may produce these changes. If this is true, we need not imagine numerous intermediate now-extinct forms. Moreover, a basis for reversibility is understandable in this case. Increase in number of parts is probably more common than is ordinarily supposed.

Increase and decrease in number of parts are probably achieved by very few changes in the genetics of a plant. This idea has been enunciated by Stebbins (1967), who has given good examples of increase in number of floral parts. Understanding of the adaptive nature of increase or decrease seems essential. For example, Grant (1950a) has suggested that predation by beetles involved in pollination might account for increase in number of achenes in Fragaria.

Increase in number of stamens seems accepted by morphologists as possible, although an interpretation toward numerous stamens is much less frequent than an interpretation of decreasing stamen number. A group in which stamen increase has probably occurred is Myrtaceae. In this family, large, numerous stamens may represent adaptations to bird pollination. The beetle syndrome also may involve increase in stamen number (see section 12).

Increases in the number of ovules within flowers seem possibilities accepted by morphologists, although they do not seem to find very many examples of this. Orchidaceae would be an example of increased ovule number. Decrease in ovule number can also be expected, and is selected much more often as the hypothesis of any particular worker. One example of this is Canright's (1960) statement that in Magnoliaceae, there is a "definite tendency toward reduction in number of ovules". Actually, there is, in my opinion, no evidence that more than two ovules per carpel is primitive in Magnoliaceae. Canright does not present any reason for his interpretation, nor does he mention what dispersal type might be primitive and thus account for the ancestral multiovulate condition he hypothesizes.

Change from superior to inferior ovary might involve merely a small shift in the site of meristematic activity of primordia. Thus numerous intermediate stages may
not be involved phylogenetically—perhaps just a few. If the same dispersal mechanism (e.g. berry) characterizes both a superior and inferior ovary in a group, or an intermediate stage, a relatively drastic change from superior to inferior ovary would be possible. Change in the other direction, from inferior to superior ovary seems likely in the case of Tetraplasandra gymnocarpa (Araliaceae), as noted by Richard H. Eyde (pers. com.). Because this change has probably involved no change in pollination or dispersal mechanisms one can hypothesize relatively rapid, sudden change here, too. There are no intermediate stages evident in Hawaiian Tetraplasandra species, and one would expect at least a few if the transition had involved numerous stages developed over a long period of time. Preservation of various stages in evolution of genera is particularly characteristic of Hawaiian plants.

Likewise, so-called peloric forms of zygomorphic flowers may involve only a single gene pair, and one can imagine a change to (or from) zygomorphy can take place relatively suddenly. Change from zygomorphy to actinomorphy seems possible provided that zygomorphy of a pronounced sort is not developed. Zygomorphic results from changes relatively late in the ontogeny of a flower. Thus neoteny would produce actinomorphy. An interpretation very much like this was offered for Downingia humilis by Kaplan (1968). The corolla of *D. humilis* is not quite actinomorphic, but it is much less zygomorphic than are the corollas of other species of *Downingia*. The corollas of *D. humilis* are also rather small.

8. Stages in ontogeny have been claimed to be of value in interpretation of floral evolution. However, ontogeny of flowers may be expected merely to exhibit the most efficient means of producing a structure, beginning with an initial or group of initials. The nature of ontogeny in angiosperm structures makes unlikely the probability that any historical stages will be preserved. In animals, closed system of growth and complex embryology make "ontogeny recapitulates phylogeny" a possibility, although probably merely as a byproduct of the fact that earlier stages are more difficult to modify, later stages easier, in embryology, and complexity of development offers a great number of stages. This is not true in plants, and stages in development of floral organs should be regarded merely as preformations of mature shapes, not as relictual images:

The fact that ontogeny does not tend to retain stages of phylogenetic significance was clearly demonstrated to me during my work on Gongylocarpus (Carlquist & Raven, 1966). In this genus, fruits and seeds are borne embedded entirely within the pith, so that stems take on a galled appearance. This unique and amazing fruit type is not at all elucidated by ontogenetic studies. A special meristem pushes the ovules and associated structures into the pith. How did such a meristem originate? There is no indication. There are no indications of intermediate structures on the way to this unique mode of fruit development, nor are there any indications of whether this change occurred suddenly or by way of numerous stages.

Ontogeny of flowers of Ranunculaceae (Sprotte, 1940; Tepfer, 1953) is said to feature characteristics of foliar ontogeny, such as marginal meristems, in the case of development of carpel and other floral parts. This is cited as evidence for a leaf-like nature of floral appendages. However, the degree of resemblance between floral appendages and leaves in ontogeny should be interpreted first as the degree of resemblance between examples of these categories. In other words, if a carpel of a particular plant strongly resembles a leaf, it may be expected to have ontogeny similar to a leaf—but ontogeny itself will give no more evidence than the mature appearance itself gives.

In fact, ontogeny of carpels is usually not strongly foliar in its various stages. This fact was stressed by Grégoire (1938) when he concluded that flowers and their appendages are not directly comparable to stems and leaves. Distinctive aspects of carpel ontogeny also proved persuasive to Troll (1932, 1939) in his development of the idea of a peltate carpel, and has also been a line of investigation used by those who have taken up peltate
concepts, such as Leinfellner. I find that carpels are obviously structures different from leaves, so differences in development are to be expected. Some students who designate some carpels as "peltate" and others as "epeltate" are, in my opinion, attaching too much significance to ontogenetic data as well as other considerations.

In recent years, advocates of the classical theory have stressed resemblances between carpels and conduplicate leaves. This comparison may be misleading, for it implies that the more leaflike a carpel is, the more primitive—which may not be true at all. At any rate, the ontogeny of carpels presumed primitive by adherents of the conduplicate interpretation is not at all like that of a leaf. The work of Tucker & Gilford (1966a, 1966b) illustrates this. They say (1966b), "the use of the term 'conduplicate' for *Drimys* carpels is an oversimplification which emphasizes the similarity to a foliar structure. In *Drimys* the term is not particularly appropriate; the insertion and the activity of the adaxial meristematic lip ('cross zone') impose upon the carpel a radically different pattern of ontogeny from a typically conduplicate structure. It is conduplicate only in the region above the level of the lip; below this level there are no margins. The carpel grows upward as a tube, by cell division and enlargement throughout."

