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A Revision of the Tribal and Subtribal Limits of the Heliantheae (Asteraceae)

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ABSTRACT

Robinson, Harold. A Revision of the Tribal and Subtribal Limits of the Heliantheae (Asteraceae). *Smithsonian Contributions to Botany*, number 51, 102 pages, 210 figures, 1981.—The tribe Heliantheae is expanded to include the genera previously placed in the tribe Helenieae and many genera from the Senecioneae. Thirty-five subtribes are recognized and described, and the more than 265 genera are listed with known, validly described synonyms. A theoretical key to subtribes is provided. Various structural and chemical characteristics are reviewed, and emphasis is given to resin duct patterns, presence of fiber-sheaths in disk corollas, and patterns of striations in achenes. The Heliantheae is considered a member of the subfamily Asteroideae in a position parallel to and more advanced than the Eupatorieae.

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Contents

A Revision of the Tribal and Subtribal Limits of the Heliantheae (Asteraceae)

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Introduction

The tribe Heliantheae is generally known for such members as the sunflowers (*Helianthus*), the ragweeds (*Ambrosia*), the cockleburs (*Xanthium*), black-eyed Susans (*Rudbeckia*), commonly cultivated members of the Coreopsidinae (*Coreopsis, Cosmos,* and *Dahlia*), and the marigolds (*Tagetes*). More notable to students of the tribe is the diversity reflected in the many obvious taxonomically useful characters. Variations in sexuality of flowers including ray flowers that are completely sterile, extremes in palea development including ornate or greatly expanded forms, and a great variety of achene and pappus shapes have resulted in the acceptance of well over 200 traditional genera in the tribe. The obvious diversity and the often primitive aspect of members of the tribe have caused some authors to assign to it a central and ancestral position in the family, and in recent decades the group has been subjected to more revisions at the generic level than any other comparable group of plants. The increasing efforts in the tribe have also provided great amounts of chemical and cytological data for various members. Nevertheless, until recently, the overall understanding of the tribe has rested on a treatment that is over a hundred years old.

Recent studies have shown a contrasting picture of the understanding of various taxonomic levels in the Heliantheae. Because of the wealth of structural features, the true diversity of the tribe has been obvious, and only comparatively minor alterations of generic concepts have been necessary. However, the adoption of nearly correct generic limits in the Heliantheae has not been matched by equally correct ideas regarding the limits of the tribe or the relationships between the genera. The present effort is directed toward this problem.

The present study has evolved from an initial need to publish various results from identification and floristic work. As the full taxonomic implications of some structural features have become apparent, it has become desirable to provide a general revision of the tribe. The revised subtribes will be used in floristic treatments of the tribe in Ecuador and Peru now in preparation, and they provide a refined basis for evaluating cytological data that is being fully treated in another publication. The present revision utilizes new characters discussed in recent studies such as striation of achene walls (Robinson and Brettell, 1973b), resin duct patterns in the flower (Robinson, 1979b), and fiber sheaths in the corolla (Robinson, 1978a). The study also incorporates improvements from the recent revision of the tribe by Stuessy (1977), while avoiding a number of fea-

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tures of that revision believed to be in error. The limits of the tribe are redefined to include the related genera that have been placed in the Helenieae and Senecioneae, and the relationships of the Heliantheae to the other tribes are considered. Conclusions regarding the relationships are discussed in the light of the ancestral position in the family given to the tribe by Cronquist (1955).

Completion of the present paper has been delayed to take advantage of the published results of the Reading Symposium on the Biology and Chemistry of the Compositae (Heywood et al., editors, 1977), which were not available until the spring of 1978. The parts of the symposium that are most important for this study are the systematic reviews of the Heliantheae by Stuessy, of the Helenieae by Turner and Powell, of the Tageteae by Strother, and of the Senecioneae by Nordenstam. Various chemical reviews, such as those of the Heliantheae by Swain and Williams and of the sesquiterpene lactones by Herz, also are important, but data on polyacetylenes are taken primarily from the book by Bohlmann et al. (1973). Chromosome data have been evaluated in a separate study (Robinson et al., in press), but the conclusions are incorporated into the present paper. Throughout the study, a primary source has been the continuing microscopic examination of floral parts mounted in Hoyer's solution (King and Robinson, 1970).

The present paper is designed to achieve three primary purposes: to examine the origins of some previous concepts of the Heliantheae, to describe and evaluate characters of potential taxonomic value in the tribe, and to align and describe the 35 subtribes that are recognized in this study.

ACKNOWLEDGMENTS.—Many people are to be thanked for their contributions to this study. The drawings of the achene and head structures have been prepared by Alice Tangerini of the Department of Botany. The series is based on an earlier unpublished series prepared for me in 1972 by Rebecca D. Brettell. The microphotographs were taken by Victor E. Krantz, staff photographer, National Museum of Natural History. The paper has benefitted from the work of various authors cited as well as from conversations with a number of synantherologists, including Jose Cuatrecasas, Vicki Funk, R. M. King, Guy Nesom, David Rindos, and John Strother.

Historical Considerations

The taxonomic history of the Heliantheae revolves around a limited number of interesting and influential treatments produced during the last 170 years. In almost every case, features of these treatments have been retained in recent classifications of the tribe, and often this seems to be strictly on the basis of tradition. A review can be instructive, to the extent that reasons for past concepts, whether correct or not, can be recognized. The tribe's history is discussed here in the light of my present concepts. My judgments of some works may seem overly kind or harsh independently of the extent to which I consider them to be correct; I admit being influenced by my perception of whether various works represent a proper use of the information available at the time they were produced. In general, those treatments that I consider most flawed in their conclusions are the ones that I find to be seriously flawed in their basic approach.

The tribe Heliantheae was first named by Cassini in 1819. One of the more useful summaries of salient features was provided by Cassini in his article on the Helianthees in volume 20 of the *Dictionnaire* (1821:370).

> La calathide est ordinairement radiée, souvent incouronnée, quelquefois discoïde. Le clinanthe est ordinairement squamellifère, souvent inappendiculé, jamais fimbrillifère. Les squames du péricline sont ordinairement unisériées ou bisériées, égales ou peu inégales, souvent imbriquées. Les feuilles sont ordinairement opposées, souvent alternes, souvent trinervées. Les tiges sont ordinairement herbacées, souvent ligneuses. Les fleurs sont ordinairement jaunes, souvent blanches, quelquefois purpurines.

The tribe included the subgroups Prototypes, Rudbeckiées, Coréopsidées, Héléniées, Tagétinées, and Millérinées. The only major element of the present concept that Cassini omitted was the Ambrosiées, with its various specializations of unisexual heads, fused heads, and free anthers, which Cassini placed in a separate tribe.

The work of Cassini presented for the first time the primary characters that have been used in constructing most subsequent classifications of the Asteraceae, including those of Bentham and Hooker (1873) and Hoffmann (1890–1894). The use of the characters has led to a partial restoration of the tribal concepts of Cassini in the latter classifications. However, one essential quality of Cassini's concept of the Asteraceae was lost by most subsequent workers: his recognition of the discrete nature of most of the tribes of the family. Bentham and those who followed his system seem to consider the tribes as mere nodes in a continuum.

In a diagrammatic representation of the family, Cassini (1816–1817) arranged the tribes in a circle, which, in many details, anticipated the presently accepted two-parted concept of the Asteraceae (Robinson and Brettell, 1973d; Wagenitz, 1976; Carlquist, 1976).

A final consideration regarding the Cassini work concerns the sense in which he used the term "affinités." It is possible that Cassini was influenced by his contemporary Lamarck, although he would not have been able to openly espouse evolution when publishing in the *Dictionnaire* edited by Cuvier, who was Lamarck's most outspoken opponent. Certainly, the comparative phyletic accuracy of Cassini's work is in clear contrast to the classifications of his immediate successors who used totally nonevolutionary approaches to classification.

One can only speculate about what would have happened if subsequent authors had built directly upon the work of Cassini. Instead, the year of Cassini's death saw the publication of the appallingly simplistic and superficial study by Lessing (1832), which presented a classification that emphasizes the most obvious characters and ignored all subtleties. In one case Lessing described the new genus *Astemma*, without benefit of material, on the basis of the erroneous suggestion in the original description that *Monactis dubia* H.B.K. might be dioecious. The uninsightful nature of the work is probably traceable in no small part to the extreme youth of the author (1809–1862). Unfortunately, Lessing was followed closely in the treatment of the Compositae by de Candolle (1836–1838). An important aspect of the Lessing and de Candolle treatments was the placement of most yellow-flowered radiate members of the family in a single tribe, Senecioneae. This was responsible for the manner in which Bentham later treated the Senecioneae as a residuum in his classification.

The Bentham classification of the Compositae was presented in Bentham and Hooker in 1873, and a separate explanatory article was produced by Bentham in the same year. The system represents a full reinvestigation of the characters of the family with restoration of most of the essential features of Cassini's classification. The explanatory article even includes a circular representation of the tribes similar to that of Cassini. It has been argued that Bentham considered the Heliantheae the most primitive tribe in the family (Cronquist, 1955, 1977a), but the idea that the tribe was ancestral to others was Cronquist's alone.

In his treatment of the Heliantheae, Bentham introduced a degree of artificiality. The Heliantheae were rigorously redelimited to exclude groups totally lacking paleae and to exclude all groups with a well-developed, nonplumose, capillary pappus. The epaleaceous forms with reduced pappus were placed in a separate tribe, Helenieae, which was placed adjacent to the Heliantheae. The genera with a capillary pappus were placed in the more remote and extremely heterogeneous Senecioneae.

