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TRIBAL INTERRELATIONSHIPS AND PHYLOGENY OF  
THE ASTERACEAE

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## INTRODUCTION

Although smaller families of angiosperms may yield to classification problems readily, the family Asteraceae has posed unusual difficulties for plant taxonomists and phylogenists. It is either the largest family of angiosperms, as Bentham (1873) claimed, or, should Orchidaceae prove to be larger, at least the largest family of dicotyledons. Correlated with its large size are its excellent dispersibility, its explosively rapid evolution, its array of numerous instances of parallel evolution within the family, and its capability for colonizing and adapting to a wide variety of ecological habitats in a weedy fashion (Burt, 1961). The consequences of these characteristics are manifold, and the psychological reaction of the plant taxonomist is appropriately laden with blockages. For example, this "most natural" of all families of angiosperms (Bentham, 1873) continues to be subjected to splitting into two (e.g., Cichoriaceae) or more families, although those who do this do not all seem to regard the family as polyphyletic. Segregate families are still ranged beside each other in classification systems. The unity of Asteraceae can be cited on numerous bases, and continues to be emphasized, most notably and recently by Fairbrothers et al. (1975), who have found sesquiterpene lactones throughout the family.

The parallelisms pandemic in Asteraceae have led taxonomists to seek one or several conservative characters, often without any basis but intuition, and to deduce lines of relationship and specialization accordingly. Parallelisms must not be mistaken for polyphyletic origin of the family. There is no convincing evidence that Asteraceae is a polyphyletic group, but there is evidence that particular characters have shown similar shifts two or more times. For example, all-ligulate heads of flowers have evolved in the mutisiad *Glossarion* (Carlquist, 1957c) as well as the tribe Cichorieae. There is no evidence from fossil pollens yet that the family is earlier than Miocene (Germeraad, Hopping and Muller, 1968; Muller, 1970). Macrofossils appearing to be capitula have been claimed from Oligocene (see Small, 1919, and Cronquist, 1955), but such a fossil as *Paleanthus problematicus* from the Cretaceous of New Jersey (Newberry, 1896) is very likely not a composite but a cycadeoid inflorescence.

Probably no single character within the family is free from parallel

evolution. For example, styles and stigmas like those of Senecioneae may be found in heleniad Heliantheae (Carlquist, 1956) as well as in other tribes. *Fitchia* has stigmatic branches fused nearly to their tips, as do most Mutisieae (Carlquist, 1957c), yet *Fitchia* is clearly a member of Heliantheae (Carlquist, 1957b). Raylessness has evolved many times in tribes that are undoubtedly primitively radiate, but that does not indicate affinity among the rayless genera. These examples are obvious ones, but more subtle parallelisms occur and must be taken into account. One should not be surprised that taxonomists have avoided grappling with larger groupings in this worldwide family, only a fraction of whose species are known to the most astute botanist. The more one searches for "reliable" or "conservative" characters whereby to delimit tribes or demonstrate phyletic, the more one finds exceptions. The alternatives available to the taxonomist or phylogenist are virtually all untenable.

The most rational option that workers have followed is the construction of natural groupings of genera based on a critically sifted analysis of as many characters as possible (the "sifting" involves perception of parallelisms). Cassini's (1834) division of Asteraceae into tribes has persisted to the present day. Obvious to the student who views Cassini's work is his method of discerning fundamentally distinct genera (distinct by virtue of a number of characters), then ranging around these tribal "types" genera similar in most or many of these features. This process, not unlike that of numerical taxonomy and computer-formed dendrograms, is an obvious starting point. This method fails where parallelisms are not perceived, where genera are transitional between tribes (and are perhaps, therefore, "non-missing links"), or where salient aberrant characters have been evolved (e.g., *Adenocaulon* or *Coulterella*).

With respect to structuring phylogenies within Asteraceae, pitfalls are also difficult to avoid. One must remember that characters, not genera or tribes, are primitive. For example, I have been misquoted to the effect that I believe Mutisieae to be the primitive tribe of Asteraceae. I believe that there are a few genera of Mutisieae with a large number of characters primitive for the family, but that does not make those *genera* primitive—they also have some specialized features. Even if those mutisioid genera have numerous primitive features, calling Mutisieae a primitive tribe is a misconception. Yet in more than one phylogenetic treatment of Asteraceae, characters alleged to be primitive are listed, and the discerning reader of those studies can identify the genus that contains all of these features. Thus, a "primitive genus" has been selected, and characters and their modifications read out accordingly. The circular reasoning in this method is obvious. However, if one attempts alternative methods to designate primitive or specialized features, one cannot cite thoroughly reliable criteria. Related families could furnish suggestive criteria—if we were certain of which families were related to Asteraceae and which characters in those families are primitive. Consensus and tradition are insufficient grounds for acceptance of either taxonomic treatments or phylogenetic sequences. However, lines of evidence such as anatomy, palynology, and cytology are now sufficiently developed so that a new summary can be made. I am presenting my thoughts on the

family because the past two decades have seen considerable work published on Asteraceae, because I have an interest as a result of the cumulative experience of my own research in the family, and because my esteemed colleague, Dr. Robert F. Thorne, has urged me to summarize my thinking. Indeed, he and I are in close agreement with regard to the conclusions below. I did, in fact, propose a sort of phylogenetic summary of the family (1961, pp. 135–140). However, that summary seems to have escaped notice because it is embedded in a book on plant anatomy.

### GROSS MORPHOLOGICAL CHARACTERS

*The pollen presentation mechanism: styles.*—Bentham (1873) quite rightly cites style-branch morphology as tribal characteristics, while noting that exceptions or ranges of character expression occur in virtually all of the tribes. The range in style features within the family as a whole can be summarized as follows (tribes cited as examples do contain exceptions):

- (1) Style branches long (Vernonieae, Cichorieae, Eupatorieae), of medium length (Astereae, Heliantheae, Senecioneae, Inuleae), or short, branches fused nearly to the tip (Anthemideae, Arctoteae, Calenduleae, Cardueae, Mutisieae).
- (2) Stigmatic hairs covering the entire inner surface of the branches (Cichorieae, Cardueae, Eupatorieae, Heliantheae, Vernonieae) to restriction of stigmatic hairs to marginal bands (other genera of Heliantheae; other tribes).
- (3) Pollen-collecting hairs on the outer surface of style branches prominent (e.g., some Vernonieae) to hairs sparser (e.g., some Cichorieae).
- (4) Pollen-collecting hairs scattered on the outer surface of the style branches (Vernonieae, Eupatorieae, Cichorieae) to hairs localized at the tips of branches (Senecioneae, Anthemideae) or in a ring below the forking of the branches (Cardueae, Arctoteae) or restricted to the deltoid tips of the branches (Astereae, Calenduleae, Heliantheae).
- (5) Style branches acuminate (Cichorieae, Vernonieae) to acute (Astereae, some Heliantheae) or clavate (Eupatorieae, Inuleae) rounded (Arctoteae, Cardueae, some Mutisieae) or blunt (Anthemideae, Senecioneae).

The prevalent view is that the vernoniad-type style is primitive (e.g., Cronquist, 1955), in that it shows the least "modification" or localization of functions on particular portions of the style: long acuminate branches bearing collecting hairs scattered on the outer surface above and below the point of bifurcation, with an even coating of stigmatic hairs on the inner surfaces of the branches. I tend to agree with this. However, I wish to stress two points that have escaped mention in literature on Asteraceae:

- (1) There is undoubtedly reversibility in all of the features cited above, and different style types can coexist in a single head. For example, in *Chaptalia nutans* Hemsl. (Mutisieae), the female marginal flowers



have vernoniad-type styles, whereas the bisexual flowers have short, nonspreading rounded style branches. The latter type characterizes heads of Mutisieae which primitively lack differentiation among flowers of a head (e.g., *Stenopadus*, *Hesperomannia*).

- (2) Style branch length and morphology are integral parts of the floral biology of a species. For example, the style dimorphism cited above for *Chaptalia nutans* suggests that the styles of female flowers expose maximum areas of stigmatic hairs, whereas the styles of the bisexual flowers are more efficient, by virtue of their knoblike tips, at pushing masses of pollen out of the tube of united anthers, exposing it to a pollinator at the anther tips. This dimorphism would tend to retain the seed-setting capacity of all flowers while offering possibilities for outcrossing. More drastic differentiation can be found in styles of Asteraceae with all-female and all-male heads (e.g., Ambrosinae of Heliantheae), but degrees of style dimorphism are common in all the radiate tribes (Asteroideae of this study), where ray flowers are usually female (occasionally bisexual, as in *Wyethia*) and disc flowers are usually bisexual (occasionally male: some Inuleae). Some illustrations of style dimorphism are offered by Uexküll-Gyllenband (1901).
- (3) The forms of style branches are, in close correlation with the above statement, adapted to particular modes of pollination and, more significantly, genetic systems. The mode of self-pollination of flowers of Asteraceae in which style branches recurve so as to pick up pollen from the collecting hairs is well known. On the other hand, selfing may occur if style branches are short and some pollen grains fall into the cleft of the style as it elongates, while the remainder of the pollen remains on collecting hairs and is available for outcrossing (some Anthemideae).