Kaplan (1967), in comparing ontogeny of *Pereskia aculeata* and *Downingia bacigalupii* flowers alleges that ontogeny of the former, which features marked radial expansion, shows cauline origin of the inferior ovary, whereas the ontogeny of *Downingia* which features development of a concavity early in ontogeny and vertical elongation, demonstrates the appendicular theory. Interpretation of ontogeny in this way does not seem justified, because the different modes of ontogeny relate to obvious differences in proportion and other features. The long floral tube and clear epigyny of *Downingia* are foreshadowed by the early concavity and vertical elongation, not any appendicular mode of origin. The broad disc-like shade of the floral cup in *Pereskia* and near-hypogynous condition are related to the relatively late radial expansion of the floral axis. Kaplan writes, "in order to arrive at the most accurate judgment of the homology of the inferior ovary, it is necessary to combine the closely-related approaches of comparative morphology, vascular anatomy, and ontogeny (including histogenesis). This statement has an appealing quality to it, but should be rejected: accretion of dubious or incorrect interpretations or of irrelevant "evidence" is no service to morphology.

9. The leaf-like or bract-like nature of sepals or calyx lobes is related to their function as floral coverings, exposed directly to the environment and capable of photosynthesis. The fact that sepals typically have leaf-like venation can be related to a greater degree of transpiration and photosynthesis and a greater longevity as compared to petals or corolla lobes, which are non-photosynthetic and typically exposed only briefly. In many fruits, especially those with inferior ovaries, calyx lobes participate in the composition of the mature fruit, and so their vascularization might be expected to be greater than that of petals:

Sepals typically have three traces related to three gaps, and this is interpreted as evidence that sepals originated from bracts or leaves, rather than from sporophylls (Eames, 1931; Rao, 1951). There are many instances in which leaves are not trilacunar, and of course there are many instances of trilacunar sepals and calyx lobes. The wide range of venational conditions alone would tend to inhibit one from using this character for morphological interpretation. Another irony in this respect is that when Eames first proposed derivation of sepals from bracts or leaves, the primitive nodal type in angiosperms was thought to be trilacunar; now the 2-trace unilacunar is considered primitive. If the latter is primitive, we would expect sepals to be primitively unilacunar also, provided venation were valid evidence.

However, similarity in contemporary functions—and thereby also structure—between sepals and leaves should not be interpreted as evidence of phylogenetic derivation of one category of appendage
from another. Obviously parallel evolution between sepals and leaves is not only possible, it is very likely in a plant group with the tremendous plasticity of angiosperms, and in structures with the great diversity within each category. An interesting, if not vital indication of similarity between sepals and leaves might be obtained by physiological tests: transpiration rates, photosynthetic ability, etc. This might give us ideas of selective factors which would permit parallel evolution in the two categories of organs.

10. Vascularization of petals or corolla lobes is related to function: display of shapes and colours suited to pollination mechanisms. The relatively moderate basal vein trunks of petals are related to the brief periods during which they typically are exposed, the thinness of corolla structures, and their lack of photosynthesis. Veins of a petal may be much branched, related to width of the petal expanse. Venation is not a valid line of evidence to show that petals are derived from stamens or other organs.

Eames (1931) claimed that petals are primarily and primitively 1-trace organs, and that this is an evidence that they have been derived from stamens by sterilization. This interpretation has been used more recently by Rao (1951) and Moseley (1958). The fact that there are transitions in structure between typical stamens and typical petals in Nymphaeaceae seems to have influenced Moseley, and he envisions intermediate structures — broad, petal-like stamens — as a primitive type from which both petals and filiform stamens have been derived. Although I earlier accepted this interpretation (Carlquist, 1961), I now believe that this view is not justified by the facts.

One question, in the case of Nymphaeaceae, is why Nymphaea shows transitional structures, whereas in other genera of the family, such as Nuphar, structures transitional between petals and stamens do not occur.

Transitional structures are not a good source of evidence in any case. For reasons inherent in morphogenesis, some situations would be expected to feature transitional structures. In many Asteraeae, involucral bracts range from multilacunar in wider, outer bracts, to unilacunar in narrow, innermost bracts. This can hardly be regarded as evidence that wider bracts are derived from narrower bracts. In cones of Pinus, the lowermost ovuliferous scales are ordinarily small and sterile, as are sometimes the uppermost as well. There are transitions among various ovuliferous-scale types within a cone, but this is not evidence that one type has been derived from another.

We lack a discussion, in the case of Nymphaeaceae, of how anatomy of floral parts is related to pollination mechanism. Stamens and petals of the types found in Nymphaeaceae are adapted to particular pollination mechanisms—probably beetle pollination—and have a high selective value in their present conformation. If this were not true, we would expect them to be changing rapidly or becoming extinct rapidly. There is a tacit assumption by Moseley that primitively Nymphaeaceae had only structures intermediate between stamens and petals, and that these formed a successful pollination system. This seems unlikely; it requires one to believe that flowers with intermediate structures rather than well-differentiated ones would constitute a successful pollination presentation and pollination scheme for Nymphaeaceae, yet we are not told what that scheme was.

By no means all petals are 1-trace organs. The trilacunar condition is, in fact, more widespread than current generalization might suggest. Trilacunar petals can be found in such “ranallean” families as Degeneriaceae (Swamy, 1949) and Calycanthaceae (Tiagi, 1963). Assuming that in angiosperms at large the unilacunar 1-trace condition is commonest, however, I think that physiological considerations give an obvious and compelling explanation. The thin, membranous nature typical of many petals seems related to relatively restricted vascular supply. Moderate vascular supply of petals might also be related to rapid expansion of petals as anthesis approaches: if veins are relatively few and
consist of annular and helical tracheids only, the expansibility of the petal would theoretically be greater. Duration of petals seems in my experience correlated with richness of vascular supply. Because many petals last only for a day, a single trace is an obvious correlation. Thick petals or corolla lobes of greater duration have either more than three traces at the base or, if a single trace only, more numerous tracheary elements in this trace. Studies of corolla morphology which examine the relationship between nature and richness of venation and the factors given above are needed.