General patterns that are preserved in the present treatment can be detected in the Bentham organization of the two tribes Heliantheae and Helenieae. The Heliantheae are basically paleaceous, connecting through the partly epaleaceous Madiinae to the totally epaleaceous Helenieae. Within the paleaceous Heliantheae, the first subtribes are epappose, progressing through more completely pappose forms and ending with the well-developed radial pappus of the Galinsoginae. The paleaceous, mostly epappose groups show one further trend from types with separate strictly male and female flowers to those with heterogamous heads. These patterns are believed to represent phyletic trends in the tribe. Two subtribes in Bentham's treatment of the Heliantheae that were characterized by reduced numbers of flowers in the heads are considered here to have been artificial.

The Bentham system was perpetuated essentially intact by Hoffmann in *Die natürlichen Pflanzenfamilien* (1890–1894).

Small (1917–1919) proposed a phylogeny of the family which patterned the relationships closely after Bentham's system. *Senecio* was selected as the ancestral genus because it had the most species and the widest distribution. Small might have drawn some support from the extreme diversity of the Senecioneae as delimited by Bentham, but this was not considered. Small's concepts have no present support.

The essential points of the more recent phyletic system of Cronquist (1955) continue to have some support (Conquist, 1977a; Turner, 1977). The system virtually enshrines the work of Bentham as perceived by Cronquist in what should be called the "heliocentric theory of the Compositae." The Heliantheae are considered the ancestral stock of the family, giving rise directly to all the other tribes but one. The family is seen as a near continuum, with the exception of the Lactuceae, which are held unnaturally distinct because of their ligulate heads and latex. Almost all phyletic stages in the family are presumed to survive, with the extant helianthean genus *Wyethia* closely approximating the ancestor of the family. Highly specialized structures such as the pappus are presumed to be in their primitive form when they have a shape more like a calyx, and involucral bracts are presumed primitive when they look more leafy.

The present paper not only disagrees with various conclusions of Cronquist, but also with some of his methods of approach. The 1955 paper tried to interrelate the tribes of Bentham without a proper foundation study of tribal limits. Cronquist did doubt the naturalness of the Helenieae as a separate tribe from the Heliantheae, but one of the primary examples he cited was the misplaced asterean genus *Rigiopappus*. Cronquist relied heavily on secondary sources and on studies at the floristic level. This superficial approach resulted in every morphological convergence being misconstrued as a reflection of close relationship. Circular reasoning was employed to justify the ancestral position of the Heliantheae, that tribe being said to have primitive character states, but the character states being determined as primitive primarily by the fact that they are found in the Heliantheae. Finally, Cronquist completely overlooked the fact that many members of the Eupatorieae share the same "primitive" character states as the Heliantheae, and that the former tribe would be more ancestral according to his own criteria.

Carlquist (1957) published a study of the genus *Fitchia*, which used microcharacters in reference to some tribal and subtribal relationships of the Heliantheae. *Fitchia*, with its ligulate heads, was shown to be a member of the Heliantheae near the Coreopsidinae, with no direct relationship to the Lactuceae in which it had been placed by Bentham. Carlquist showed that other distinctive insular genera were also related to the Coreopsidinae, and he made observations on the basic dissimilarity of the two genera *Lagascea* and *Coulterella* then placed in the subtribe Lagasceinae.

In recent years, three significant papers on relationships within the Heliantheae have been published by Stuessy. The first (Stuessy, 1973) initiated the much needed dismemberment of the subtribe Melampodiinae. The second (Stuessy, 1976) reduced the subtribe Lagasceinae to synonymy, placing *Lagascea* in the Helianthinae and suggesting a position for *Coulterella* near *Flaveria*.

In the third paper, for the Symposium on the Biology and Chemistry of the Compositae, Stuessy (1977) presented a complete survey of the Heliantheae, including some elements such as the Bahiinae and Gaillardiinae from the Helenieae. *Schistocarpha* and *Neurolaena*, transferred to the Heliantheae from the Senecioneae by Robinson and Brettell (1973b), were accepted, but other genera, including many from the Helenieae and two from the traditional Heliantheae, were referred to the Senecioneae. Stuessy was not able to take advantage of the information in the symposium contribution of Nordenstam (1977), where various helianthean genera were rejected from the Senecioneae. The Tageteae were not considered by Stuessy and were treated as a separate tribe in the symposium (Strother, 1977). *Marshallia* was considered by Stuessy as possibly Eupatorieae, but the eupatorian *Isocarpha* was included, apparently because of its well-developed paleae and its resemblance to *Spilanthes* in habit.

In the Stuessy survey, the name "Helianthinae" was used correctly for the typical element, which had been under the name "Verbesininae" in the works of Bentham and Hoffmann; however, there was a confusing reintroduction of the name "Verbesininae" for a segregate subtribe containing many genera, including *Lagascea*. The name "Ecliptinae," dating from 1831, was resurrected for a largely natural group of genera that previously had been distributed among four different subtribes. Stuessy was able to present an entirely natural concept of the Ambrosiinae as a result of his 1973 work. The subtribe Engelmanniinae was created, being properly removed from the Melampodiinae, but its ties to the Ecliptinae were not recognized. The Coreopsidinae was enlarged to contain a number of related genera, but a few other unrelated genera were included, and the distinctive obcompressed disk achene was not mentioned, although it had been noted in older literature. The Gaillardiinae was redelimited with great accuracy, but was considered close to the Helianthinae, possibly because of the superficial resemblance between *Gaillardia* and *Rudbeckia*. The artificiality of some subtribes such as the Milleriinae and Neurolaeninae was greatly increased by Stuessy. Among the genera placed in the Neurolaeninae was *Bebbia*, which had been traditionally correctly placed in the Galinsoginae. Also, the transfer of *Spilanthes* from the Verbesininae to the Galinsoginae was inexplicable, being counter to all recognized evidence regarding achene structure.

One of the most notable features of the Stuessy survey is the great faith placed in chromosome numbers, some relationships between genera seeming to be based on this characteristic alone. A diagram of hypothetical evolutionary relationships suggests three main lines for the tribe, the first with $X = 15$, 16, and 17, the second with $X = 12$, and the third with $X = 8$ and 9. Such a proposal conflicts with the evidence of extensive instability in chromosome number in many subtribes of the Heliantheae.

The symposium treatment of the Helenieae (Turner and Powell, 1977) is most notable for the complete dissolution of the tribe. A number of subtribes are recognized that combine genera from the traditional tribes Helenieae and Senecioneae. Unfortunately, the resulting groups are placed mostly in the Senecioneae.

Helianthean elements, including those rejected from the Heliantheae and Helenieae by Stuessy (1977) and Turner and Powell (1977), are excluded from the Senecioneae in the symposium treatment of the latter tribe by Nordenstam (1977). Eighteen characters are cited that indicate the helianthean rather than senecionean nature of the genus *Arnica*, including phyllotaxy, nectary shape, presence of numerous corolla hairs, achene wall with a carbonaceous layer, shape of achene hairs, pollen structure, epidermal structure and UV patterns of the rays, embryo sac with 2 antipodal cells, presence of apomixis, serological data, chromosome number, presence of helenanolides, and the lack of both furanoeremophilines and pyrrolizidine alkaloids. Many of the characters apply equally well to other helianthean genera that are to be rejected from the Senecioneae.

The chemical evidence regarding the tribal position of *Arnica* has been clarified further by Robins (1977), especially in regard to pyrrolizidine alkaloids. The presence of a senecionean type of pyrrolizidine alkaloid is noted in *Doronicum*, a genus often placed close to *Arnica*. The chemistry reinforces conclusions based on structural details, that the two genera are not closely related, and *Doronicum* is properly placed in the Senecioneae.

As the present study has progressed, a number of individual contributions on the genera *Lundellianthus* (1978a), *Kingianthus* (1978b), *Podachaenium* (1978c), *Alloispermum* (1978d), and *Smallanthus* (1978e) have been published by the author. The last four of these involve the recognition of subtribally distinct elements within traditional genera of the tribe. Three papers (Robinson, 1978g, 1979a, 1980a) have validated 16 subtribes, including 15 established as a direct result of the study. Information on the distribution of corolla fibers in the Ecliptinae was introduced in the paper on *Lundellianthus* (1978a), and various characters including resin ducts have been discussed in relation to the limits of the Galinsoginae (Robinson, 1979b).

A separate series of studies has led to the recognition of a new subtribe, Espeletiinae, including a number of new genera (Cuatrecasas, 1976), which are adopted in this treatment.

Review of Taxonomic Characteristics

Almost any genetically controlled feature of a plant is potentially useful in taxonomy at some level. Even so, the value of any one character is reliably determined only by comparison with a phylogeny obtained from maximum correlations between all available characteristics. Still, the stability of some features might be predicted on the basis of the function that they serve. Many microstructures are basic to survival and are modified only at great risk. Many parts involved in pollination are factors in species isolation and vary in the process of speciation. Various secondary metabolites are defensive in nature, as discussed by Cronquist (1977b), and taxonomic significance can vary greatly. General chemical types are often of phyletic significance, but individual compounds usually vary with the tastes or tolerances of herbivores or parasites. In most cases, the absence of a character is found to be less significant than variations in a character that is present.

The following survey includes traditional characters used in the classification of the Heliantheae (some of which have been overemphasized) and other characters that previously have been ignored. Such features are all of potential use in generic delimitation and should be included in any analytical generic descriptions. Not all are as useful above the generic level.