With respect to this last point, I was struck by the fact that the styles of *Fitchia* and *Stenopadus* (genera one would expect to possess outcrossing ability) are long, but have short branches that open only a little. If the vernoniad style is primitive, *Fitchia* (Heliantheae) and *Stenopadus* (Mutisieae) must represent a modification, exhibiting fusion of the style branches. These short segments do bend outward in late anthesis in *Fitchia*, at least. During early anthesis, however, the style branches are appressed to each other. Thus, there is a strong possibility for outcrossing, with only a moderate amount of selfing. Stress on outcrossing as opposed to autogamy would be expected in evolutionary lines of considerable longevity. The risk to such populations is that the small area of stigmatic tissue exposed may result in failure of many flowers in a head to be fertilized. Indeed, heads of *Fitchia speciosa* Cheeseman do show a rather low seed set (original observation, based on a population of *F. speciosa* near Honolulu). However, lowered percentage of seed set and exogamy is typical of trees of stable forest, such as *Fitchia*, whereas autogamy is characteristic of weedy annuals. *Helianthus annuus* L. has the capability for both outcrossing and, by virtue of style-branch recurvature, autogamy, and this flexibility is undoubtedly

related to its genetic variability and weedy capabilities. Such wind-pollinated weeds as *Ambrosia*, with unisexual heads, achieve high seed set by great abundance of pollen, coupled with prominently exposed style branches.

Broadening of style branches, as in Anthemideae, Calenduleae, Eupatorieae, Heliantheae, and Inuleae, would tend to have the effect of maximizing both pollen-presenting and pollen-receiving surfaces. Likewise, distribution of stigmatic hairs in marginal bands, which tend to receive pollen grains on the sides of the branches, not just on their inner surfaces, would result in greater accessibility of receptive surfaces. Aggregation of flowers in a capitulum results in a high probability that an insect will visit several flowers in a head before moving on to another head, and thus exogamy tends to occur. This can be seen when an insect bearing pollen lands on a radiate capitulum, visiting a ray flower (female) first, thus tending to pollinate the ray flower with pollen from another head, a head either on the same or a different individual plant. When one considers that only a single ovule per flower can be fertilized, and thus only a single pollen tube per flower is required for fertilization, Asteraceae show remarkable maximization of pollen presentation and pollen reception. This feature tends to lend itself to insuring pollination of all flowers in a head (e.g., as an insect traverses the capitulum) if the species is not self-sterile, and achieves the high fertility characteristic of weedy species.

Bisexual flowers of Asteraceae are protandrous. This, coupled with the variations in style morphology, forms the basis for great flexibility. In the case of a radiate head, the ray flowers may be receptive before disc flowers, and are available for outcrossing at that time. The sequence in anthesis from outside to the center of a head makes probable that outermost flowers in a head will be fertilized by pollen from another head, whether they are ray or disc flowers. As the capitulum ages, the innermost flowers finally become receptors only, and thus would also tend to receive pollen from another head. On morphological grounds only (Uexküll-Gyllenband, 1901) the opportunities and modes for various degrees of exogamy and autogamy (neglecting genetic factors for self-sterility) are numerous. Highly flexible genetic systems coupled with high fertility are keys to the evolutionary success of the family.

*Anthems*.—Variations noted by Bentham (1873) and others include the following ranges:

- (1) Anthers with long distal appendages (stamen tips) to anthers that lack any extension of the connective beyond the anther sacs.
- (2) Anthers with long tails at the bases of anther sacs (Mutisieae, Cardeae) to anthers with no appendages on anther bases.

Here again, the tribes show modalities in both of these features—modalities sometimes useful for taxonomic purposes. However, the nature of stamen tips probably represent portions of a pollen-presentation system. A circle of long anther tips would serve as a deep cup of pollen grains at an early stage in anthesis, and would lend itself to precision in pollination. Very short or no stamen tips would tend to result in scattering of pollen by an insect from one

flower to another. *Achillea* (Anthemideae), in which flat corymbs of heads are known to be beetle pollinated, benefits from broad pollen-presenting surfaces unhindered by intrusions by stamen tips. The length of stamen tips also tends to be related to flower form, with longer stamen tips more common in flowers with long, narrow corollas. A tall cup formed by stamen tips would tend to make pollen more accessible to a pollinator than would pollen recessed deep within a flower. Length of anthers is also roughly proportional to length of corolla.

Similar considerations apply to basal appendages on anthers. The action of these during opening of a flower does not seem to have been described adequately, and the assumption one would gain from the literature is that they are passive parts of the flower. However, tailed anthers show a high degree of correlation with long, narrow flowers (Cardueae, Mutisieae), whereas tailless anthers occur in shorter, cuplike flowers. One can speculate that anther tails function in position of anthers during anthesis, as in Ericaceae.

*Involucre*.—An involucre consisting of numerous spirally arranged imbricate bracts characterizes the vast majority of Asteraceae. Exceptional are Senecioneae, most genera of which have a single cylinder of bracts, sometimes connate, and a few Heliantheae (Lagasceinae; outermost receptacular bracts of Madinae; a few "heleniad" genera). The Madinae are interesting in the cylinder of outermost receptacular bracts between ray and disc flowers (receptacular bracts may also be present throughout the head, as in *Hemizonia*). *Raillardella* was not recognized as a member of Madinae because in all but two rare species, ray flowers are lacking, but in those two species they are present outside the cylinder of bracts, certifying the genus as a member of Heliantheae subtribe Madinae rather than Senecioneae (Carlquist, 1959a). A similar situation occurs in the madinean genera *Wilkesia* and *Dubautia* (including *Raillardia*), so that the apparent involucre of the discoid heads consists of receptacular bracts only.

There seems no special selective advantage of the *Senecio*-type involucre over the imbricate type overwhelmingly predominant in the family. Both types show equal capability for reflexing in fruit, so that functionally they are equivalent. Although Small (1919) argued for primitiveness of senecionean features within the family, no other author has seriously considered the senecionean involucre anything but a specialization, and even in Senecioneae, some genera (e.g., *Tetradymia*) show overlapping or imbrication of bracts of the single cycle, so that the single cycle of connate bracts is probably not primitive even within Senecioneae. If indeed the spiral of involucre bracts is primitive in Asteraceae, one can say that a primitive feature has been retained in all but a few genera. One may also note that within the involucre, spiral phyllotaxy is continued in arrangement of flowers, even in Senecioneae. If spirally arranged involucre bracts are primitive in the family, as seems highly likely, it may be an expression of alternate leaf phyllotaxy as primitive for the family as well (Leonhardt, 1949).

Tribal characteristics involving the involucre are few; one can cite the scarious-margined nature of involucre bracts in Anthemideae, however.

The presence of receptacular bracts ("paleae") is of considerable signifi-

cance. Intergradation of involucre bracts into receptacular bracts would be expected to be a primitive feature in Asteraceae. Bracts subtending individual flowers in an inflorescence are all but universal in angiosperms. However, retention of bracts within a capitular inflorescence depends on selective value: in Dipsacaceae, for example, bracts are hooked and serve in dispersal.

Heliantheae contain a large number of genera with receptacular bracts. This is doubtless one of the prime reasons why such authors as Cronquist (1955) regard Heliantheae as a "primitive tribe." However, many helianthids lack receptacular bracts, notably the genera formerly segregated as the tribe Helenieae. More significantly, receptacular bracts occur in certain genera rich in primitive features in other tribes. For example, *Stenopadus* and *Stomatochaeta* (Mutisieae) have slender vascularized receptacular bracts that almost certainly must be regarded as vestiges of a primitive condition (Carlquist, 1958a). *Wunderlichia* (Mutisieae) has bristlelike receptacular bracts. Some genera of Cardueae have vascularized receptacular bracts (Napp-Zinn, 1956). In Vernonieae, *Bolanosa*, *Centauroopsis*, *Diaphractanthus*, and *Heterocoma* have well-developed receptacular bracts (Hoffmann, 1890; Augier and Du Merac, 1951). A few Anthemideae have vascularized receptacular bracts (Napp-Zinn, 1956), and receptacular bracts can be found in the subtribe Bupthalthinae of Inuleae. Even Small (1919) concedes the primitiveness of presence of receptacular bracts in Asteraceae, but is confounded by attempting to reconcile this with the supposed primitiveness of features of Senecioneae. He can cite only *Raillardia* (= a section of *Dubautia*), which is clearly helianthid, not senecionean (Carlquist, 1959a), a teratological head of a *Senecio* found on an herbarium specimen, and a few species of *Senecio* with sparse bristles on the receptacle.