Factors such as the above might give us explanations for other tendencies in petal construction, such as the presence of predominantly dichotomous venation. Other explanations for dichotomous or flabellate venation might be recent phylogenetic widening of a petal, or the tendency of some petals to be much wider in their distal portions. Such possibilities are mentioned for leaf venation in Stylidiaceae (Carlquist, 1969). Dichotomous or flabellate venation occurs in petals of Ranunculaceae (Arnott & Tucker, 1963, 1964) and has been said to be related to vestiges of ancient venation patterns. This explanation seems unacceptable. Dichotomous or flabellate venation occurs in petals of a wide variety of angiosperms, particularly monocotyledons. The genus Calochortus (Liliaceae) displays this well. Likewise, dichotomous venation in angiosperm leaves cannot be interpreted as vestigial, although Foster (1968) seems obviously tempted by that explanation.

11. The 1-trace nature of most stamens is related to their filiform nature and the brevity of their exposure. Stamens with more numerous traces or with branched traces are more massive, have longer duration, or broad surfaces are related to particular modes of pollination, particularly beetle pollination. Stamens with laminar form and more elaborate venation need not necessarily be interpreted always as primitive; these may be adaptations derived from narrower stamens.

As in other parts of the flower, decrease and reduction in venation has been hypothesized quite uniformly. This interpretation does not seem to have been challenged where stamens are concerned—but a challenge is needed, in my opinion. Angiosperms with numerous characters alleged to be primitive do not by any means all possess laminar stamens with numerous veins. Flat 3-trace stamens can be found in Musa (Fig. 18) and other genera of the Zingiberales, as mentioned by Eames (1961). Such stamens cannot be regarded as primitive in these families; they probably represent relatively recent adaptations to ornithophily. Such interpretations also seem likely to Sterculiaceae and Bombacaceae. These families have richly-veined stamens (Heel, 1966). Fremontodendron californicum (Fig. 19) has five stamens united into a tube at their bases; three veins run the length of each of the stamens. Of these, the median veins are larger. Branches of each of the three veins occur in the region of the anther sacs. Similar but richer venation characterizes flowers of Cheirostemon (Cheiranthodendron) platanoïdes (Fig. 20). Five veins per stamen occur in this plant, which probably represents an adaptation to either bird pollination or bat pollination. Retention of more elaborate venation as vestiges in these genera of Sterculiaceae seems very unlikely. These flowers are exceptionally large for Stercuhaceae and these genera have few characteristics one could term primitive.

If adaptation to particular modes of pollination can be accompanied by development of 3-trace massive stamens, laminar or otherwise, can we unquestioningly regard these features as primitive in any family of angiosperms? The recent view (e.g. Canright, 1952) is that primitive stamens are flat, have sporangia embedded in the surface rather than on the margins, and have more than a single vein. In Magnoliaceae, such stamens occur, but there are also narrow 1-trace stamens with marginal anther sacs (e.g. Michelia) or filiform stamens which are extrorse, as in Liriodendron (Fig. 15). Are the stamens of Michelia and Liriodendron specialized, as Canright (1952) claims? Actually one might with better justification read the series in reverse.
Flowers of Magnoliaceae are specialized in a number of respects, as is the wood. Canright (1960) states that "the gynoecium is in marked contrast to the androecium of the Magnoliaceae, where primitive forms of microsporophylls are retained by a number of species". Why should the gynoecium be so markedly out of synchronization with the androecium? Is perhaps the interpretation wrong?

I find that one of Canright's correlations, that of broad stamens with tropical habitat in Magnoliaceae, does not hold true. When one looks at one of the features regarded by Canright and others as primitive—anther sacs embedded in the surface of a broad stamen—one receives some surprises. In some of the genera with this stamen type, such as *Nuphar* (Fig. 12), anther sacs are embedded in the adaxial surface. In others, such as *Degeneria* (Fig. 7) and *Liriodendron* (Fig. 15) the anther sacs are in the abaxial surface. Which type is the primitive condition—or is either type necessarily primitive? The irony is further increased by other examples.

In Lauraceae, outer stamens are introrse, inner stamens extrorse, so that both types are represented in a single flower, as shown for *Umbellularia* (Fig. 17). Keng's (1965) drawings of *Illicium* anthers suggest sacs embedded on the adaxial surface, but his photographs of sectioned material indicate an essentially marginal position. As the photograph in Fig. 5 suggests, thecal position in *Illicium* is probably halfway between the adaxial surface and a marginal position.

If one considers the "ranalian" families with notably primitive wood structure, such as the vesselless families Trochodendraceae, Tetracentraceae, Amborellaceae, and Winteraceae, one finds that stamens are not at all laminar, anthers sacs are marginal, and only a single vein per stamen is present. In Winteraceae, anther sacs tend to be terminal, as shown for *Drimys winteri* (Figs. 1, 4) and illustrated by Sampson (1963) for *Pseudowintera*. Terminal anther sacs characterize Annonaceae, such as *Asimina* (Fig. 10) and *Annona* (Fig. 11).

Marginal anther sacs characterize most "ranalian" families, such as Calycanthaceae (Fig. 9).

The strong diversity of stamina types in "ranalian" families is to me the striking feature that needs explanation. Is not the simplest explanation that these all represent various modes of adaptation to particular pollinators (chiefly beetles—but in many distinct ways)? Narrow stamens with marginal anther sacs might well represent the basic type from which the others have been derived; this is the least difficult hypothesis. Adaptation to beetle pollination does include exposure of large zones of pollen, and usually exposure over relatively long periods of time. The stamens in the genera named above are usually fleshy, corresponding perhaps to this longevity. Beetles make visits to flowers chiefly in order to forage on pollen (Faegri & Pijl, 1966), so large quantities of pollen are understandable lures. Those authors also note the attractiveness of heavy, oily fragrance.