HABIT.—Cronquist (1955) favored a herbaceous ancestor for the Asteraceae, but since the various studies of wood anatomy of the family by Carlquist (1966), there seems to be general agreement by all, including Cronquist (1977a), that the ancestor was woody. This ancestral condition of the family is presumed to extend to most of the individual tribes, particularly the Heliantheae. The pattern of relationships within the tribe accepted in the present paper in no way conflicts with this view, and partial support is provided by the evidence that $X = 19$ is functionally the ancestral number for almost all of the extant members of the tribe.

The annual habit occurs widely in the tribe and is common in diverse subtribes such as the Galinsoginae, Dimeresiinae, Madiinae, and Baeriinae. The same subtribes are characterized by chromosome numbers of $X = 10$ or less. It is my present view that both annual habit and low chromosome number represent derived conditions in the tribe, being found primarily in three separate evolutionary lines, each of which contain numerous closely related subtribes showing the more common perennial habit and higher chromosome number.

PHYLLOTAXY.—The spatial relationships of leaves, especially as they effect the distribution of flowers in an inflorescence, may have functional importance in a plant. However, the often utilized simple difference between opposite and alternate leaves on vegetative stems does not seem to be under strict constraints, and it seems useful to keep in mind the simple physiological basis of the character. In the meristem, auxin from each growing point suppresses the development of new growing points in its immediate vicinity. Patterns of distances between the central growing point and those leaf primordia already formed in the meristem determine whether one or more new primordia will develop during each plastochron. Distances in the meristem have no direct relationship to the ultimate width of the stem, as can be seen in the mature stems of many alternate-leaved Espeletiinae. Near or at the time of inflorescence formation, there is a tendency for the meristem to become more conical, and the reduction in primordium distances may suppress the opposite-leaved condition, even when that condition is present in the basal part of the plant. A rare reversal of this is seen in *Espeletia*, where the vegetative parts bear alternate leaves, but the bracts of the lateral inflorescences are opposite.

Whatever the basis, the opposite- versus alternate-leaved condition shows some interesting patterns in the family at species, generic, and tribal levels. It is notable that two of the three tribes in which opposite leaves predominate are the Heliantheae and Eupatorieae. Still, both of these have many alternate-leaved species and genera. Opposite-leaved exceptions also occur in basically alternate-leaved tribes, including *Baccharis spicata* (Lam.) Baillon and *B. corymbosa* (R. & P.) Pers. in the Astereae, *Luciliopsis* in the Inuleae, *Chuquiraga oppositifolia* Don in the Mutisieae, and various species in the Senecioneae, including two species of *Herodotia* and most species of *Gynoxys*. In the Vernonieae, a few species of *Vernonia* such as *V. stellata* (Spreng.) Blake of Brazil and *V. sparrei* H. Robins. and *V. harlingii* H. Robins. from Ecuador have opposite leaves (Robinson, 1976b, 1979c), and both opposite and whorled leaves occur in the African *Bothriocline* Oliv. ex Benth.

To the extent that it can be seen to work, phyllotaxy should be used in identification and minor phyletic speculation, but the character seems very unreliable at higher levels of classification. Phyllotaxy is certainly not sufficiently reliable for speculations at the family level, as attempted by Cronquist (1955).

SECONDARY AND TERTIARY HEADS.—The reduction of individual heads and their enclosure in a secondary or even tertiary involucre occurs sporadically in the family. A clear example of secondary heads in the Heliantheae is *Lagascea* (Stuessy, 1978). Here, one can see a true involucre of semi-paleaceous aspect around each flower, and a secondary involucre is formed around the cluster. Elsewhere in the family, *Echinops* has flowering structures variously interpreted as secondary or tertiary heads. Expression of genes seems to be transferred from one structure to another. Furthermore, the physiological machinery by which plants developmentally differentiate their parts seems to fail in such complex inflorescences, producing structures that are morphogenetic hybrids.

INVOLUCRE.—Contrary to the generalization of Wagenitz (1976), subimbricate or imbricate, scalelike involucral bracts occur widely in the family in both subfamilies. It is my belief that they are the primitive type in the family. The various other types, such as 1-2-seriate interlocking form in the Senecioneae or the herbaceous form of many Heliantheae, are endemic to their tribes, and they seem specialized. Cronquist (1955) holds the herbaceous involucral bract of the Heliantheae as primitive because of its greater similarity to the vegetative leaf with which it is homologous. This ignores the fact that the involucral bracts are bud-scales, a type of structure widely produced by higher plants without recourse to intermediate forms.

Actually, most hypotheses on the origin of the asteraceous head do not take into account adequately the budlike nature of the head and the probability that it was a specialization associated with seasonal flowering.

PALEAE.—In the Heliantheae, all variations of palea development are represented, including the most persistent and most foliaceous types in the family. The paleae represent the subfloral bracts that are theoretically present in all heads, and there is a tendency to interpret the most prominent and most foliaceous types as primitive. The Heliantheae with the larger paleae, however, are among those with more herbaceous involucral bracts, and it seems likely that the two homologous structures are both specialized in their leaflike aspects.

Traditionally the tribe has been restricted to those members having paleae, and the epaleaceous members have been placed in a separate tribe, Helenieae. More recently the palea character has been given less support, and Cronquist (1955, 1977a) has recommended reduction of the Helenieae to synonymy. A few of the epaleaceous elements were placed in the Heliantheae by Turner and Powell (1977). Most members of the present concept of the Heliantheae are paleaceous, and it is probable that this is the primitive condition in the tribe. Isolated examples, such as *Eclipta* with its filiform paleae and the epaleaceous *Geissopappus* group in *Calea*, evidently are reduced from more paleaceous forms. In contrast, the paleae in the Madiinae, especially those on the disk as in *Blepharipappus*, the paleae in *Hymenopappus newberryi* (A. Gray) Johnston, and the tendency toward a single row of paleae in *Helenium* and *Gaillardia* seem to represent revived structures in subtribes where expression of paleae is usually suppressed. It is probable that the paleaceous *Varilla* is related to the epaleaceous Clappiinae, as indicated by Turner and Powell (1977), but I interpret the unusual form of paleae in *Varilla* as another example of a reversion from epaleaceous ancestors. Such palea variations should not always be interpreted as reduction series in the Heliantheae or in any other tribe. In the Eupatorieae, paleaceous types occur sporadically, and at least some seem definitely to have immediate ancestors that were epaleaceous, indicating that caution is needed in interpreting the structure.

The variations in palea development in the tribe should not be overemphasized, however. The present analysis of the Heliantheae indicates that, with the few exceptions, the epaleaceous members of the tribe are more closely related to each other than to the paleaceous members. This suggests more integrity for the "Helenieae" than is allowed by Cronquist (1955, 1977a) or Turner and Powell (1977). The present study shows, nevertheless, that the epalecaeous subtribes are best included in the Heliantheae.

SEXUALITY OF FLOWERS.—The Heliantheae show great variety in the distribution of partially to completely sterile flowers in the heads. The basic pattern of all radiate Asteraceae, the female ray and the bisexual disk flower, is found in most members of the tribe. There are many scattered examples of secondary loss of rays, and in a few examples such as *Tridax*, some species have zygomorphic bisexual peripheral flowers (Powell, 1965).

Numerous Heliantheae in the paleaceous series possess a trait seen in the family only in the advanced members of the subfamily Asteroideae and a few genera of the remote tribe Mutisieae: the suppression of the gynoecium in some flowers. In the extreme, whole heads are functionally male while other heads are female. The two types of heads occur on the same plants in many Ambrosiinae, while *Podanthus* of the Ecliptinae is dioecious. *Petrobium* of the Coreopsidinae has been credited with dioecy, although this has been questioned (Carlquist, 1957; Stuessy, 1977). A third supposedly dioecious genus, *Astemma*, definitely is not (Robinson, 1976a).

A common specialization in the tribe is the functionally male disk flower. The character has been a primary basis for the traditional concepts of the Milleriinae and Melampodiinae. In such cases, the disk style may or may not be defective as in *Melampodium*, where branches and stigmatic surfaces are not formed. Such species may have a compensating expansion of the ray styles, as in *Rensonia* and *Smallanthus*. The reliability of the character in the Melampodiinae has recently been questioned by various authors (Stuessy, 1973; Turner, 1978a), and various members of the subtribe have been transferred to other subtribes which include genera with bisexual disk flowers. The present treatment confirms many of these observations and makes similar revisions in the Milleriinae.

A nearly unique development in the Heliantheae is the completely sterile ray flower. Both stamens and styles are lacking. This specialization occurs in all radiate members of the subtribe Helianthinae and also occurs in many other genera, such as *Encelia*, *Oyedaea*, *Balsamorhiza*, and others in the Ecliptinae, *Montanoa* in the Montanoinae, and all members of the Rudbeckiinae. The sterile ray seems restricted to the paleaceous members of the tribe, but seems rather randomly distributed within that series, being precluded only in those members with functionally male disk flowers.

At present it is thought that numerous parallelisms are involved in the distributions of various sexual functions in the heads of the Heliantheae. In the various combinations, only the obviously nonfunctional have been avoided, such as gynoecial suppression in both ray and disk flowers. A particularly notable example of variation in a closely related group is the occurence of sterile rays, functionally male disk flowers, and fertile achenes in both ray and disk flowers among species presently placed in the genus *Wedelia* (McVaugh, 1972).