In the tribes other than Heliantheae, presence of receptacular bracts can be regarded as a primitive and relictual feature with little negative selective value, so that bracts have persisted. In Heliantheae, receptacular bracts are more prominent. Although a primitive feature, receptacular bracts in Heliantheae may be well developed because they have been integrated into the dispersal mechanism (or other aspects of floral biology) of the capitulum. For example, heads of some Heliantheae may not reflex at maturity, but instead shatter (*Coreopsis*, *Fitchia*), and receptacular bracts may aid in separating fruits which might otherwise cling together. In heads of other Heliantheae with receptacular bracts persistent on the receptacle, dispersal of fruits may be by a shakerlike mechanism, perhaps aided by pecking motions of birds as well as the jostling in windy conditions. Where the dispersal mechanism in Asteraceae is by a reflexed circle of pappus bristles, as in Astereae, Cichorieae, etc., presence of receptacular bracts would interfere with dispersal and thus would be of negative selective value. Contributions concerning dispersal biology by Burt (1961) and Zohary (1950) are noteworthy, particularly because they combine morphology with flowering habits and dispersal mechanisms. Field studies are much needed in regard to interpreting morphology of fruits. In some cases, the significance is obvious, as in the fruits of *Chrysanthemoides monilifera* L. (Calenduleae), which have a fleshy brown exocarp and which I have seen eaten by birds.

The calycine nature of pappus was long ago established (Lund, 1872),

although confirmation has come subsequently (Carlquist, 1957b; Ramiah and Sayeeduddin, 1958). Most interesting in this regard is the work of Sattler (1973), who demonstrates five pappus primordia, alternating with corolla lobes, in both *Tragopogon* and *Tagetes*. Presence of five pappus primordia in *Tragopogon* is particularly noteworthy, because the mature pappus consists of numerous bristles in which neither pentamery nor alternation of five bristle groups with corolla lobes is evident. The idea that pappus is a secondary structure and not calycine (e.g., Small, 1919) is definitely not supported.

Asteraceae can be characterized as a pioneering group, often found on widely scattered sites of a disturbed nature. Excellence of dispersal is a requisite for a pioneering group to reach these sites. To be sure, the family has invaded "old, stable habitats," but probably secondarily, and loss of dispersal has often occurred accordingly (Carlquist, 1974). However, the likelihood seems to be that early in evolution of the family, evolution of a superior dispersal mechanism was linked with explosive spread and rapid radiation. Thus, conversion of calyx into bristles or scales that show little resemblance to typical calyx is an adaptation that one would expect to have occurred rapidly in early representatives of the family. Also involved in this modification is the fact that with the development of an involucre, the pre-anthesis protective function of a calyx has been superseded. The loss of calycine appearance of pappus in the vast bulk of the family is therefore quite understandable. The occurrence of calycine features in helianthad genera such as *Wyethia*, *Lagascea*, and *Fitchia* (Carlquist, 1957b) may well be relictual, but if so, one must not expect these composites to be primitive in all features; for example, *Lagascea* has one-flowered heads grouped in capitula of the second order.

*Foliage*.—The majority of Asteraceae have alternate leaves, although genera with opposite leaves may be found in scattered genera in most of the tribes (for figures, see Bentham, 1873). There is a preponderance of opposite leaves only in Eupatorieae and in some subtribes of Heliantheae. Cronquist (1955) probably considers opposite leaves primitive for the family on account of his tendency to consider characters of genera in Heliantheae, subtribe Verbesininae as primitive and also because of the opposite-leaved conditions in families he considers to be related to Asteraceae (Rubiaceae, Dipsacaceae, Valerianaceae). However, I believe that in agreement with Leonhardt (1949) we may consider alternative leaves as primitive instead. Some will say that there can never be any "hard evidence" on this point. Seedling phyllotaxy is also inconclusive. At best, it would indicate opposite leaves as basic to a few subtribes (e.g., Coreopsidinae and Madinae of Heliantheae), but not for the family as a whole.

No constant foliar conditions can be cited as tribal characters, only "tendencies" with numerous exceptions (e.g., highly dissected leaves in many Anthemideae; prickly leaves in most Cardueae).

*Growth form*.—Because most botanists live in areas where herbaceous composites are abundant, they have an impression of the family as quite herbaceous. However, the family as a whole has an aspect of great flexibility with

respect to growth form and degree of cambial activity and therefore woodiness. I have postulated (1966b), based on anatomical reasoning and on familiarity with genera from various tribes that a shrub or subshrubby form might be primitive for the family. There are a number of trees in the family, trees with quite normal woody appearance (one must not be misled by the often-mentioned Afroalpine *Dendrosenecios*, which have a special growth form that is undoubtedly derived from herbaceous ancestry). However, arborescence has probably been evolved many times independently in the family, just as the annual habit has. If one agrees that the family as a whole had a shrubby or subshrubby ancestry, a number of the tribes appear nevertheless to be radiations based on herbaceous stocks. For example, Cardueae is overwhelmingly herbaceous, and I doubt seriously that anyone would wish to derive this tribe from the rosette trees *Centaurodendron* and *Yunquea* of the Juan Fernandez Islands or from the Canary Island species of *Centaurea*. The same holds for Cichorieae. The Juan Fernandez rosette trees (*Dendroseris* sensu lato) appear clearly secondarily woody, whereas relictual genera suspected as primitive in numerous respects, *Dubyaea* and *Sorosieris* (Stebbins, 1940) or *Scolymus*, *Hymenonema*, and *Hypochoeris* (Stebbins, 1953) are clearly herbs as are most other Cichorieae. If, as Stebbins (1953) contends, *Scolymus* tends to link Cichorieae, Cardueae, and Arctoteae, these three tribes probably arose from an herbaceous ancestry. Calenduleae appear to be an offshoot of Senecioneae, as claimed by Cronquist (1955), and seem basically herbaceous. The only shrubby genus, *Chrysanthemoides*, has successive cambia (Carlquist, 1966a) and a determinate growth form (the first-formed inflorescence terminates growth of the main stem, and so forth with lateral branches, so that no "leader" shoot develops). These characteristics suggest secondary woodiness for *Chrysanthemoides*. The remaining tribes (Astereae, Eupatorieae, Heliantheae, Inuleae, Mutisieae, Senecioneae, and Vernonieae) appear to stem from at least somewhat woody ancestors. The great flexibility of Asteraceae in evolving herbaceousness or increased woodiness is undoubtedly one of its reasons for evolutionary success. Such tribes as Anthemideae and Senecioneae show how easily more woody or less woody growth forms can be evolved.

### ANATOMICAL CHARACTERS

*Pollen*.—Earlier work on pollen of Asteraceae showed them to be characterized by tricolporate echinate sphaeroidal grains with a transverse furrow in the endexine perpendicular to each colpus, and with a tectate exine. Variations on this pattern proved to be many and diverse (see especially Wodehouse, 1935, and his earlier papers cited therein; and Erdtman, 1952). However, the basic type described above can be found in all of the tribes. Detailed studies of pollen of some additional groups are now available, such as those of Wagenitz (1955) on *Centaurea*, Payne and Skvarla (1970) on *Ambrosia*, Liens (1968, 1971) on Inuleae, and Tomb et al. (1974) on Cichorieae.

However, surveys of exine layers in the family have been presented, such as that of Stix (1960), and the details have been rendered more precise in



the survey of Skvarla and Turner (1966a). These studies have had as a goal the elucidation of variation in exine structure and its application to the taxonomic system. In fact, they reveal an enormous amount of diversity. My own preference would be for ultrastructural surveys based on nonacetylated grains. However, the structural modes shown would probably not be altered appreciably. Studies with transmission electron microscopy (Skvarla and Turner, 1966a) have shown that an endexine, which may or may not be lamellate, is present. Between endexine and ectexine a space, termed the cavus, is present in most species studied. The cavus appears to be a harmomegathic device to accommodate changes in pollen grain volume (Payne and Skvarla, 1970), changes greater than the colpi can accommodate. Some species apparently lack cavi: *Moquinia velutina* Bong., *Artemisia cana* Pursh, *Liabum caducifolium* Robinson & Bartlett, and *Vernonia pacchensis* Benth. (Skvarla and Turner, 1966a). One might speculate that lack of cavi is correlated with ability of colpi to accommodate extremes in volume change as a grain dries out. The ectexine consists of columellae arising from a foot layer and joining upwardly to form a tectum. One or more additional layers of columellae may be present external to the first layer of columellae, or an almost reticulate arrangement of columellae, as in Cichorieae (Tomb et al., 1974) or in *Inula britannica* L. and *Iva annua* L. (Skvarla and Turner, 1966a) may occur.