Because beetles are crude or random in

Figs. 9-12 — Fig. 9. *Calycanthus occidentalis*, central portion of longisection of flower. From plant cultivated in the Rancho Santa Ana Botanic Garden, Claremont. Carpels in pale circular area near bottom of photo; above them, staminodes; outside of staminodes are the stamens, which are latrorse. Staminodes, stamens, and inner tepals are tipped by white oil-rich bodies; pollen is scattered on the inner tepals. x 3. Fig. 10. *Asimina triloba*, flower showing numerous stamens in a globose arrangement around the several carpels. Photographed in its native habitat, near Bloomington, Indiana. x 1.5. Fig. 11. *Annona cherimoya*, immature fruit, left, showing numerous carpels; flower at right, has numerous stamens, which dehisce apically, surrounding the carpels. The 3 perianth segments are succulent. From specimen cultivated in Santa Barbara, California. x 2. Fig. 12. *Nuphar luteum* var. *polysepalum*, portion of flower; androecium shows part of stamens already dehisced (below), pollen visible against the purplish part of the stamens; stamens are introrse; note numerous prominent stigmas above. From a plant cultivated at the Rancho Santa Ana Botanic Garden. x 2.
Figs. 9-12
their approach to flowers, broad pollen-bearing zones and broad stigmatic areas are advantageous. Special food bodies may be present (Grant, 1950b), as at tips of stamens or staminodes of Calycanthus (Fig. 9), or beetles may chew on floral appendages in some cases.

Even within a single family, considerable diversity in the pollen-presentation mechanism may occur. In Magnolia grandiflora, stamens as they drop fall into the cup-like tepals, and may provide a broader pollen-bearing zone and perhaps tend to make beetles eat pollen of fallen stamens while fresh pollen is thereby saved on the anthers still attached. In Liriodendron, stamens do not fall into the tepals (Figs. 14, 15). Nectar can be found as a film over the broad orange-coloured concavities of the tepals (Fig. 14). Pollen falls into this nectar film, and thus is retained within the flower; pollen mixed with nectar provides both a potential food source and also a mixture likely to make pollen adhere to an insect. Pollen becomes scattered into the tepals in Calycanthus (Fig. 9) and Nuphar (Fig. 12), providing increase in the pollen-bearing zone of the flower. Display of stamens in all of the genera mentioned above offers exceptionally broad pollen-bearing areas even before scattering of pollen into the perianth.

The various adaptations for beetle pollination in these "ranalean" families have probably been achieved independently. There is no justification for selecting one genus—say Magnolia—and then attempting to derive the other types from it. This is the more difficult hypothesis because Magnolia is specialized in one direction, just as Annona is in another, and Calycanthus in still another. The laminar stamen type of mechanism (and one should say "types", because different laminar types are involved) represents only one of these tendencies. The richer venation of laminar stamens has proved tempting to those who believe in vascular conservatism. However, if stamens are larger and broader, one would expect, for physiological reasons, richer venation, and increase in vascularization seems as acceptable a hypothesis in stamens as decrease. The non-ranalean examples cited indicate likelihood of increase in vascularization, and this could occur within the "ranalean" families as well. All arguments in favour of laminar stamen structure as primitive are, in fact, circular.

Families with fascicled stamens have been claimed to be primitive in that characteristic. Wilson (1965) has claimed this for Dilleniaceae, as has Kawano (1965) for Clusiaceae. There is, in my opinion, no anatomical evidence to support this view; if venation is not reliable, as suggested above, there is no criterion by which anatomy of fascicled stamens could indicate phylogenetic primitiveness of fascicled stamens. The fact that Clusiaceae and Dilleniaceae are thought to be related to "ranalean" families is not really pertinent, but it is probably the most important factor that has tempted some plant anatomists to regard fascicled stamens as primitive.

12. The primitive placement of ovules on carpels seems more likely to have been marginal than laminar or submarginal. How leaf-like angiosperm carpels primitively were is open to question. Although stigmatic areas are uniformly interpreted as decreasing phylogenetically, they may be capable of increase also:

Obviously carpels were always sporophylls, they were never leaves. However, adherents of the classical theory often seem unconsciously motivated to find that the more leaf-like a carpel is, the more primitive it is. Obviously there is no evidence that this is true. We do not know the appearance of pre-angiosperm sporophylls or even of carpels of early angiosperms. They could just as easily have been narrow and rachis-like as broad and foliar (although there is really no evidence for the former either). One could, by sheer speculation, say that presuming the carpel to be a lateral appendage of the same morphological homology as a leaf, it could have been narrow or even linear, but became broader during the process of closure. Very likely we will never have much evidence on the nature of early carpels and pre-carpel sporophylls. This continuing
Figs. 13-16 — Flowers and fruits of Magnoliaceae. 

**Figs. 13-15.** *Liriodendron tulipifera*, from specimens cultivated in Claremont, California. 

**Fig. 13.** Fruits, showing samaroid carpels some of which have already broken away from the elongate receptacle. × 1. 

**Fig. 14.** View of inner tepal from above, showing glistening surface covered by nectar; numerous pollen grains were embedded in this nectar. × 2.5. 

**Fig. 15.** Lateral view of flower, tepal removed to show the extrorse stamens still covered with quantities of pollen (both extrorse and introrse stamens occur within Magnoliaceae); behind stamens is the gynoecium, carpels attached to the elongate receptacle. × 2.5. 

**Fig. 16.** *Magnolia grandiflora*, fruit, showing bright red-orange seeds hanging from dehisced carpels by means of thin fibrous funicle remnants. From plant cultivated in Claremont, California. × 1.
Figs. 17-20
lack of evidence is probably exasperating and tantalizing to morphologists, some of whom eventually refuse to concede this lack of evidence, and adopt something as usable evidence.

Paleobotanical evidence is often cited as the criterion on which floral theories will stand or fall, and such evidence is demanded by some workers. Such a position is rather naive: we can misinterpret relationship and morphological nature of fossil plants (especially when they are fragmentary). The chance of finding a fossil that shows ancestral carpel form is vanishingly small—and would we recognize it if we saw it, or would we misidentify it because of preconceptions?

In this connection it is interesting to note that no contemporary seed plants have leaf-like megasporophylls. There is no evidence that Cordaitales, Ginkgoales, Coniferales, Cycadeoideales or even Cycadales ever had leaf-like megasporophylls. Cycas megasporophylls do offer a hint of leaf-like structure, but one must note that the proximal ovule-bearing part of this sporophyll is not the part with laminar vestiges at all, for malformed pinnae occur on the non-ovuliferous distal part.