RAY COROLLA.—The tip of the limb of the ray is basically three-lobed. In most Heliantheae, however, the median of the three lobes is reduced or even completely lacking. The third lobe is more prominent in a number of subtribes such as the Gaillardiinae and Coreopsidinae, and it has been useful in this study in redelimiting the Galinsoginae and Milleriinae.

The cells of the ray surface have been studied recently by Baagøe (1977a,b, 1978). The length and bulge of the cells is often consistent in related groups. The shape of the cells of the upper surface is usually directly correlated with that of the cells on the inner surface of the disk corolla lobes.

DISK COROLLA.—Many genera of the Heliantheae have disk corollas containing fibers along the veins of the throat. These may occur in sparing amounts or can form complete sheaths. In genera such as *Borrichia* and *Rensonia*, the fiber-sheaths extend into the lobes, and *Synedrellopsis* has supplementary strands of fibers between the veins of the throat. All the genera showing such fibers share carbonized achenes without striations and have black anthers. Some of the genera having fiber-sheaths have obvious relatives that lack the character, but all the genera having the character are members of the Ecliptinae, and the character apparently is unique to that subtribe. The genera with fibers seem to form three groups within the subtribe. The primary group has already been recognized in large part by Stuessy (1977) on the basis of other characters. It centers around *Wedelia* and includes *Delilea* and *Synedrellopsis* of the traditional Milleriinae, *Rensonia* and *Schizoptera* from the Melampodiinae, *Synedrella* and *Calyptocarpus* of the traditional Coreopsidinae, and the genera placed by Stuessy in his subtribe Engelmanniinae.

FILAMENTS.—Pubescence on the filaments occurs sporadically in the Heliantheae. The most notable examples are *Guardiola* of the Guardiolinae, *Viguiera dentata* (Cav.)Spreng. of the Helianthinae, *Rojasianthe* of the Ecliptinae, *Cosmos* of the Coreopsidinae, and the uniquely glandular-haired *Venegasia* of the Chaenactidinae.

ANTHER THECAE.—Many genera of the Heliantheae have anthers that blacken at maturity due to pigments in the outer layer of the thecial wall. This blackening sometimes extends to the anther appendage, where it may be useful as a species character (Heiser, 1957; Robinson, 1979d). Such blackening is rare outside of the Heliantheae, but it is found in some genera such as *Munnozia* in the Liabeae and in the appendage of *Perezia* in the Mutisieae.

In the Heliantheae, the black color of the anthers is sometimes poorly developed in subtribes where it normally occurs, but there are many significant groups in which it is characteristically lacking. Pale anthers are a useful key character for distinction of the subtribe Ambrosiinae (Stuessy, 1977). The pale anthers found throughout most of the epaleaceous subtribes tend to support the distinctness of that series within the tribe.

The seemingly black anthers of some genera such as *Smallanthus* and *Icthyothere* show a more reddish color under the microscope, and anthers of the Madiinae are often quite reddish. Anthers of the anomalous *Marshallia* tend to be violet. In the Neurolaeninae, the *Calea* group can be delimited by anther thecae with a distincive yellow color. In various genera such as *Guardiola* and *Schistocarpha* the dark anthers may be greenish.

ENDOTHECIAL CELLS.—A basic feature of the anthers of most angiosperms is the thickenings in the walls of the endothecial cells that function in the opening of the valves. In some families such as the Melastomataceae and in genera such as *Solanum* where the anthers open by pores, the thickenings are lacking. In the Asterales, pollen release is facilitated by a plunger action of the style, and the essential function of the endothecial thickenings apparently is diminished, as evidenced by variations and reductions in the patterns. Dormer (1962) has provided a preliminary classification of these patterns; the two most important types are "radial," where the thickenings are evenly distributed along both the lateral and transverse walls, and "polar," where the thickenings are restricted to opposing walls, either the lateral or the transverse.

The radial pattern of thickenings seems characteristic of fully functional angiosperms, and it seems primitive in the asteralean line. Since the point of origin of the plunger-type style is not known, the earliest possible point for reduction of endothecial patterns is not known. It is notable that the Eupatorieae have only a few minor variations on the radial design, while the Heliantheae and most other tribes have primarily variations of the polar patterns.

The majority of Heliantheae have endothecial thickenings polarized on the transverse walls. Radial patterns occur in a few isolated groups in the tribe, some species of *Melampodium* and *Dahlia*, the genus *Lasthenia*, the subtribe Ambrosiinae, and most members of the subtribe Rudbeckiinae. Another variation in the tribe involves polar thickenings on the lateral walls, as in two species of *Tridax* and the genera *Chamaechaenactis* and *Oxypappus*, all of which apparently represented isolated occurrences.

A significant trend in the number of thickenings and the shape of the endothecial cells is seen in the subtribes once placed in the Helenieae. The Peritylinae and Baeriinae have short cells with 2–5 thickenings on the transverse walls, which reach an extreme in the radial patterns of *Lasthenia*. Genera of the Chaenactidinae such as *Palafoxia*, *Florestina*, and *Schkuhria* have short cells with single thickenings. Other genera of the subtribe, such as *Arnica* and its relatives, and the genera of the Gaillardiinae have longer elliptical cells with 1 or 2 thickenings at the ends.

ANTHER APPENDAGE.—In the Heliantheae, the anther appendages are usually ovate with a constricted base. Such appendages relate the tribe to the Anthemideae-Astereae-Inuleae-Senecioneae series, which has appendages usually constricted at the base and sometimes constricted throughout. The anther appendages of the Heliantheae usually have a radiating pattern of cells that might reflect an expansion of a basically narrower structure. In contrast, the appendages of the Cichorioideae and the tribe Eupatorieae are basically as broad as the thecae and have no radiating cell patterns.

The presence of hairs or glands on the appendage in the Heliantheae is not regarded here as primitive, but as a transfer of a character commonly occurring elsewhere in the plant. Such anther pubescence is also seen in the Inuleae, in *Cyathodine jacquemontii* Gagnep. of the Astereae (Fayed, 1979), and in the more remote tribe Vernonieae.

STYLE.—Pubescence on the style base occurs in only two tribes of the Asteraceae. In the Eupatorieae, the character is widely distributed, and there is even one example of hairs on the nectary (King and Robinson, 1974). In the Heliantheae, hairs are found on the style base in three genera of the Chaenactidinae. The presence of such hairs supports the general impression of relationship between the two tribes. Other tribes apparently have completely lost the potential to produce such hairs. The form of the pubescence does not directly parallel that elsewhere on the plant, and its presence does not seem to represent a simple transfer of characters. The potential to produce hairs on the base of the style is widespread in the angiosperms and is regarded here as primitive among the advanced families.

The presence of two distinct stigmatic lines on each style branch seems basic in the subfamily Asteroideae, whereas a continuous stigmatic inner surface is characteristic of the Cichorioideae.

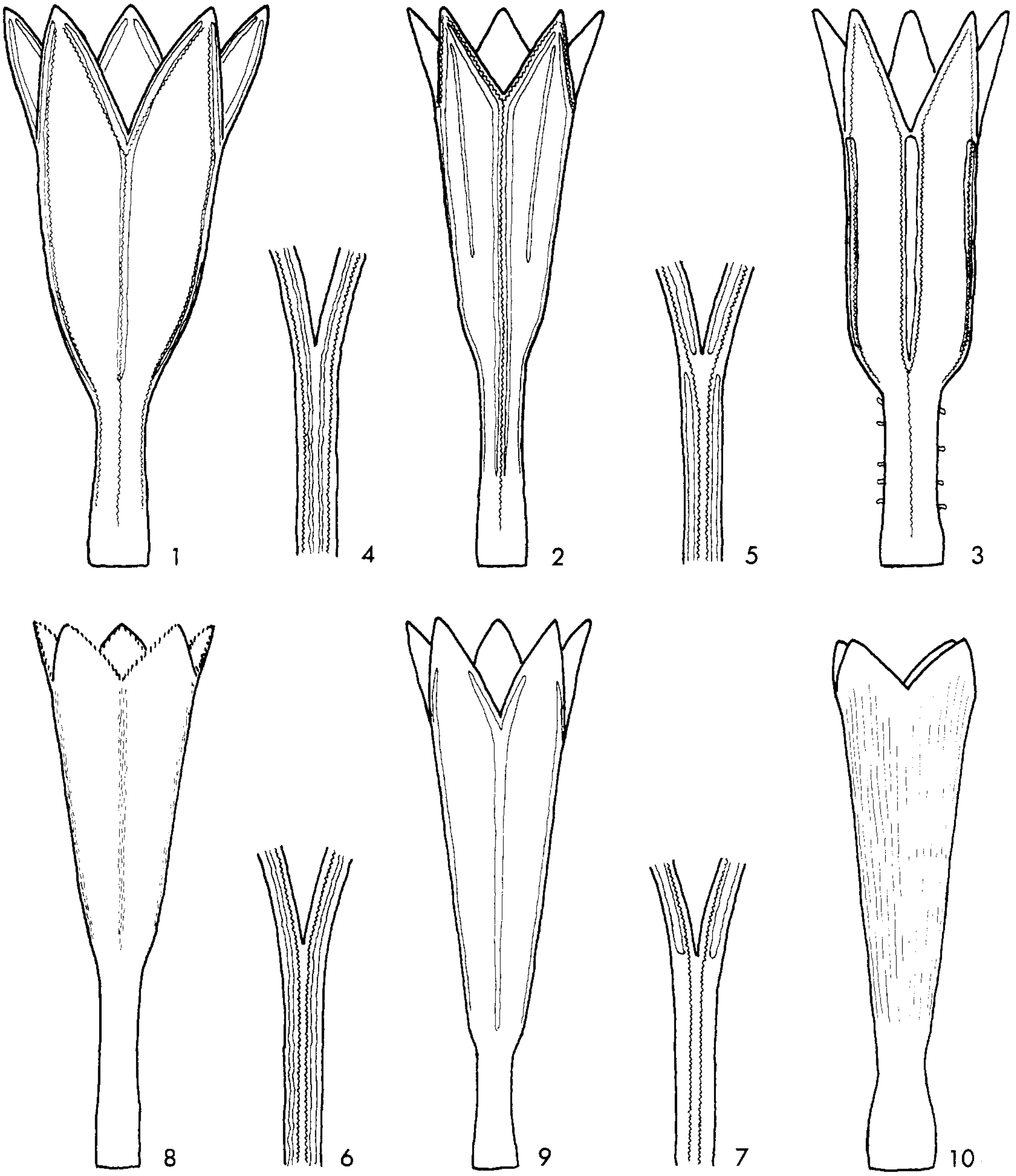
There are fused stigmatic surfaces in the cacalioid Senecioneae and in many Heliantheae, but these occur in groups showing no other cichorioid features, and these exceptions in the Asteroideae are regarded as specialized. Most Heliantheae have two stigmatic lines, but fusion seems to have occurred separately in a number of subtribes in the paleaceous series. Fused surfaces are characteristic of the Helianthinae and Zaluzaniinae, and they occur in many Ecliptinae and some Coreopsidinae. The Galinsoginae, which resemble the Helianthinae in many ways, are sharply distinguished by the presence of two stigmatic lines. The lines are often very close, and the division difficult to see in some Heliantheae with two lines, including some of the Galinsoginae.