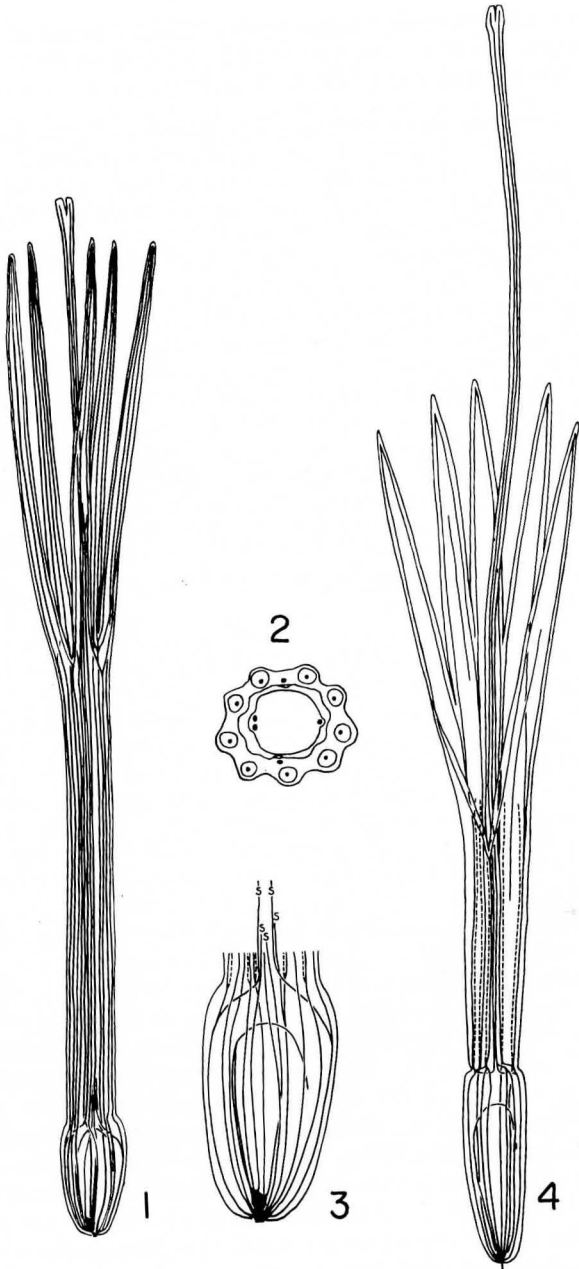
Repatterning of ectexine appears to be an evolutionary characteristic of Asteraceae. For example, within a single genus, such as *Anthemis*, some species have a single layer of columellae, others have two. Although Skvarla and coworkers recognize three types of ectexine patterns in Asteraceae ("anthemoid," "helianthoid," and "senecionoid"), they admit two or all three can be found within a single tribe or genus (Skvarla and Turner, 1966b). Large columellae in the inner ectexine layer combined with small columellae in outer ectexine seem to demonstrate relationship between Mutisieae and Cardueae. This relationship is abundantly clear on the basis of features other than pollen, however. Skvarla and Turner (1966a) are very aptly restrained in claiming far-reaching taxonomic or phylogenetic significance for their studies. One could claim, on the basis of data now available, that an ectexine consisting of a single layer of columellae, as in Astereae, Eupatorieae, Heliantheae, and Senecioneae, represents a primitive condition. This conclusion would, however, be based on the assumption that exine layering proceeds from simpler to more complex, which may not necessarily be so. One might equally well postulate that a reticulate-columellate condition, as in Cichorieae (Tomb et al., 1974) or *Gundelia* (a genus of disputed affinities to Arctoteae, Cichorieae, and Cardueae: see Stix, 1960) is primitive in ectexine structure, and that from an unstable reticulate-columellate condition both the one-layered and two-layered conditions have been derived. Conceivably, one could even postulate a two-layered condition as primitive. Even in Mutisieae, such a genus as *Hesperomannia* (Marticorena and Parra, 1975) seems to show intermediacy between a one-layered and a two-layered tectum, with a tendency toward reticulate patterning of ectexine columellae. At present, ultrastructural studies seem to show that greater diversity rather than uniformity characterizes at least the majority of tribes,

as in the survey of Inuleae by Liens (1968, 1971). Conceivably, ultrastructural pollen studies may prove most useful at the generic or specific level, or in relationship to modes of pollination biology.

*Floral Venation.*—Although I have been skeptical of the usefulness of floral venation patterns in phylogenetic studies, there does prove to be a startling convergence among certain genera of Heliantheae, Mutisieae, and Veronieae thought to have numerous other primitive characteristics. We can hardly overlook this convergence, because the same basic pattern has been preserved (in my interpretation) independently in three tribes; the vast majority of genera and species in all tribes have simplified venation patterns, patterns that conform to a pattern functional for small disc flowers but not congruent with venation patterns in any family claimed related to Asteraceae. For example, the absence of a midvein in corolla lobes of most Asteraceae has a functional explanation: the fused lateral veins extending downward from sinuses of the corolla into the achene are adjacent to filament bundles, with which they fused; thereby, veins supply both androecium and corolla in the most efficient manner possible. Illustrations of this simplified type of venation are given elsewhere (Koch, 1930a, 1930b; Carlquist, 1957b); the flower of *Hesperomannia arborescens* A. Gray subsp. *swezeyi* (Degener) Carlquist shown here (Fig. 4) has portions of midveins in the corolla and more than five bundles in the achene wall, but otherwise conforms to the simplified pattern.

One would expect, in a precursor of Asteraceae, that corolla lobes would have midveins as well as lateral veins (probably fused beneath the sinuses, as in most Asteraceae, although the laterals are not fused in a few, such as *Schlectendalia luzulaefolia* Less, Figs. 5, 7). A flower in which fused laterals and midveins are present would, if these bundles extend downward into the achene, have a circle of ten bundles in an achene as seen in transection. One might also expect carpellary bundles: one midvein and two lateral bundles for each of the two carpels. The adjacent laterals might fuse, so that four rather than six carpellary bundles would be present. Carpellary bundles would lie internal to the circle of 10 achene-wall bundles, as seen in a transection of an achene. The four carpellary bundles would extend upward into the style. These conditions are perfectly realized in the mutisioid *Stenopadus* (Carlquist, 1957c). Very nearly the same is the venation of *Wunderlichia tomentosa* Glaziou of the Mutisieae (Figs. 1–3). In *W. tomentosa*, only two carpellary bundles can be seen in the achene transection shown as Fig. 2, but had the transection been taken at a higher level (see upper portion of achene in Fig. 3), four carpellary bundles would be seen: there is a fusion of two of the carpellary bundles with the achene-wall bundles. A similar condition, with only two carpellary bundles, is seen in *Schlectendalia luzulaefolia* (Figs. 5–7). Both *Wunderlichia* and *Schlectendalia* have median veins in corolla lobes and 10 achene-wall bundles, as well as four stylar bundles (a short fifth bundle in the flower of *Wunderlichia* studied, Fig. 3). The reader may recall that *Stenopadus* and *Wunderlichia* are unusual among Mutisieae in retaining receptacular bracts. *Hesperomannia arborescens* subsp. *swezeyi* (Fig. 4) retains midveins in some





corolla lobes, nine of the ten achene-wall bundles (in the flower figured), but otherwise is of the simplified type characteristic of most Asteraceae.

In Vernoniaceae, genera and species with vestiges of what is interpreted here as a primitive pattern may be found. Exemplary in this respect is *Proteopsis sellowii* Sch. Bip. (Fig. 8). Only two style bundles and no carpellary bundles are present, but the corolla and achene-wall venation are otherwise like the patterns of *Stenopadus* and *Wunderlichia*.