There is no reason to believe that laminar placentation—ovules scattered over the inner surface of the carpel—is a primitive characteristic, although some have claimed this (e.g. Eames, 1961). The systematic distribution of this character—Nymphaeaceae, Butomaceae, Lardizabalaceae, and the helobiod families—alone would make this interpretation suspect. The adaptive significance of laminar placentation is not obvious. One might hypothesize that it is a way of increasing ovule and seed number, just as some angiosperms have enormously expanded placentas that fill the locule or locules of a syncarpous gynoecium. There are no groups of vascular plants known in which sporophylls bear a scattering of sporangia on the adaxial surface, so that the ancestry for laminar placentation seems very dubious.

Similar criteria militate against adoption of a submarginal position of ovules as a primitive feature of angiosperms. This hypothesis, invented by Bailey & Swamy (1951) and expounded by Periasamy & Swamy (1956) and Swamy & Periasamy (1964), has been rejected by Puri (1961). Eames (1961) regarded submarginal placentation as more primitive than marginal. He was, of course, forced to this interpretation by a conservative view of carpels with bundles distal to (more marginal than) the ovule-bearing ventral bundles. Moseley (1965, 1967) believes that orientation of ventral carpellary bundles—how many degrees they are inverted from normal orientation—offers hope for distinction between "classical" (marginal placentation) and "conduplicate" (submarginal placentation)—he evidently believes both types exist or existed. To me, the plasticity of the vascular system is relatively great, so this subtle characteristic seems a very unlikely one to be conservative, and is insufficient and too variable to serve for such an alleged distinction.

The submarginal placentation hypothesis can now be put into historical

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Figs. 17-20 —Fig. 17. *Umbellularia californica*, one flower and parts of others are shown; the 6 outer stamens, each opposite a tepal, tend to be introrse, whereas the 3 inner stamens tend to be extrorse to latrorse; note that stamens are filiform at base. From a specimen cultivated in the Rancho Santa Ana Botanic Garden. × 8. Fig. 18. *Musa cavendishii*, flower at left viewed from adaxial side, flower at right viewed laterally. Flower at right shows the large flat stamens prominently exserted, the style, shorter, in center of flower. From a specimen cultivated in Santa Barbara, California. × 2.5. Fig. 19. *Preontiodendron californicum*, flower, showing 5 stamens, united at bases; each stamen contains 3 veins. From specimen cultivated in the Rancho Santa Ana Botanic Garden. × 1. Fig. 20. *Cheirostemon* (*Cheiranthodendron*) *platanoidei* (*Sterculiaceae*), flower shows 5 stamens, united at bases, in fan-like arrangement; stigma between the anthers and front perianth segment. Each stamen contains 5 veins. From a specimen cultivated in Santa Barbara, California. × 0.75.
perspective. It was a result of discovery and description of *Degeneria* and, at the same time, the study of certain other carpels of "ranalean" plants. Indeed, the submarginal hypothesis probably would not have been invented without the carpels of *Degeneria vitensis* and of certain species of *Drimys* section *Tasmannia*—particularly the oft-cited *D. piperita*. When we look at the *Degeneria* and *Tasmannia* carpels as biological phenomena rather than primarily as histological ones, we discover some interesting features not hitherto appreciated. 

*Degeneria* has a single large carpel (Figs. 6, 8). The *Tasmannia* species *Drimys*, which are dioecious (*D. lanceolata*, Fig. 2) have fewer carpels each. In this respect there is a contrast with species of section *Drimys*, such as *D. winteri* (Fig. 1), in which flowers are bisexual but, more importantly, have numerous carpels. Carpels of *D. winteri* have restricted stigmatic areas (Fig. 3). Can this be a correlation with the more numerous carpels? Are the prominent stigmatic crests in the *Tasmannia* species of *Drimys* and in *Degeneria* compensations for the smaller number of carpels? *Degeneria* has a large number of seeds in its large, single carpel; there are only 1-3 seeds per carpel in *D. winteri*. The size of the stigmatic crest might bear a direct relationship to carpel number, carpel size, and ovule number per flower. Also, one can note that with a circle of carpels (Fig. 1), stigmatic crests would be inaccessible if they extended all the way down the ventral faces where carpels are almost in contact with each other. Maximum of stigmatic surface, as in *D. lanceolata*, may be related to dioecism, more restricted stigmas to the hermaphroditism of *D. winteri*. If these different carpellary conditions have adaptive significance, one cannot rule out the possibility that evolution of the dioecious *Tasmannia* species of *Drimys* has featured elongation of stigmatic crests.

If stigmatic crests have elongated, development of additional veins in them would not be unexpected, for veins related to large areas of exposed stigmatic papillae are typical of a number of angiosperms. Veins supernumerary to the ventral veins are claimed by Swamy (1949) in *Degeneria*, and probably do occur there, although a flower I sectioned (Fig. 8) lacked them. Occurrence of such veins characterizes a very small number of angiosperms—they are absent in many where one might expect them on the basis of the hypothesis that they are relics of vanishing margins. In fact, the physiological correlations suggested would explain the few instances of these veins, and one need not invoke a static, archival interpretation of veins.

13. The open carpel is an ontogenetic matter, and openness is not a reliable indicator of primitiveness. In essence, carpels of the vast majority of angiosperms are open, because in terms of ontogeny the typical pattern of carpel and ovary development includes origin as primordia open during early stages, closed only relatively late in ontogeny. Many angiosperms with relatively specialized features have carpels open to some degree at anthesis. Some ovaries are stipitate; this feature is probably not a primitive one.

Those who choose to regard an unsealed stigmatic passage to the interior of the carpel or ovary as a vestige of a primitive mode of construction tend to pick examples that suit their purposes, such as the carpel of *Degeneria* (Fig. 8), and to neglect those that do not. Admittedly, carpels that open during maturation of seeds, as in *Firmiana*, should not be considered pertinent. However, what of the angiosperms with carpels open at anthesis? For example, Payne & Seago (1968), who regard carpels of *Akebia* (Lardizabalaceae) as primitive in their unsealed (at anthesis) nature cite *Drimys* and *Degeneria* conspicuously, but do not mention that similarly unsealed gynoecia characterize such genera as *Sparganium*, *Hillebrandia*, *Reseda*, various *Araceae*, etc. Moreover, one wonders why, if *Drimys* primordially had stigmatic crests along the length of the carpels as in *D. piperita*, we see no trace of this fusion below the stigmatic crest in carpels of *D. winteri* (Fig. 4), *Pseudowintera*, etc. Because closure of carpels takes place ontogenetically in essentially all angiosperms, and this closure can occur at various times, even
late in fruit formation, with little or no relation to phylogenetic position, failure of closure of carpels in flowers at anthesis of a wide variety of angiosperms is understandable.