RESIN DUCTS OR CANALS.—Resin or secretory ducts occur widely in the Asteraceae. Ducts in vegetative tissues have been extensively studied by Col (1899–1904). Anderson (1970) has studied secretory canals in floral parts of members of the Astereae, and in various reports has emphasized the wide distribution of these structures in various tribes, even though they are often difficult to observe. Actually, ducts are often very obvious because they often contain highly colored resin. The numerous reddish ducts in the involucral bracts and the paleae of many Coreopsidinae are sometimes useful in recognition of the subtribe. The first significant detailed study of secretory ducts in flowers of the Heliantheae seems to have been in certain Coreopsidinae and in the closely related Fitchiinae (Carlquist, 1957). Ducts in some other genera such as *Flourensia*, *Helianthus*, and *Wyethia* were also noted in the study. Colored ducts seem to reach their greatest development in the Coreopsidinae, where they appear in the anther appendges (Robinson and Brettell, 1973a) and in the achenes of some genera. Colored ducts are not found in the anther appendages or achenes in the other subtribes of the Heliantheae.

The color of the resin ducts has proven useful in the study of the tribe, and the chemical basis of the color should be studied more extensively. The distribution of some compounds might be determinable by simple visual examination. Different types of chemicals might be involved. A preparation shows that resin in the style tips of *Echinacea* has some reddish pigment that might be derived from the surrounding tissue. The pigment presumably is an anthocyanin. Nevertheless, the ducts have been noted as the site for polyacetylene compounds, and it seems these are a primary source of the colors. Sørensen (1977) indicates that the ducts in some cases are colored red because of polyacetylenes containing the unstable dithiin ring. The genera listed as having such compounds by Bohlmann et al. (1973) have shown little or no reddish resin in this study, but my observations have been mostly restricted to dead material in Hoyer's solution.

On the basis of the survey of material in Hoyer's solution, the majority of the subtribes lack colored resin. It is particularly rare in the epaleaceous series. The lack of colored resin in the Ecliptinae of the paleaceous series is notable because of the marked color of the resin in some of the subtribes with which it previously has been confused. The resin is rather reddish in a number of subtribes, including the Coreopsidinae and Neurolaeninae. The Helianthinae and Galinsoginae (the two subtribes marked by the presence of the polyacetylene dehydrofalcarinone) have a yellowish resin. The Desmanthodiinae also have yellowish resin, but they have not yet been analyzed chemically.

The relative positions of the ducts in the corollas and styles are also taxonomically significant. In the throats of the disk corollas, the ducts and veins show three basic patterns. The first pattern (Figure 3) is rarest, where one duct is between two veins, as in *Varilla*. This pattern occurs to a lesser extent in such genera as *Clappia* and *Clibadium* and is slightly developed in *Unxia*. The second pattern (Figure 1) is most common, with one duct inside of the vein. This can be seen most clearly in the Neurolaeninae, where the duct is colored, but is also typical of such subtribes as the Ecliptinae. The third pattern (Figure 2) has the ducts paired, one duct on each side of each vein in the disk corolla throat. Such a pattern is seen in most Galinsoginae, in many Helianthinae, and



Figures 1–10.—Resin duct and fiber patterns in flowers of the Heliantheae: 1–3, corollas with veins as zigzag lines and with resin ducts as paired lines (1, *Calea eitenii* H. Robins., with one duct overlying each vein in corolla throat; 2, *Schistocarpha bicolor* Less., with ducts paired along each vein of throat; 3, *Varilla mexicana* A. Gray, with single duct between paired veins of throat); 4–7, styles with relative positions of veins and resin ducts (4, *Galinsoga* type; 5, *Tridax-Lagascea* type; 6, *Helianthus* type; 7, *Heliomeris* type); 8–10, corollas of Ecliptinae with patterns of fibers (8, *Synedrella nodiflora* (L.) Gaertn., with sheaths restricted to veins of throat; 9, *Rensonia salvadorica* Blake, with sheaths extending into lobes; 10, *Synedrellopsis grisebachii* Hieron. & O. Kuntze, with fibers dispersed in corolla throat). (Corollas redrawn to appear equal in size.)

in the Desmanthodiinae. When only one of the ducts is evident, that duct is located to one side of the vein rather than inside. In both the first and second patterns, the ducts continue upward along the margins of the corolla lobes. In the third pattern, the ducts of the corolla lobe are inside the veins and are sometimes remote from the margins.

The resin ducts in the style usually are outside of the veins, although this is sometimes difficult to see. In groups with colored resin, such as the Helianthinae, Galinsoginae, Neurolaeninae, and Desmanthodiinae, the reliability of the character can be tested. In the Helianthinae, the ducts in the shaft of the style are outside of the veins and extra ducts are sometimes present. In most Helianthinae, the ducts continue outside the veins upward into the branches, as shown by Carlquist (1957) in *Helianthus*. The few exceptions include *Lagascea* and *Alvordia*, where the ducts of the style branches are inside the veins. In *Tridax balbisioides* (H.B.K.) A. Gray, *T. brachylepis* Hemsl., and *T. tambensis* Hieron., the duct arrangement of *Lagascea* is equalled, being outside in the shaft and inside in the branches, but other Galinsoginae and all Desmanthodiinae and Neurolaeninae I have seen have the ducts inside the veins throughout the style or collateral with the veins. There are further examples of discontinuity of the ducts at the base of the style branches, especially in *Heliomeris* of the Helianthinae, which is unique in that the resin ducts seem to be restricted to the branches. Also, the ducts seen in *Spilanthes* in the Ecliptinae are inside the veins in the style branches, rather than outside as is normal in *Acmella* and other genera in that subtribe.

ACHENE WALL.—The surface of the achene provides a number of taxonomic characters. The "zwillingshaare" have been reviewed by Hess (1938), but they have proven of limited use in the present study. The hairs are particularly dense and long in many Gaillardiinae and in *Dyscritothamnus* of the Galinsoginae. Such hairs otherwise are most notable for their absence (along with the pappus) in sporadically occurring "calvous achenes." A minor achene wall specialization, cortication, is seen in *Borrichia*, undoubtedly associated with the maritime habitat of that genus. A distinctive regular pattern of short epidermal cells is found in some genera such as *Polymnia* and *Unxia*. The extensive layer of hard fiber development in the genus *Montanoa* contrasts sharply with the extensive layer of soft tissue in the genera *Smallanthus* and *Ichthyothere*, but all share a tendency for elaboration of the wall that is most common in the subtribes with paleaceous receptacles and functionally male disk flowers.

As presently viewed, the most significant feature of the achenes is the presence or absence of the carbonization or black layer formed by the materials known as phytomelanins. The carbonized layer with the accompanying microscopic punctate appearance is found only in the tribes Eupatorieae and Heliantheae. Phytomelanins are present in all the genera brought to the Heliantheae from the Senecioneae except *Psathyrotes*, but they are absent from all true Senecioneae. The tribes that lack phytomelanins and micropunctations have cells in the walls of the achene containing prominent raphides. In the Heliantheae two subtribes, the Gaillardiinae (including the Psilostrophinae) and the Marshalliinae, lack phytomelanins and have raphides. The two subtribes are not closely related, and the lack of phytomelanins in the Gaillardiinae is evidently a derived condition. The Marshalliinae are near or possibly in the tribe Inuleae, being out of the main line of helianthean development. If phytomelanins are a primitive feature of the family, then their absence in the Gaillardiinae, in the advanced Asteroideae including *Marshallia*, and in the subfamily Cichorioideae all represent independent losses.