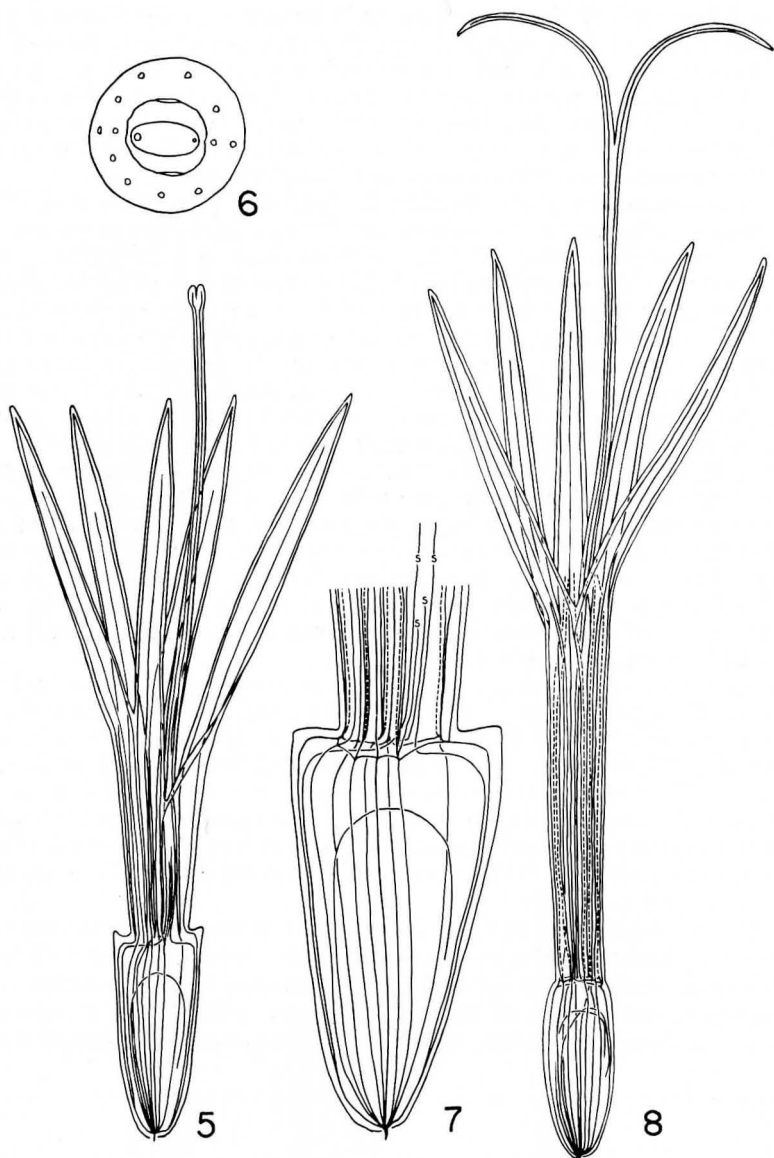
In Heliantheae, the genera *Fitchia*, *Helianthus*, *Oparanthus*, and *Wyethia* have four bundles per style; median corolla lobe bundles are present in all of these genera (Carlquist, 1957b). In *Helianthus* and *Fitchia*, the numerous finer bundles in the achene wall probably represent carpellary bundles (departure of these bundles from the base of the ovule trace in *Helianthus* suggests this), but the large number of these bundles is probably the result of a secondary increase in vasculature, perhaps in relation to large achene size. In *Wyethia*, carpellary bundles are evident in the top of the achene, since they separate from achene-wall bundles below the achene apex with its interconnections among achene wall bundles (Carlquist, 1957b).

Thus, Heliantheae do not show in a single genus the pattern suggested above as a primitive pattern, but the genera of helianthads cited do have all portions of that pattern. If only one tribe, or two closely-related tribes showed the "primitive" pattern, I would suspect the possibility of secondary increase from a simpler pattern—perhaps because of floral size. However, the floral size of the genera cited is not at all the same. Portions of the "primitive" venation pattern have been reported by Stebbins (1940) in genera of Cichorieae he regards as relictual.

The presence of a bifurcate ovule trace is associated with the "primitive" floral venation pattern in *Fitchia*, *Hidalgia*, and *Wyethia* (forked several times in *Wyethia*), of the Heliantheae, as well as *Wunderlichia* (Fig. 2) and *Stenopadus* (Carlquist, 1957c) of Mutisieae and *Proteopsis* (Fig. 8) of Vernoniaceae. This can be most easily interpreted as a primitive feature. I am not prepared to suggest that a divaricate ovule trace represents a vestige of an ancestral biovulate condition, however; the report of occasional biovulate achenes in *Wyethia* (Stebbins, as quoted in Cronquist, 1955) is suggestive, but not in itself conclusive.

In my 1969 paper, I pointed out that increase in number of vascular strands as well as reduction should be expected. The numerous achene-wall bundles of *Helianthus* and *Fitchia*, as well as the numerous bundles in corolla lobes of *Fitchia mangarevensis* F. Brown (Carlquist, 1957b) and *F. rapensis* F. Brown (Carlquist and Grant, 1963) seem to represent increase in vascula-

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Figs. 1-4. Venation of flowers of Mutisieae.—1-3. *Wunderlichia tomentosa* (Glaziov 21684; UC).—1. Venation of flower; stamen traces omitted.—2. Transection of ovary and contained ovule; veins shown in black; circles surrounding achene-wall bundles represent sclerenchyma.—3. Enlarged portion of ovary to show venation; traces to style labeled "s"; traces to stamens shown by broken lines.—4. *Hesperomannia arborescens* subsp. *swezeyi* (Brown 1244; BISH). Flower drawn to show venation; stamen traces shown by means of broken lines. (Figs. 1, 4:  $\times 3$ ; Figs. 2, 3:  $\times 6$ .)



Figs. 5-8. Venation of flowers of Mutisieae and Vernonieae.—5-7. *Slechtendalia luzulaefolia* (Leitz 2433; UC).—5. Venation of flower; stamen traces omitted.—6. Transverse section of ovary and included ovule; small open circles represent veins.—7. Enlarged ovary and adjacent portion of corolla to show venation; traces to style labeled "s"; traces to stamens shown by broken lines.—8. *Proteopsis sellowii* (Mexia 5872; UC). Flower drawn to show venation; stamen traces shown by means of broken lines. (Fig. 5:  $\times 6$ ; Figs. 6-8:  $\times 12$ .)

ture. Increase in floral vasculature over basic patterns have been figured by Carlquist (1967) in *Dendroseris littoralis* Skottsberg ligule tips and by Manilal (1971) in disc corollas of *Gaillardia* and *Tithonia* and in ray corollas of *Ximenesia*, *Tithonia*, *Verbesina*, *Calendula*, etc.; I interpret these as secondary increase in vasculature, not relictual presence of primitive patterns. Reduction from the basic pattern would be indicated by the figures of Manilal for disc flowers of *Ageratum conyzoides* L., *Artemisia vulgaris* L. (the latter with small flowers owing to adaptation to wind pollination), and ray corollas of *Aster molliusculus* Wall., *Chrysanthellum indicum* DC., *Acanthospermum hispidum* DC., *Blainvillea acmella* (L.) Philipson, *Blumea eriantha* DC., *Artemisia vulgaris*, *Cyathocline purpurea* (Don) Kuntze, and *Gnaphalium pulvinatum* Delile. Small flower size would seem to dictate venation reduction in these more than any other factor. Burt (1961) has noted the ease with which larger flowers (primarily ray flowers, but also disc flowers) can be achieved by selection and breeding in cultivated Asteraceae; concomitant increase in venation can doubtless be demonstrated in these (e.g., the cultivated sunflower: Carlquist, 1961).

My 1961 phylogeny of floral venation patterns in Asteraceae took into account the marginal flowers of the head as well as disc flowers. I made the distinction between ray flowers and ligulate flowers, a distinction made by most workers who have studied the family. Ligulate flowers are restricted to Cichorieae by definition, although they have also been evolved in the mutisoid genus *Glossarion* (Carlquist, 1957c). Ligulate flowers can be identified by virtue of their exclusive presence throughout a head and by the corolla form, deeply slit on the adaxial side, forming a flat, five-toothed structure, with veins outlining each of the five teeth. Ray flowers, on the other hand, basically exhibit three teeth at the corolla apex; veins outline the three teeth. Veins representing the "missing" two teeth are present at the margins of the ray corolla; these veins often terminate freely. Ray flowers of *Zinnia elegans* Jacq., figured by Manilal, have the venation of a ligulate flower but are not toothed. An exception of this sort does not, in my opinion, vitiate the distinction between ray corollas and ligulate corollas. Ray flowers of various composites show more than the basic number of veins, probably in response to natural selection for increased ray corolla size.

The bilabiate flowers of most subtribes of Mutisieae are only slightly modified disc flowers. Some Cardueae, such as certain species of *Centaurea*, show some degree of zygomorphy in corollas peripheral in capitula, but these flowers are still clearly modified disc flowers. *Stokesia* (Vernonieae) is distinctive in having at the periphery of the head flowers the corollas of which correspond to the ligulate definition, although disc flowers are present in the center of the head.

An interesting question arises with respect to Arctoteae. If one divides the Asteraceae into two subfamilies, Asteroideae (the "helianthoid line" of my 1961 treatment) and Cichorioideae ("mutisoid line," op. cit.), to which subfamily does Arctoteae belong? The only characteristic discordant with placement in the mutisoid line would be if the peripheral flowers of arctotid heads are ray flowers rather than ligulate-type flowers. Cronquist

(1955) believes that Arctoteae do have ray flowers. However, I think that these flowers of Arctoteae, like those of *Stokesia*, are of a ligulate type. This seems confirmed by the five-toothed corollas of peripheral flowers in heads of the arctotid *Didelta* (Hoffmann, 1890) and other Arctoteae. Thus, I believe that for this and other reasons (presence of laticifers, type of styles, presence of cynaroid-type leaves in arctotid genera which seem transitional to Cardueae) Arctoteae should be placed in subfamily Cichorioideae. I also believe, contrary to Cronquist (1955) that the tribes of Cichorioideae (Arctoteae, Cichorieae, Cardueae, Eupatorieae, Mutisieae, Vernonieae) are not derived from ancestors with ray flowers. I see no evidence in any of these tribes of ancestral presence of ray flowers, and there is every reason to believe the tribes basically have capitula composed of actinomorphic disc flowers only, a condition still shown (in a slightly modified form) by *Fitchia* of the subfamily Asteroideae, in my opinion.