Eames (1961) cited stipitate carpels as primitive, claimed that sessile ones are specialized. Little comment by workers other than Eames has been devoted to this concept. Eames's contention is based on the alleged resemblance between the stipe of a carpel and the petiole of a leaf, a view which in turn depends on the supposition that the carpel primi-
tively closely mimics a foliage leaf. The perils of interpretation such as this seem obvious. This case exemplifies the way that morphology has been ill-served by excessively literal interpretations. Can one explain occurrence of stipitate carpels and ovaries in other terms? I believe so. The relationship of a stipitate ovary to nectaries — placement of bulky carpellary tissue out of the path of access to nectaries — seems worth exploration.

14. Various evolutionary rates can be expected among the organs within a flower, but gross differences in synchronization might be expected to be exceptional. Correlations among characters within a given plant can be abused easily in both directions: occurrence of primitive characters in a given plant tends to influence workers into reading too large a number of the other characters as primitive. The opposite tendency, that of finding too few or none at all, is represented in the literature. However, the designation of one primitive character (to agree with a given theory) in a relatively specialized plant should be avoided, unless there is good supporting evidence.

There are enough valid or probable examples of different degrees of synchronization in evolutionary rates so that any investigator can find any precedent for interpretation he wishes. For example, Sarcandra has vesselless xylem, yet flowers hardly any aspect of which could be called primitive. In this instance, rapid and sensitive adaptation to a new pollination mechanism might explain this. Likewise, a genus not often cited as primitive, Cornus, has exceptionally pri-
mitive secondary xylem, but notably specialized flowers. Understanding of what causes relatively large differences in evolutionary rates in a particular group ought to concern plant morphologists, but usually they do not explore these possibilities because they would have to develop information on a wide variety of ecological topics.

Within a given group, the most common condition is a relatively comparable degree of evolutionary advancement among the various floral and vegetative characteristics. The irreversible qualities of the major trends of xylem evolution (Carlquist, 1961) makes them good criteria against which phyletic advancement of other features within plants can be measured. We might be suspicious where only a single characteristic within a flower is considered as primitive. For example, the stamens of Degeneriaceae, Himantandraeaceae, and Magnoliaceae are claimed to be highly primitive (Can-
right, 1952), yet secondary xylem of these families is moderately specialized (Canright, 1955). Similar considerations apply to Nymphaeaceae. Of the families with vesselless and therefore highly primitive xylem (Trochodendraceae, Tetra
centraceae, Amborellaceae, Winteraceae), none of them have the laminar condition often claimed to be primitive in the Magnoliaceae and allied families.

The "ranalian" families have been anatomically investigated actively in the past two decades, notably by Bailey and his associates. Bailey, who was well acquainted with wood in these families, and who knew that in some cases primitive wood structure characterized them, was understandably interested in seeing what other features of a primitive nature might be synchronized with wood anatomy. In the many papers Bailey co-authored on these families, papers too widely cited to need repetition here, Bailey is never as explicit in the designation of floral characters as primitive or advanced as he is in designation of wood characters. Bailey's unwillingness to go on record with detailed phyletic interpretations in floral anatomy can be contrasted with the relative freedom with which Eames offered them. Bailey's
restraint very likely was based on his convictions that floral characters cannot be interpreted evolutionarily with certainty in many cases—they are reversible all too easily. Bailey probably did not wish to express any conclusion likely to be overturned later. One notes with interest the fact that of recent plant anatomists with a large output of papers, Bailey’s views have been challenged only in a relatively small number of cases.

Those who look to the “ranalean” families as a rich assemblage of primitive expressions in angiosperms often do not note the tremendous diversity in this group in expression of various characteristics. If the “ranalean” families contain primitive carpellary structure, why are other families in this group so highly specialized in gynoecial structure? If some do have primitive gynoecia, why have such structures survived? Do they represent early adaptations in which the selective value of particular features has remained the same? We need answers to questions of this nature, instead of dogmatic principles. Unfortunately, most morphologists would be more at ease in a scheme of dogmatic interpretations in which the phyletic value of any floral feature could be established and related easily to a scale of primitive to advanced. This has been the appeal of Eames and other workers, for explicitness is generally preferred to vagueness. However, these workers are too explicit and literal in interpretations.

15. Syndromes for particular pollination types might be relatively conservative, if they are extreme enough. However, many groups seem to have a versatility in pollination mechanisms, and are reversible. Anemophily produces a syndrome of rather drastic alterations and might be the least reversible of pollination syndromes:

The beetle-pollination syndrome, mentioned earlier, seems related to broad expanse of anthers and stigmas; one form of these is represented by the laminar stamen in the case of the androecium, and broad stigmatic areas can be offered by conduplicate carpels. “Ranalean” families with these particular expressions might represent early adaptations which have survived with relatively little change, perhaps because the relationship with pollinators has remained relatively constant. Beetle pollination is believed to be an early mode of pollination in the history of angiosperms (Grant, 1950a).

There is a distinct possibility that laminar stamens and conduplicate-type carpels developed several times independently and perhaps were not even present during origin of angiosperms.

Numerous parts in flowers has been stressed as a primitive feature in angiosperms. This characteristic may be related to beetle pollination. Not only do numerous stamens and stigmas offer broad targets for crude pollinating agents, they can also offer sacrificial tissue on which beetles (or other insects) could forage. This suggests that adaptation to beetle pollination might involve either preservation of numerous parts or increase in number of parts. The latter has undoubtedly occurred in some beetle flowers—but which? Do Magnoliaceae represent an increase in number of parts? If a flower of Drimys or Bubbia is taken to represent a more primitive condition, Magnolia would clearly represent increase in number (and size) of stamens and carpels.

The presence of large numbers of sclereids in carpels (Zygogynum, Galbulimima, Degeneria) might represent structures to deter predation. Likewise, the position of carpels in Calycanthus (Fig. 9), Eupomatia, and other “ranalean” genera might represent protection of ovules against foraging beetles, in accordance with the theory of Grant (1950a).