In the Heliantheae that have carbonized achene walls, there are often strands or interruptions in the carbonized layer that are referred to here as striations. These are the internal features that can be seen macroscopically as fine longitudinal streaks on the common sunflower seeds. The striations are not vascularized and they do not seem to be structurally related to the supernumerary vascular strands that have been mentioned by

Carlquist (1957) and Stebbins (1977). Such striations are found in the Heliantheae, but they do not occur in the Eupatorieae. Striations seem to be basic to the Heliantheae, and their complete absence from some groups such as the Clibadiinae, the Ecliptinae, and the Neurolaeninae is regarded as a significant specialization. All forms of striations may not be equivalent. Rather broad bands of cells interrupting the carbonized layer occur in *Bidens*, but these are structurally different from striations in other groups. The Coreopsidinae surveyed have otherwise lacked striations. In the genera *Melampodium* and *Smallanthus* of the Melampodiinae, the carbonized areas are strongly convex with the striations recessed. In other groups such as the Helianthinae and Galinsoginae, where striations have a high reliability, the carbonized layer is flat and in the same plane as the striations. In some genera such as *Acanthospermum*, the achenes seem to lack striations, but one or two strands of clear cells have been seen. In *Montanoa*, regular recessed striations are present, but they are difficult to see because of the dense layer of fibers. The costate structure of the achene wall in the subtribes Clappiinae, Flaveriinae, Jaumeinae, and Varillinae represent outward projections of the carbonized layer that have no apparent relation to striations.

CARPOPODIUM.—The basal callus or carpopodium represents the abscission zone at the base of the achene. The variations that often are taxonomically useful also are functional. The asymmetric form of the Galinsoginae leaves an isolated plate that seems to be pulled loose from the receptacle as it dries. The form in the Neurolaeninae is similar, but differs by the firmer cells on the inner surface. Both contrast strongly with the bilobed form as seen in the Helianthinae, which seems to bite itself loose from the receptacle as it matures.

At least some of the asymmetry of the carpopodium in the Heliantheae may be traced to the presence of paleae. In *Calea*, the epaleaceous species (*Geissopappus*) have more symmetrical carpopodia than the paleaceous species. As a further indication of its unique position, *Marshallia* has a symmetrical annuliform carpopodium in spite of the presence of stout paleae on the receptacle.

PAPPUS.—The morphology of the pappus varies greatly in the family, making it useful in identification. But this same variability creates a need for caution in using the pappus as a guide to relationships. The pappus is widely accepted as a remnant of the calyx, and Cronquist (1955) assumed that the more calyx-like, 5-awned, squamose forms were primitive in the family. This idea tended to support the concept of a primitive Heliantheae, since most genera with a capillary pappus had been systematically excluded from the tribe as delimited at that time. This idea overlooked the highly specialized nature of the pappus and presumed the unlikely multiple derivation of a complex capillary pappus from simpler types.

Further evidence on the primitive pappus form is gained from the redelimitation of the Heliantheae, which shows a well-developed capillary pappus in members of both the paleaceous and epaleaceous series. There is no reason to regard the subtribes that are involved (the Galinsoginae, Neurolaeninae, and Chaenactidinae) as more specialized than any others in the tribe. In contrast, the Gaillardiinae, with the most calyx-like pappus of 5 awns, seems clearly specialized in at least the achene wall structure and the chemistry.

At this time, I regard the pappus as the product of a "primordium field" around the periphery of the upper callus of the achene. I believe the primitive form among extant Asteraceae has numerous primordia in one or more series, arranged without direct correlation to other structures of the achene. The derived forms are reduced, with segments limited to positions over the main veins of the achene. The well-developed capillary pappus may contain vascularized bristles, as in *Helogyne* of the Eupatorieae and some Chaenactidinae of the Heliantheae.

The exact equivalence of some pappus structures in the Heliantheae remains in question. Pappus awns of many Heliantheae and relatives of the *Encelia-Verbesina* group in the Ecliptinae look superficially similar, but the former are often dehiscent at the base with a texture more like a true pappus. In the *Encelia-Verbesina* type, the awns are structurally continuous with the body of the achene and often are connected to wings of the achene. Equivalence is cast in doubt further by the form in *Perymeniopsis* of the Ecliptinae, where the two clusters of setae at the outer and inner limits of the pappus are attached at a level below that of the median squamellae (Robinson, 1978f).

The calvous-achened condition occurs sporadically in the Asteraceae in individuals of species normally having a pappus. The condition is particularly common in the subtribe Heliantheae (Robinson and Brettell, 1972b; Robinson, 1977).

SEED COAT.—The surface of the ovule seems to be of particular interest in the Heliantheae, being ornamented in many members in a way not seen in related tribes such as the Eupatorieae. The ornamentation of the ovule surface is much in need of a survey, and it must be observed with care to insure that the correct layer is obtained in a comparable stage of maturity. Nevertheless, on the basis of slides prepared primarily for other purposes, it has been possible to make the following general observations.

A basic type of ornamentation in the tribe is exemplified by *Alloispermum* in the Galinsoginae (Figure 16), which has sinuous lateral walls and distinct annulations on the surfaces. Variations include elongate, nearly straight-walled, densely annulated cells, as in *Acanthospermum* in the Melampodiinae, and more quadrate, irregularly lined cells, as in *Verbesina* or *Eleutheranthera* in the Ecliptinae (Figure 17).

The Coreopsidinae seem to be characterized by firmer-walled cells having straight sides and no annulations (Figure 18). The character is sufficiently marked to support the separation from the subtribe of *Guardiola*, which has elongate, densely annulated cells (Figure 15).

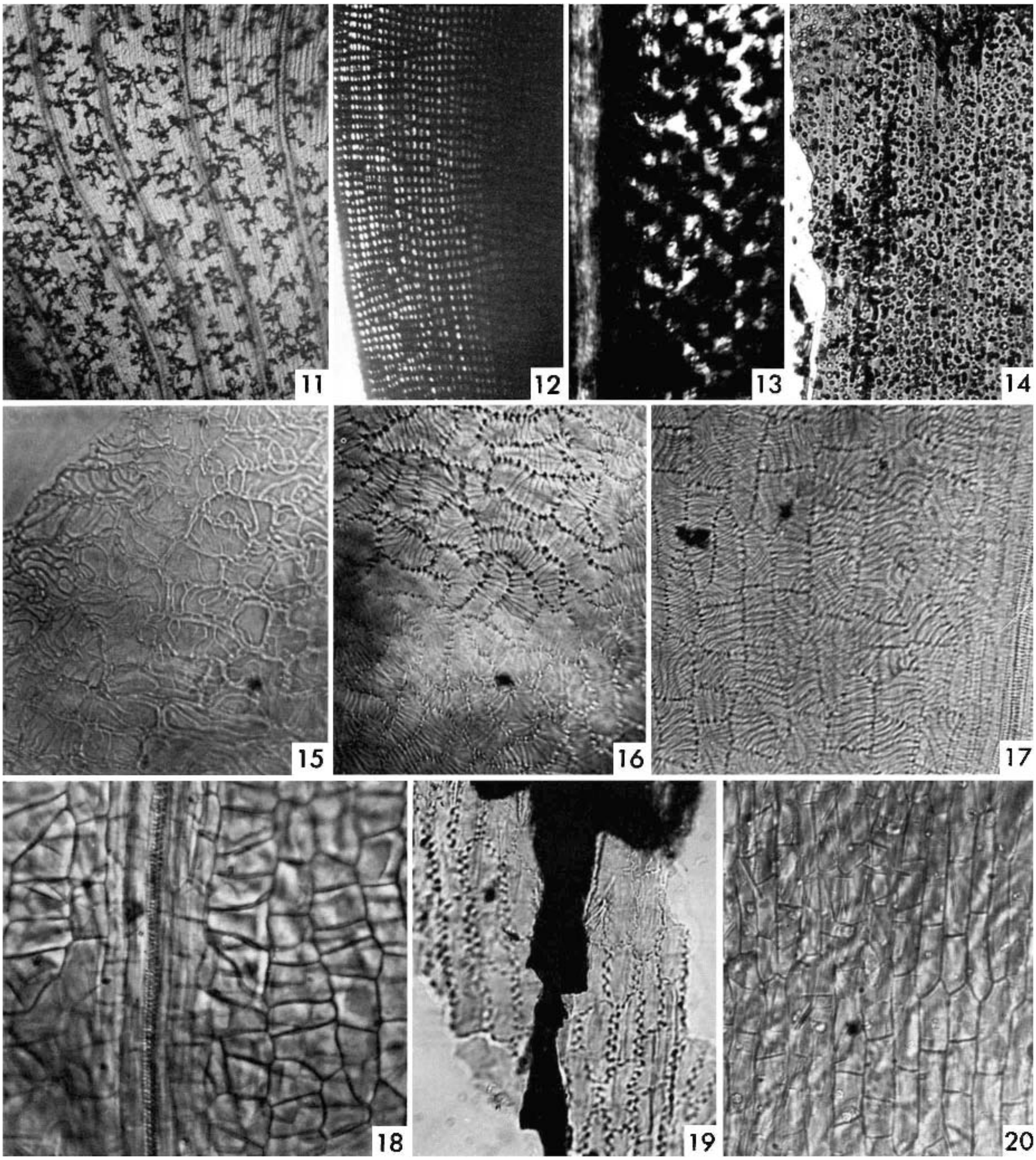
Among the epaleaceous subtribes of the Heliantheae, there are significant differences in the seed coat. The Pectidinae have ornamented cells with distinct annulations. A few subtribes such as the Flaveriinae have cells with only small thickenings along the lateral walls (Figure 19). Ornamentation apparently is lacking in the main series of epaleaceous subtribes, including the Hymenopappinae, the Peritylinae, the Baeriinae, the Chaenactidinae, and the Gaillardiinae.