*Secretory canals, laticifers, and laticiferous cells.*—Occurrence of these structures was studied by Col (1899). Augier and du Merac (1951) have expanded Col's work and summarized data in a sophisticated graphic form. I have added data on secretory canals in Heliantheae (1957b) and on secretory canals of an incipient nature and on laticiferous cells in Mutisieae (1958a). Two phenomena appear to characterize Asteraceae in regard to these structures:

- (1) There is a tendency for tribes and genera to have either secretory canals or laticifers but not both. They may even contain similar substances. The occurrence of sesquiterpene lactones in Asteraceae with either laticifers alone or secretory canals alone (Fairbrothers et al., 1975) suggests this.
- (2) The underlying genetic ability to form either type of structure seems basic to Asteraceae; they may have even originated in Asteraceae independently of other families, and have undoubtedly originated more than a single time in Asteraceae. For example, Heliantheae have secretory canals but not laticifers, yet laticiferous cells occur in *Parthenium* and *Picradenia* (Augier and du Merac, 1951).

Although our picture of occurrence of these structures is far from complete in Asteraceae, the following tentative conclusions may be drawn. In Asteroideae, all tribes basically have secretory canals in root, rhizome, aerial stem, and leaves (they may be absent in small or reduced organs). This statement encompasses Anthemideae, Astereae, Calenduleae, Heliantheae (including Heleniae), and Senecioneae. Presence in lower portions of the plant but not in upper portions characterizes some species. For example, secretory canals are present in roots only of Calenduleae, *Helenium tenuifolium* Nutt., and the subtribe Gnaphalinae of Inuleae. As noted, laticiferous cells are known to occur in the subfamily Asteroideae only in *Chrysanthamnus*, *Parthenium*, and *Picradenia*; their occurrence in these genera can hardly be a relictual phenomenon; it probably represents a *de novo* introduction of this cell type.

In the subfamily Cichorioideae, at least some species of all tribes have both secretory canals and laticifers or laticiferous cells except for Eupa-

torieae (only secretory canals, present in all plant portions). Cichorieae are widely known to have laticifers; all Cichorieae do have anastomosing laticifers in all parts of plants as far as is known, but in addition, *Scolymus* and *Scorzonera* of this tribe have secretory canals in roots. Cardueae characteristically have secretory canals, but laticifers occur in all portions of *Cardopathium*, and laticiferous cells occur in aerial stems of *Cirsium* and *Lappa*. Arctoteae have secretory canals in roots only (e.g., *Ursinia*, *Arctotis*); laticifers occur in roots and aerial portions in *Gundelia*, and in aerial portions of *Gazania* (laticiferous cells in roots of *Gazania*). Vernonieae have secretory canals in roots only, but laticiferous cells have been found, in addition, in all portions of the plant in *Heterocoma*. Mutisieae present a complicated picture, ranging from absence of either structure (*Chaptalia*, *Barnadesia*) to presence of laticifers throughout the plant plus secretory canals in roots only (*Warionia*) to presence of laticiferous cells plus secretory canals (*Berardia*, *Gongylolepis*). Mutisieae never show either secretory canals or laticiferous structures prominently developed (Carlquist, 1958a), and are thus a germinal group. One might expect that primitively in Asteraceae, rudiments of both laticiferous structures (perhaps as laticiferous cells) and secretory canals (perhaps narrow canals) might have been present. One can hypothesize that as the various tribal stocks evolved, elaboration of secretory canals "shut out" development of laticifers, or vice versa. The two systems, although morphologically different and also different to a large extent in nature of contents, may contain some of the same compounds, if the data of Fairbrothers et al. (1975) on sesquiterpene lactones are applicable.

With the exception of Eupatorieae, then, tribes within Cichorioideae all contain various expressions of both laticifers (or laticiferous cells) and secretory canals. This tends to unify Cichorioideae as a subfamily, in contrast to Asteroideae, where secretory canals are present, highly developed, laticifers not reported, and laticiferous cells present only in a few genera. The state of our knowledge concerning chemistry of contents of these structures is only beginning, but we still have knowledge of only a small sampling of the family. This is underlined by presence of cells in which contents can be categorized only very imprecisely as "resinous or milky" in *Atractylis*, *Carduus*, *Carlina*, *Chardinia*, *Cirsium*, *Cousinia*, *Galactites*, *Gazania*, *Jurinea*, *Onopordon*, *Silybum*, *Stachelina*, *Vernonia*, and *Warionia* (Metcalf and Chalk, 1950). All of these genera belong to tribes of the subfamily Cichorioideae, and the nature of these cells may indicate less specialization in the secretory systems of that subfamily.

*Wood Anatomy.*—When I began my studies of wood anatomy of Asteraceae with a study of Mutisieae (1957a), I was hopeful for emergence of data applicable to taxonomic or phylogenetic problems. However, as this series of 13 papers progressed, culminating with a summary (1966b), I was forced to conclude that the variations observed yield minor taxonomic dividends, but provide compelling evidence of evolutionary adaptation to the various ecological regimes Asteraceae occupy. The features of an "average" wood of Asteraceae are adaptive in moderately dry circumstances (Carlquist, 1966b), and I would hypothesize that the family originated under such ecological

regimes and has invaded both wetter and drier areas numerous times in independent phylads within the family. The "average" wood of Asteraceae is like that of other dicotyledon families. I would not be able to distinguish, on the basis of wood sections, asteraceous wood from those of Boraginaceae, Hydrophyllaceae, Lamiaceae, Scrophulariaceae, and some other families. If wood of Asteraceae lacks criteria for discerning relationships, it yields a remarkable wealth of information about the ecology of particular species, for reasons more completely described in my 1975 book. In my survey of wood anatomy of Asteraceae, I found nothing that would contradict the unity of the family: its woods are variations on a single plan.

*Embryology.*—Although embryological studies on Asteraceae continue to emerge, we may take the summary of Davis (1966) as representative. The thrust of her summary for the family is the remarkably unvaried pattern in all basic embryological features throughout the family. Such variations as take place can be regarded as minor and characterize only one or several species. Two embryo sac types have been found within a single species, and even within a single head of a species, showing that deviations from the *Polygonum* type should not be regarded seriously. The uniformity of the family in so many features gives no aid to those who wish to segregate Cichorieae as a separate family, nor will it aid, apparently, in delimitation of tribes or other natural groupings. The tendency for antipodal cells to become haustorial occurs independently in the most disparate genera (Davis, 1966), and does not take the form seen in Campanulaceae in any case. Small's (1919) stress on this feature as indicative of relationship between Asteraceae and Campanulaceae is not justified, and the aggressive antipodals in Asteraceae can only be explained as parallelisms.

*Trichomes.*—I have hypothesized (1958b, 1961) that two basic types of trichomes occur in Asteraceae: uniseriate nonglandular and biseriate glandular on the same plant. This hypothesis seems justified by presence in genera of both Asteroideae (e.g., *Layia*) and Cichorioideae (e.g., *Hesperomannia*: Carlquist, 1957d). To be sure, there is a great deal of variation and elaboration of both types (Carlquist, 1958b, 1959b, 1959c, 1961; Ramayya, 1962a, 1962b) has taken place independently in all of the tribes. From the data available, no tribal or subfamilial lines in trichome types emerge. Uniseriate glandular trichomes also occur in both subfamilies: *Eupatorium odoratum* L. (Eupatorieae), *Lactuca sativa* L. (Cichorieae), and *Flaveria australasica* Hook. (Helianthae), for example (Ramayya, 1962a). My data and those of Ramayya suggest that further research may confirm my hypothesis of the two trichome types as primitive in Asteraceae. However, a fascinating variety of modifications of the glandular and nonglandular types await study and application to taxonomic and phylogenetic problems within the family. Tribal lines will probably not emerge, but trichomes of particular forms may characterize genera or groups of genera.

#### CHROMOSOME NUMBERS

Our chromosomal knowledge of Asteraceae has broadened rapidly. Asteraceae provide convenient material partly because of the gradate sequence



of development of flowers within a capitulum, the reasonable size and number of chromosomes, and the easy availability of sufficient flowers and of large numbers of species. Chromosomal studies in the family reveal that evolutionary repatterning of chromosomes is active; this results in interesting, although at times confusing patterns, difficult to interpret.