We need not hypothesize relictual preservation of a single method of pollen presentation in “Ranales”—the original one, if it is still extant, would be difficult or impossible to identify. Structures related to beetle pollination are not only quite diverse within the “ranalean” families, they have been evolved many times within angiosperms, including even Asteraceae; a single original adaptation to beetle pollination, even within the primitive families, seems unlikely.

Plant anatomists tend sometimes to analyze one floral structure independently of the others. Because the entire
flower is a unit involved in pollination and dispersal, individual organs cannot be studied in an isolated fashion for meaningful results. Wind pollination is a case in point, for nature of stamens and pollen is one aspect, but nature of perianth is obviously also part of this syndrome, as is condensation of inflorescence, reduction in flower size, increase in number of flowers, etc. Where so many concomitant and deep-seated changes are involved, irreversibility becomes a strong possibility. Some plants (e.g. Lithocarpus) seem only part-way toward anemophily, however, and thus potentially are reversible. The one clear instance of evolution of entomophily from anemophily, Dicrornena, is an obvious exception to the usual trend from entomophily to anemophily. It should probably be considered a secondary level of entomophily, not a reversion to entomophily.

Because of the relative irreversibility of the wind-pollinated syndrome, groups which became anemophilous relatively early in the history of the angiosperms have probably continued in this condition intact. Some angiosperms may have been static for a long time, and the beetle-pollinated syndrome may not be the only static mode, or may not be nearly as static as the wind-pollinated syndrome.

16. Dispersal syndromes influence floral anatomy and must be taken into account when analyzing vascularization and ontogeny. Texture and size of carpels relate to dispersal mechanisms, and nature of venation bears relationship to texture and size. Degree of carpel cohesion, adnation to receptacle, etc., are also related to dispersal mechanism in many cases, and venation must be expected to be present in relation to these adaptations. Elongate receptacles, stipitate ovaries, etc., may bear relationships to dispersal mechanisms.

No one can seriously contend that exceptionally long receptacles, as in Myosurus (Ranunculaceae) or Magnoliaceae are a primitive feature. In Magnolia (Fig. 16), display of large seeds hanging on fibrous funicles relates to arrangement of carpels on an elongate axis. In Liriodendron (Fig. 13), a totally different fruit-type, Samaroid carpels, is served by the elongate receptacle form. There is no reason to believe that either Magnolia or Liriodendron represents the primitive dispersal type in angiosperms.

One of the ironies inherent in recent investigations of "ranalean" carpels is that venation has been analyzed with little regard to the dispersal mechanism of a given species. Presence of numerous veins in carpels such as those of Drimys has tempted some to regard these carpels as more leaf-like and therefore more primitive than, say, those of Ranunculus. Such differences are those of a larger, fleshy fruit versus a small, dry achene. Likewise, the presence of additional veins in more than one series in some larger carpels should never have been interpreted as evidence for "gonophylls" (see point 5 above). We need exploration of the relationship between fruit type and venation; the relationship is, in fact, probably a rather exact one. Because we know that fruit types can change easily in angiosperms and are interconvertible, the likelihood that veins in fruits can be interpreted as vestiges is a very poor one. Because carpel veins are simply precursors of fruit veins, conservatist views of carpellary veins must be viewed skeptically.

17. Phylogenetic and taxonomic positions of genera are important in analysis of phylleis of anatomical characteristics. Few anatomists have devoted sufficient attention to matters of relationship. A number of points in even the best classification systems are still dubious and controversial. There is, however, no value in comparing anatomical results with outmoded classification systems — or no systems at all. Anatomists should strive to demonstrate relationship; the tendency of too many studies is to state that genera studied are exceptionally isolated.

Studies on floral anatomy often show selection of materials based on availability, rather than pertinence, or whether species or genera form a series on the basis of gross morphology, or whether gross morphology suggests particular taxa to be rich in primitive or specialized features. One good example of failure in this regard is the development of
ideas concerning the crucifer gynoecium. Most papers which dealt with this topic analyzed whatever crucifers were available, regardless of whether they were typical or exceptional, in which subfamilies of Brassicaceae they were located, or what modifications particular genera might show for dispersal mechanisms. Until the relatively recent work of Puri there was no effort to introduce to crucifer studies two families known to be closely related to Brassicaceae: Capparaceae and Moringaceae. Instead, in many of the crucifer gynoecium papers, we find repeated mentions of Papaveraceae, and comparisons of poppies with crucifers. In fact, Brassicaceae, Capparaceae, and Moringaceae are probably not at all related to Papaveraceae (Thorne, 1968). If this is true, comparisons between these two groups were largely a waste.

If one is investigating a particular taxon, viewing putatively related taxa may be quite time-consuming, and is difficult to do in a meaningful fashion. Comparative studies of this sort can, if not handled carefully, could be overwhelmed by an excess of data, and require excessive time in performance. At the other extreme, however, meaningful comparisons can easily be missed if too few comparisons are invoked.

Studies on "ranalian" families have, in recent years, tended to avoid comparisons with "non-ranalian" families. Because quite primitive wood structure can be found in such "non-ranalian" families as the woody Saxifragaceae ("Hydrangeaceae", etc., of some authors), Theaceae, and others, we might better search from primitive floral characteristics outside of "Ranales" in the future.

The "broadened outlook" advocated by Bailey (1949) has been greeted with approval by morphologists, largely because most think they are already employing "broadened outlooks". Where taxonomic groups are concerned, relatively few anatomists are "broad"; one can be sympathetic to this, for a grasp of numerous anatomical characters within particular plants and then also throughout angiosperms is very difficult to acquire, if not literally impossible. However, one ought to be skeptical of conclusions in anatomical studies which invoke only a limited comparison to putatively related groups. The significance of any anatomical structure depends on its systematic distribution—we must know whether it occurs only in a single taxon and has only a special significance, or whether it might be part of a phylogenetic series, or whether the structure is merely an aberrant formation.

The fact that plant anatomists often feel ill at ease in dealing with taxonomy and phylogeny may explain why they often express their results in term of differences rather than similarities. One should not be surprised that genera regarded as distinct (but related) by taxonomists should differ in anatomical respects. When such anatomical features are discovered, this is no reason, per se, to regard the genera as more isolated than hitherto. Using anatomy to demonstrate relationships is the rarer skill, evidently.