CYTOLOGY.—The chromosome numbers of the Heliantheae are reviewed in detail by Robinson et al. (in press). An extreme instability is noted in much of the tribe, and most subtribes show evidence of aneuploid decrease from $X = 19$ or 20. The authors differ on whether the higher number is basic to the whole tribe excepting the Marshallinae, or whether polyploidy occurred independently in different lines of the tribe. Of the authors, Robinson and King favor the first interpretation, while Powell favors derivation of a few subtribes such as Galinsoginae and Baeriinae directly from the asteroidean base of $X = 10$.

The present view maintains the polyploid condition as a unifying specialized character of all the Heliantheae of both the paleaceous and epaleaceous series, with subsequent reduction in some cases reaching as far as $n = 3$.

CHEMISTRY.—A number of relationships are beginning to be proposed on the basis of various types of chemicals found in the family. Included are sesquiterpene lactones, polyacetylenes, flavanoids, cytochrome *c* amino acid sequences, and the C_4 photosynthetic pathway.

Among the sesquiterpenes, the lactones of the germacradiene derivatives have proven most taxonomically useful in studies of the Heliantheae. Pathways have been suggested and distributions of various forms in the family have been summarized in the papers of Herz (1973, 1977). A simplified version of the Herz diagram is presented here to show the sesquiterpene lactone types that are significant in systematic considerations of the Heliantheae (Figure 21). The simplest types have an undivided 10-carbon atom ring. Derived forms include two major groups. First are those in which a secondary cross-link divides the larger ring equally into two 6-carbon rings. These include the eudesmanolides, the elemanolides, and eventually in a further step to the eremophilanolides. The other group includes the



FIGURES 11–20.—Microphotographs of achene structures: 11–14, achene walls (11, *Melampodium microcephalum* Less., wall showing striations and initial phytomelanin deposition, × 110; 12, *Acmella* sp., wall lacking striations, × 110; 13, *Flaveria linearis* Lag., showing part of rib and extra knoblike thickenings in phytomelanin, × 260; 14, *Pericome caudata* A. Gray, showing second layer of evenly deposited phytomelanin, × 260); 15–20, seed coats (15, *Guardiola mexicana* H. & B., × 260; 16, *Alloispermum caracasanum* (H.B.K.) H. Robins., × 260; 17, *Eleutheranthera ruderalis* (Swartz) Sch.-Bip., × 260; 18, *Heterosperma pinnatum* Cav., × 260; 19, *Flaveria linearis* Lag., × 260; 20, *Baileya multiradiata* Harv. & Gray, showing cells and raphides, × 260).

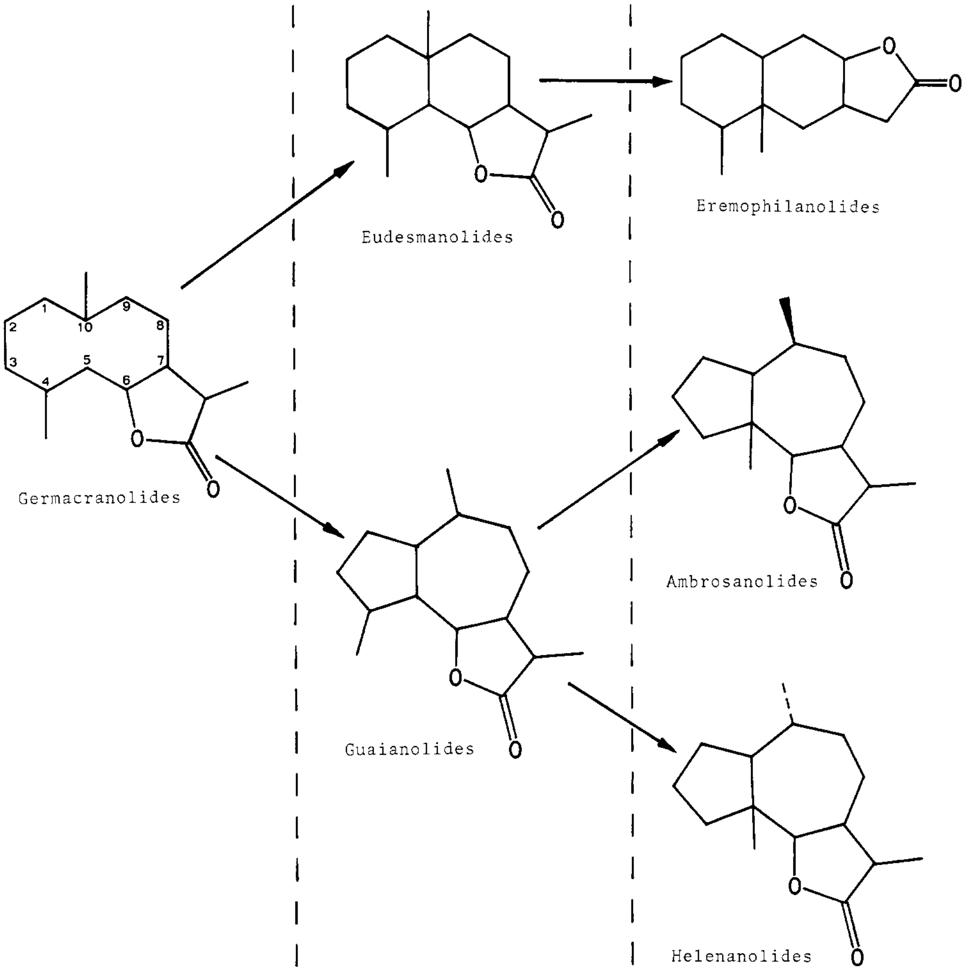
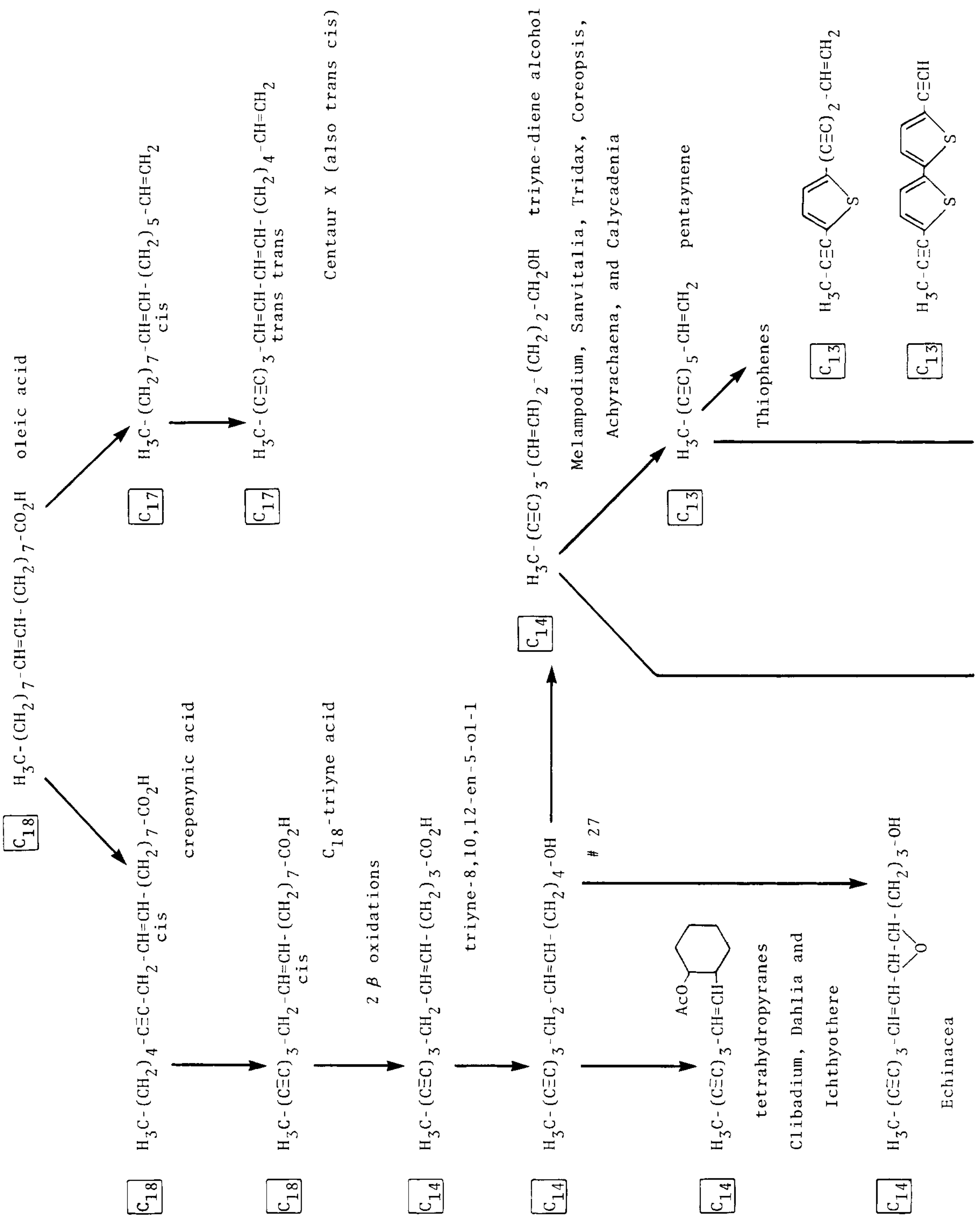


FIGURE 21.—Common forms of sesquiterpene lactones in the Heliantheae showing pathways. (Simplified from Herz, 1977.)

sesquiterepene lactones in which the secondary link divides the original ring unevenly into 5-carbon and 7-carbon rings. These lactones are the guaianolides, and by a further step the ambrosanolides and helenanolides. Most tribes of the family possess only germacranolides, eudesmanolides, guaianolides, and other comparatively simple forms and lack the lactones of the groups in which further steps are involved. Apparently the eremophilanolides, ambrosanolides, and helenanolides are produced only in the more advanced tribes of the subfamily Asteroideae.