Solbrig (1967) and Solbrig et al. (1964) make a compelling case for  $x = 9$  as the number basic to the tribe Astereae, whereas Turner et al. (1961) hypothesized that the frequency of  $n = 5$  and  $n = 4$  in the tribe suggests amphiploid origin for species and genera with  $n = 9$ . Is  $x = 10$  basic to Senecioneae, as Ornduff et al. (1963) propose? Turner and Lewis (1965) seem to prefer  $x = 5$  for Senecioneae. For Anthemideae, the number  $x = 9$  seems likely (Solbrig, 1963). In Ambrosinae of Heliantheae, Payne et al. (1964) suggest  $x = 18$  as basic, derived from  $x = 9$ . In Eupatorieae, Turner et al. (1967) propose  $x = 10$  for *Ageratum* and  $x = 10$  and  $x = 17$  for *Eupatorium*, and Turner and Flyr (1966) propose  $x = 9$  for *Brickellia*. For Veronieae, Turner and Lewis (1965) cite  $x = 9, 10, 16$ , and  $17$ . In Cichorieae, Stebbins (1953) cites data that indicate  $x = 9$  in most subtribes. In Heliantheae, chromosome numbers such as  $n = 17, 18$ , or  $19$  are frequent. In Mutisieae, the relatively small number of counts available are also of relatively high numbers, often above  $20$  (Turner et al., 1962; Solbrig, 1963; Turner and Johnston, 1961). Polyploidy seems clearly indicated for the helianthad and mutisiad numbers cited, but can the  $x = 9$  and  $x = 10$  numbers frequent in the tribes cited above be polyploid also? That seems unlikely. The number of species with  $n = 9$  or  $n = 10$  is too great. This statement requires clarification. Aneuploid series showing decrease in chromosome number correlated with specialization—for example, autogamous annuals—are of frequent occurrence, as in *Eriophyllum* and allied genera (Carlquist, 1956). There are many such aneuploid series in Asteraceae, with shift to specialized habit and other features correlated with decreasing chromosome number, and it is difficult to imagine the family derived from polyploids based on the low-chromosome number species of such aneuploid series. The base number for Asteraceae as a whole has been postulated by Raven (1975) as  $x = 9$ . I concur.

The varied chromosomal conditions in Asteraceae, ranging upward from the renowned  $n = 2$  in *Haplopappus gracilis* A. Gray, invite interpretations in terms of a broader picture of "fitness versus flexibility." Such trends would be explicable with maximum flexibility at levels near  $x = 9$ . Downward aneuploidy would be correlated with lowered recombination, and therefore lowered variability characteristic of species that spread and grow abundantly in favorable seasons of dry regions (Grant, 1958; Solbrig, 1967). Polyploidy, on the other hand, is characteristic of woodier species in relatively stable habitats. A residue of the basic stocks ( $x = 9$  or a number close to that) remains in intermediate habitats as a source for further aneuploid and polyploid derivative lines. These trends have apparently occurred numerous times independently in the family, reflecting the great evolutionary plasticity of Asteraceae. Here we see many examples of explosive evolution and the chromosomal correlations of such evolution.



## SYSTEMATICS OF ASTERACEAE

One may summarize the above information in the following form:

## Subfamily Cichorioideae:

- Mutisieae
- Vernonieae
- Cardueae
- Arctoteae
- Cichorieae
- Eupatorieae

## Subfamily Asteroideae:

- Heliantheae
- Astereae
- Inuleae
- Anthemideae
- Senecioneae
- Calenduleae

In agreement with Leonhardt (1949) and subsequent authors, Helenieae are regarded as belonging within Heliantheae. Following the majority of authors, Ambrosinae is considered a subtribe of Heliantheae. Subtribal systematics of Asteraceae are, at this point, far from satisfactory. Various authors have suggested modification of the Hoffmann (1890) scheme, but they have not attempted such revisions. Stebbins (1953) has revised subtribal lines in Cichorieae in a satisfying fashion. However, those who have advocated inclusion of Helenieae within Heliantheae have not taken the next step of integrating and sequencing the subtribes of helenioids under Heliantheae or of extracting misplaced genera. Problems of affinities of the subtribe Heleninae, some of which might belong to other tribes, have been cited by Raven and Kyhos (1961), however.

Within Asteraceae, there are some strikingly definable subtribes, such as Madinae of Heliantheae (recognized as a tribe by Jepson, 1925) or Ambrosinae of Heliantheae (recognized as Ambrosieae by numerous authors). However, the fact that these subtribes can be defined with precision should be subordinated to demonstration of close affinities. Segregation of Cichorieae as a family is definitely unwarranted. The underlying (but not expressed) rationalization for segregation of families from Asteraceae is that the family is excessively large. However, the size of the family does not change the fact that it is a natural family, well isolated from other families of dicotyledons.

With regard to natural relationships, I would like to attempt a series of hypotheses concerning interrelationships among the tribes. I would guess that Asteraceae originated in the New World, and that rapid breakup into the subfamilies occurred. If primitive features are most common in certain Heliantheae, Vernonieae, and Mutisieae, the tribes originated in the New World, if present distribution of these tribes (especially of the genera with putatively primitive features) is a criterion. Long-distance dispersal is characteristic of Asteraceae, as a generalization, so presence of Mutisieae,

Heliantheae, and Vernonieae today on continents other than North and South America is hardly surprising. Eupatorieae also seem to have a New World origin. During the early history of the family, rapid dispersal of segments of the family probably occurred, and these colonized various portions of other continents, giving rise to new tribes. Stebbins (1953) postulates an Old World origin for Cichorieae; this seems likely. In this regard, such genera as *Scorzonera* and *Scolymus* may be regarded as "non-missing links" to *Ursinia* and other Arctoteae. Arctoteae seem to be the result of explosive evolution of a stock related to a cichoriad-carduacead complex in southern Africa. *Scolymus* and *Scorzonera* approach Cardueae somewhat, and Cardueae probably had an Old World (Northern Hemisphere) origin, although they are now quite widespread. The tribes Inuleae and Senecioneae must have had rapid secondary radiations soon after their origin, so that the geographical areas of their origin are difficult to pinpoint. However, both appear Old World in their radiation and probably origin. Ornduff et al. (1963) claim Old World origin for Senecioneae, and their claim is more supportable than that of Small (1919), who believed Senecioneae originated in the Andes from South American lobelioids. Calenduleae is probably a South African offshoot of a senecionean stock. Anthemideae are centered in the Old World, Astereae in the New World, and origin in those places, respectively, may be hypothesized. The reader will note that evidence from style-branch anatomy, secretory structure specialization, and chromosome number are particularly important in these divergences; evidence from pollen ultrastructure is also compatible with this scheme. Future students can amass information that will lead to details of phyletic and divergence in the Asteroideae and Cichorioideae, and at least some details of radiation within tribes can be elucidated; the success of such efforts will depend on the scope and ability to synthesize large quantities of information by particular workers. I hope that these efforts will not be premature, for our grasp of the family is still unsatisfactory.

One obstacle to comprehension of Asteraceae that deters construction of a new system to replace Hoffmann's (1890) synopsis is the occurrence of "misplaced" or "anomalous" genera. These genera usually differ from their closest relatives in one or two misleading salient characteristics. Perhaps the classic example was *Fitchia*, variously assigned to Heliantheae, Mutisieae, or Cichorieae. My work on this genus (1957b) may be considered an "exercise in overkill," for *Fitchia* is clearly helianthad, and only its pseudoligulate flowers and lack of ray flowers misled botanists. Likewise, *Raillardella* was easily transferred to Heliantheae subtribe Madinae from Senecioneae. Evidently the possibility that there could be an alpine representative of Madinae was overlooked. Likewise, the Hawaiian genera *Dubautia* (including *Raillardia*), *Argyroxiphium*, and *Wilkesia* clearly belong to Madinae (Carlquist, 1959a); Keck (1936) is the only worker to have doubted this placement, and his reasoning is superficial.