18. Evidence for the classical theory of the flower may seem to be diminished by acceptance of the above critique. Evidence for other theories, however, would be reduced even more greatly by this critique. The classical theory, if vaguely worded, remains better supported than other theories, mostly because it is simpler, and does not require complicated hypothetical stages or morphogenetically unlikely processes for explanation of floral structure. The plasticity of angiosperms makes unlikely our ever having a great deal of solid evidence concerning phylaxis of floral structure. The classical theory can be supported by such features as the fact that the plan considered basic in it seems widely distributed and common in angiosperms considered relatively primitive in other respects, such as wood structure and pollen morphology. The classical theory was developed in terms of gross morphology originally; anatomical studies, if they do not aid in a detailed way, clearly do not negate the classical theory, unless we misinterpret them:

If we look at the alternative hypothesis, such as those of Lam, Meeuse,
Melville, etc., we see that they originate in response to several factors:

(a) Particular plants with certain exceptional morphological features are stressed by a particular author, and soon these modes of structure were regarded as basic types to which other angiosperms must be compared, from which they must be derived.

(b) The overliteral interpretation of floral anatomy by adherents of the classical theory has been apparent to some workers, who seem to view this as a weakness of the classical theory; it is, of course, only a weakness of uncritical morphologists.

(c) Various morphologists have undertaken ontogenetic studies (or other "new" approaches), and have stressed these, often using them as a way of contrasting themselves and their findings with morphologists who rely on other techniques.

(d) Morphologists, annoyed or frustrated by the enormous diversity of structure in angiosperms, have sought simple keys—keys which prove overly simple. Because good proofs of floral phylesis are lacking, a morphologist who wishes to propound a new theory cannot be discredited definitively—only by failure to secure adherents. He can always say that his theory was a "useful" one ("useful" to what or whom not indicated).

(e) Morphologists have been annoyed or frustrated by the lack of evidence linking angiosperms with other vascular plants, and have sought to construct floral theories whereby plants other than angiosperms could be shown morphologically to relate to angiosperms.

To me, all five of the above reactions are unsatisfactory, because by their nature, they tend to see a vacuum in our evidence about angiosperms, and fill it not with evidence, but with imagination. They substitute for the classical theory various theories of a more complex and fantastic nature. I have chosen to criticize adherents of the classical theory and question interpretations of "ranalian" flowers precisely because we are in danger of converting some overly literal interpretations into widely-accepted canons (e.g. viewing the Degeneria carpel or Degeneria stamens as primitive in all respects). If this happens, a simple and logical hypothesis can be subjected to eventual destruction because of the excess enthusiasm of its adherents.

Considerable damage to science can be done under the most plausible slogans. "Broadened outlook" is just such a slogan. If vascular anatomy of flowers is not, with certain exceptions, good evidence of phylesis, if ontogenetic stages are not good evidence of phylesis, are we in fact exhibiting a "broadened outlook" when we deem such data as usable evidence? A problem is not solved if misinterpreted data is added. The best interpretation of a "broadened outlook" might, in fact, be "a more critical outlook", and I suspect this is closer to what Bailey had in mind when he utilized that much-quoted phrase. One who knew the pitfalls of morphology as Bailey did might well have thought that the "broader"—the more broadly informed—one is, the more critical and therefore the more accurate one will be. I am sure that Bailey would never have endorsed the accumulation of data or the accretion of new techniques unless supervised by a critical and selective intelligence.

19. One common source of error in various theories of floral structure is fixation upon a particular pteridophyte or gymnosperm group (usually a fossil group) as a probable ancestor. The characters of that group are then, by means of appropriate diagrams, converted into whatever the author of such a theory believes to be a "primitive" angiosperm. The number of theories conceivable in this fashion is virtually endless, but none of them can be expected to have anything more substantial than an emotional conviction and a series of ingenious diagrams:

The ease of manufacturing myths concerning floral phylesis has made possible the proliferation of the theories we
see today. Part of the problem is the result of our lack of any obvious angiosperm ancestors in the fossil record. Morphologists seem to be piqued by this, and feel that such ancestors are, in fact, there, and once they find what they believe to be pre-angiosperms, then of course they can find angiosperms to simulate those ancestors.

If we assume a generalized flower along the lines of Annonales, Theales, and Rosales, such a type quite conceivably could have existed and left no macrofossil trace. If such a type of primitive flower were derived from a similar-appearing pre-angiosperm, that pre-angiosperm would by definition be called a seed fern (in the broad sense of the term "seed fern"). Types of organization in seed ferns (sensu lato) were so varied that we can easily imagine hypothetical angiosperm ancestors within that group. If we retain a vague framework of this sort, a rational approach can be obtained. Attempts to describe or find more precise ancestors will probably fail, barring a genuine breakthrough in paleobotany.

20. Taxonomic distinctions are one entirely acceptable application of data from floral anatomy. Even if the functional relationships of vascular bundles or their adaptive nature cannot be determined, applications of consistent differences in pattern or histology to the taxonomic system are legitimate and needed.

Recent work in the United States has featured chiefly work of taxonomic appli-
cability. Perhaps there is a subtle realization that evolutionary interpretation of vascular anatomy has been overextended by its more enthusiastic practitioners, and that taxonomic objectives may be the best products of studies of floral vascularization at present. Notable in this regard are papers by Eyde (e.g. 1966, 1968), and Palser (e.g. 1963; Palser & Murty, 1967). These workers evidently feel the desirability of adding to data from floral vasculature other types of anatomical data: floral histology, pollen, wood anatomy, etc., in order to present a broader assemblage of taxonomically usable material.

21. Data from teratology is not useful in the study of evolution of flowers. The use of teratological examples is a form of wish fulfillment: Whatever form one claims as a hypothetical normal form in a morphological series can be found in the realm of teratology sooner or later. The designation of particular teratological forms as morphologically significant can only represent a kind of intuition:

The majority of workers have rejected the use of teratology in evolutionary morphology, but some individuals still feel some attachment to the use of such forms. This attachment is essentially an emotional conviction, and such individuals are not likely to be persuaded against teratology. In the case of floral anatomy, application of teratology to issues already controversial can only do harm.

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