The recent accumulation of chromosomal data has influenced workers to reassign genera of Asteraceae to tribes other than those in which they have traditionally been treated. Turner and Johnston (1961) wish to reassign

*Flaveria* and *Sartwellia* from heleniad Heliantheae to Senecioneae. *Adenocaulon* remains problematic, with claims for inclusion in Heliantheae, Inuleae, and Senecioneae variously advanced (see Ornduff et al., 1963). Ornduff et al. also suggest transfer of *Crocidium*, *Dimeresia*, *Haploesthes*, *Psathyrotes*, and "perhaps" the subtribe Liabinae out of Senecioneae, but the recipient tribe or tribes for these groups is not designated by these authors. However, Skvarla and Turner (1966b) place *Crocidium*, along with *Blenno-sperma*, in Senecioneae, and Strother and Pilz (1975) place *Psathyrotes*, which they claim is closely related to *Peucephyllum*, in Senecioneae. I included *Peucephyllum* in my (1962) study of woods of Senecioneae. Powell and Turner (1963) suggest that *Varilla* (Heliantheae), *Pseudoclappia* (Senecioneae), and *Clappia* (Helenieae) form a natural group in or "near" Senecioneae, and also feel that Tagetinae, treated by Hoffmann (1890) as a subtribe of Helenieae, might be included in Senecioneae. A study by Ornduff and Bohm (1975) of *Tracyina* is a good example. *Tracyina* had been regarded as a member of Astereae, *Rigiopappus* as heleniad. Ornduff and Bohm place both genera, which are interfertile, in Astereae. The reader will note in the examples cited in this paragraph that the interfaces of Astereae, Senecioneae, and helenioid Heliantheae appear particularly difficult, and resolution of many of these genera may be difficult. On the basis of pollen study, Stix (1960) would shift *Osmites* and *Osmitopsis* from Inuleae subtribe Bupthalthinae to Anthemideae; *Platycarpha* from Arctoteae to Mutisieae; *Gundelia* from Arctoteae to Cardueae; and *Gongrothamnus* from Senecioneae to Vernonieae. The transfer of *Gongrothamnus* had been suggested on grounds other than pollen (see Stix, 1960). The proposed transfers of *Platycarpha* and *Gundelia* can be interpreted as demonstrating the closeness of Mutisieae, Cardueae, and Arctoteae, regardless of the ultimate disposition of these particular genera. Cronquist (1955) describes the history of *Adenostyles*, which has been placed in Eupatorieae by various workers, but which Cronquist feels, with support from others, is an anomalous member of Senecioneae. I feel that the position of *Grindelia* and *Remya* in Astereae is worthy of reinvestigation. Other examples of misplaced genera, some not cited as such yet, remain as interesting research projects for enterprising students of Asteraceae who are willing to understand assemblages of characters not only of the genera questioned, but of their supposed relatives in traditional treatments and proposed relatives in the potential recipient tribe. Chromosomal numbers or pollen ultrastructure alone may not by themselves be convincing, although they are appealing because of their simplicity compared to lengthy investigations of vegetative and floral anatomy. An annoying circumstance in these instances is the probability that any feature that has evolved in Asteraceae once may well have evolved more than once.

A second obstacle to taxonomic resolution of categories within Asteraceae is hinted above: transitional genera, or "non-missing links." The comments of Powell and Turner (1963) and Turner and Flyr (1966) show some of the problems involved. One should expect that in a family with such recent explosive evolution as Asteraceae, transitional forms may still be extant. Recognition of these for what they are is not so easy, however.

## RELATIONSHIPS OF ASTERACEAE

Of prime importance in analyzing relationship is a realization that no living family of angiosperms contains any genus or species ancestral to Asteraceae. This truism is applicable to any study of phylogenetic relationships, of course, but it has been forgotten all too often in practice. For example, Small (1919), by means of misinterpretation and extreme eclecticism, found many features of Asteraceae in various species of Campanulaceae, subfamily Lobelioideae. Even if Campanulaceae ultimately prove to have some relationship to Asteraceae, Small's method prevents demonstration of that. He presents no evidence linking a campanuloid stock to *Senecio*, the genus he compulsively considers primitive in all respects within Asteraceae. What we must seek in attempting to determine affinities of Asteraceae is a series of conservative (= primitive, or slowly evolving) characters shared with other families and unlikely to have arisen polyphyletically.

Following this criterion, we may more easily rule out characters than use them. The wood anatomy of Asteraceae, for example, is of a type that occurs widely among specialized dicotyledons. If I were presented with wood-section slides of Acanthaceae, Boraginaceae, Campanulaceae (including Lobelioideae), Hydrophyllaceae, Lamiaceae, Solanaceae, and other families that could be named, I doubt that I could sort them into families accurately.

Likewise, families alleged by various authors to be related to Asteraceae share with the family a common plan of pollen grain form and structure. Araliaceae (including Apiaceae: Thorne, 1968), Boraginaceae, Calyceraceae, Campanulaceae, Dipsacaceae, Goodeniaceae, Scrophulariaceae, and Valerianaceae are among families that show degrees of resemblance (Erdtman, 1952, and original observations). Only unusual types of pollen grain structure, such as the lophate grains of many Cichorieae and Vernoniaceae, could be identified as asteraceous with certainty.

The narrow tubular shape of flowers and the pollen-presentation mechanism of Asteraceae may owe their origins to evolution of the capitulum more than to affinity with other groups with pollen-presentation mechanisms somewhat reminiscent of Asteraceae (e.g., Campanulaceae and Goodeniaceae). The pollen-presentation mechanisms of Stylidiaceae are quite different from those of Asteraceae.

Chemical studies present a confusing pattern. This statement is not based on discrepancies between affinities suggested by chemistry and relationships alleged on the basis of gross morphology (indeed, one can find in chemical literature thus far support for many different purported relationships). Rather, chemical evidence should be viewed carefully and conditionally because:

- (1) Sampling has been sparse, and for some chemical categories, only a few angiosperms have been investigated.
- (2) We lack information on parallel evolution—which obviously occurs—in the various categories of chemical compounds, in part because we do not know synthetic pathways in some cases, in part because we do not know mutation capability of these pathways. Dahlgren's

(1975) system is heavily influenced by iridoid compounds (Jensen, Nielsen, and Dahlgren, 1975), for example.

- (3) We lack information about rates of evolution of compounds and their precursors.

With further work, some of these uncertainties may diminish. The presence of inulin in Asteraceae, Campanulaceae, Goodeniaceae, and Stylidiaceae (Solereder, 1908) has been cited as evidence for relationship among these families. However, other data point to affinity with Apiaceae, Boraginaceae, or Rutaceae (Hegnauer, 1964). Chemical data do not rule out possible relationship of Asteraceae with Dipsacaceae, Calyceraceae, or Valerianaceae.

Trichome types like those of Asteraceae (uniseriate nonglandular plus one or more glandular types) occur in Dipsacaceae and Valerianaceae, and with slight differences, Apiaceae, Boraginaceae, and Hydrophyllaceae (Metcalf and Chalk, 1950). Calyceraceae and Campanulaceae lack glandular hairs.

With respect to secretory structures, families cited as possibly related to Asteraceae present a mixed picture. Secretory canals are well developed in Araliaceae (including Apiaceae) and a few Rubiaceae, whereas laticifers are well developed in Campanulaceae (including Lobelioideae). Secretory cells with unidentified contents occur in Boraginaceae, Dipsacaceae, and Valerianaceae (Metcalf and Chalk, 1950).

Basic chromosome numbers may be viewed with skepticism as indicators of broad areas of relationship, but Raven (1975) reports  $x = 9$  as basic in Hydrophyllaceae and Dipsacaceae; he claims this number as basic to Asteraceae as well. Basic chromosome numbers can obviously arise in parallel fashion, so this is at best a subsidiary form of evidence.

Obviously, no single family is close to Asteraceae. This is indicated by the fact that Asteraceae are usually placed as the sole family of Asterales, or the sole family of a category of higher than ordinal rank (see Thorne, 1968; Dahlgren, 1975). One can say with some security that a stock ancestral to Asteraceae was probably semiherbaceous (neither annuals nor trees), probably with alternate leaves and with both uniseriate nonglandular and some type of glandular trichome; the inflorescence was probably at least approaching capitular form, although I tend to believe that all flowers were discoid in ancestors of Asteraceae, with a tendency toward production of zygomorphic flowers at the periphery of the head. Flowers were pentamerous, with a bicarpellate ovary; the ovary was probably already inferior, the corolla sympetalous, although these features may have been exaggerated by acquisition of capitular inflorescence structure. The ovary, if inferior, may have contained 10 ovary-wall bundles and four or six carpellary bundles; calyx was present, in a form capable of diverging into setose form; the style was bifid, with nectaries at the style base; stigmatic hairs were restricted to the inner faces of the style branches; flowers were protandrous, with five anthers. The ovary may already have been reduced to a single locule with a single ovule, although a pair of ovules and vestiges of a bilocular condition might have still been present; ovules were tenuinucellate and unitegmic with a *Polygonum*-type embryo sac. Pollen was tricolporate and tectate.

The above description of a hypothetical primitive composite contains

many features found in other families. Among those with more numerous resemblances today are most notably Araliaceae (especially Apioideae); also Boraginaceae, Dipsacaceae, and Valerianaceae, but other sympetalous families are not ruled out. This agrees with Thorne (1968).

As a final note, I would like to stress the many research opportunities Asteraceae provide. Those frightened by research in such a large family of plants should take note of the fact that studies on particular groups of Asteraceae are an integral part of our understanding of evolution of flowering plants, and few workers in plant evolution have bypassed the family altogether. Within the baffling complexity of Asteraceae still lie the rewards of seeing the active processes of evolution, not merely the relictual products of phylesis. The student can find a good introduction to the family in the paper by Solbrig (1963).

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