Until recently, the production of eremophilanolides was thought to be uniquely characteristic of the Senecioneae (Robins, 1977). More recently two occurrences have been reported in the Heliantheae, in *Dugesia* (Bohlmann and Zdero, 1976) and *Lasthenia* (Bohlmann and Zdero, 1978). Confirmation should be sought for these records. These and possibly other scattered occurrences should not be taken to reflect any particularly close relationship between the two tribes, beyond their both being comparatively advanced members of the subfamily Asteroideae.

The ambrosanolides and helenanolides are derived from the guaianolides by the formation of a quaternary carbon at the C-5 position. Both types were once called pseudoguaianolides, and


C_{18} $H_3C-(CH_2)_7-CH=CH-(CH_2)_7-CO_2H$ oleic acid
C_{17} $H_3C-(CH_2)_7-CH=CH-(CH_2)_5-CH=CH_2$ cis
C_{17} $H_3C-(C\equiv C)_3-CH=CH-CH=CH-(CH_2)_4-CH=CH_2$ trans trans
Centaur X (also trans cis)
C_{18} $H_3C-(CH_2)_4-C\equiv C-CH_2-CH=CH-(CH_2)_7-CO_2H$ cis
crepenynic acid
C_{18} $H_3C-(C\equiv C)_3-CH_2-CH=CH-(CH_2)_7-CO_2H$ cis
C_{18}-triyne acid
2 β oxidations
C_{14} $H_3C-(C\equiv C)_3-CH_2-CH=CH-(CH_2)_3-CO_2H$
triyne-8,10,12-en-5-ol-1
C_{14} $H_3C-(C\equiv C)_3-CH_2-CH=CH-(CH_2)_4-OH$
27
C_{14} $H_3C-(C\equiv C)_3-(CH=CH)_2-(CH_2)_2-CH_2OH$ triyne-diene alcohol
Melampodium, Sanvitalia, Tridax, Coreopsis,
Achyrachaena, and Calycadenia
C_{13} $H_3C-(C\equiv C)_5-CH=CH_2$ pentaynene
Thiophenes
C_{13} $H_3C-C\equiv C-$ S $-(C\equiv C)_2-CH=CH_2$
C_{13} $H_3C-C\equiv C-$ S S $-C\equiv CH$
AcO
C_{14} $H_3C-(C\equiv C)_3-CH=CH$
tetrahydropyranes
Clibadium, Dahlia and
Ichthyothere
C_{14} $H_3C-(C\equiv C)_3-CH=CH-CH-CH-(CH_2)_3-OH$ O
Echinacea

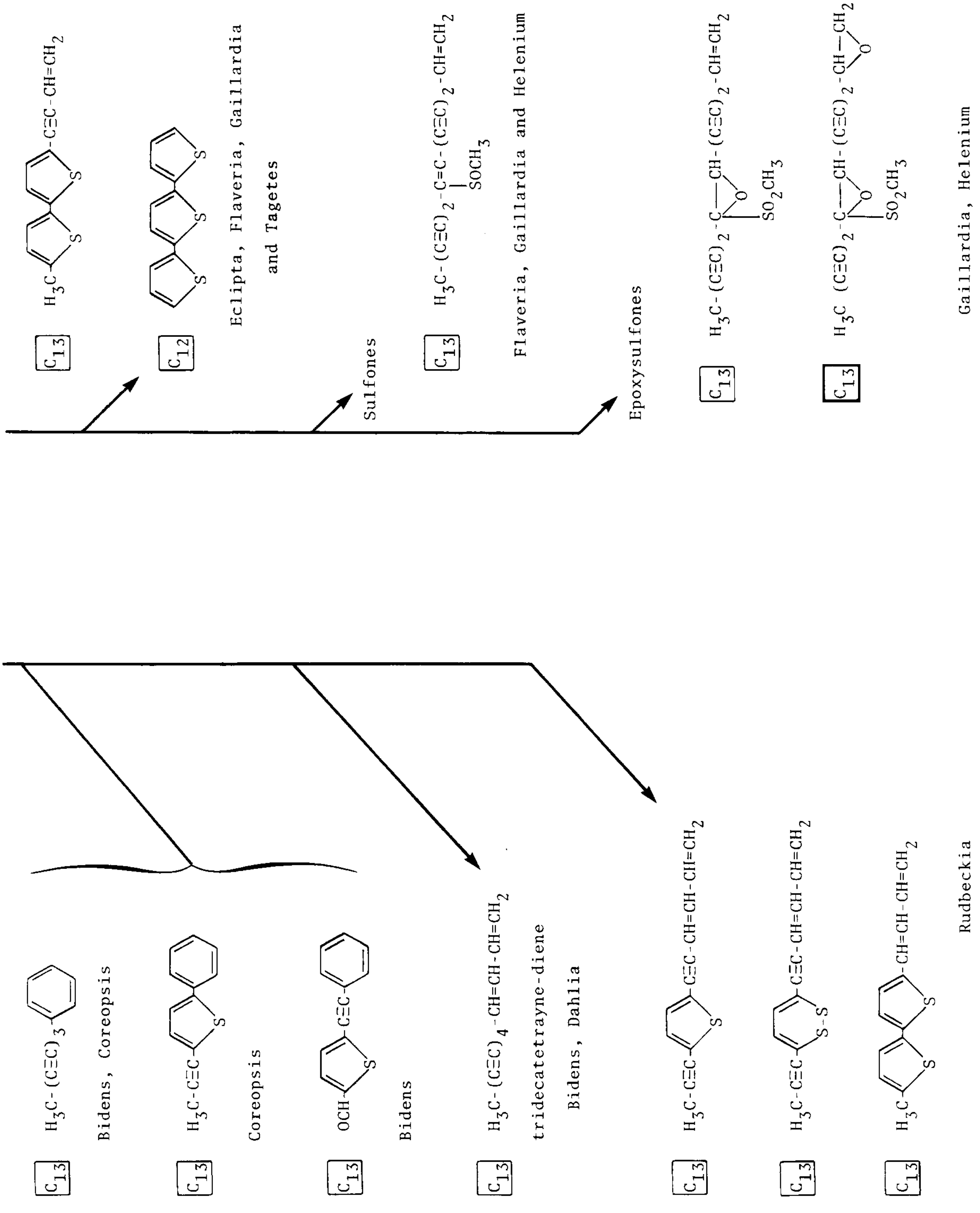


FIGURE 22.—Polyacetylenes of the Heliantheae with methyltriyne endgroups showing suggested pathways. (Based on Bohlmann et al., 1973.)

they differ technically by stereoisomerism at the C-10 position. The basic nature of this seemingly slight difference is reinforced by the different trends seen in lactone formation in the two groups (Herz, 1977), as well as by the fact that they occur in two widely separated groups of the Heliantheae. The stereoisomerism arises at the stage where the secondary cross-link is established, and thus it also occurs in the guaianolide precursors, but there is no evidence in the literature of any preferential occurrence of guaianolide stereoisomers in various Heliantheae. This might indicate that it is the elaborating enzyme systems that are selective in the guaianolide stereoisomers that they can use as a substrate.

Acetylenic compounds include the phytomelanins of the achene walls that are visible and can be surveyed by optical means. Only the presence versus absence or the pattern of deposition of the phytomelanins is considered in this study.

A great variety of acetylenic compounds is available through chemical analysis, and the structure, distribution, and chemical pathways of these have been extensively studied and summarized by Bohlmann et al. (1973). These compounds are well represented in the Heliantheae by products from a number of different pathways.

General pathways of polyacetylene formation as interpreted from Bohlmann et al. (1973) have been diagramed (Figures 22–23). All polyacetylenes are considered to be ultimately derived from fatty acids with 18 carbon atoms, passing through the sequence: oleic acid–linoleic acid–crepenynic acid, the latter being a polyacetylene. A number of pathways diverge from C_{18} crepenymic acid.

A major series of polyacetylenes has a methyl-triyn end-group on the free (nonacidified) end of the molecule. With the exception of the erratically distributed by-product, Centaur X, that has been reported in *Dahlia*, all methyl-triyn polyacetylenes in the Heliantheae are derived from C_{14} triyn-(8, 10, 12)-en-(5)-ol-(1), which is compound 27 in chapter 2 of Bohlmann et al. (1973). Four important subgroups are derived from 27. The C_{13} pentaynene series is widely distributed in the family and is the source of distinctive epoxides, epoxisulfones, dithiins, and most polythiophenes in the Heliantheae. The dithiins of the series are in the Ambrosiinae, *Melampodium*, *Milleria*, *Verbesina*, the Baeriinae, and the Chaenactidinae. The second group from compound 27 includes tridecatetrayne-diene in *Dahlia* and *Bidens* as well as thiophenes and dithiins in *Rudbeckia*. The third subgroup from compound 27 is also shortened to C_{13}, and it produced a phenol group on the initially acidified end of the molecule. The compounds of this pathway found in the Coreopsidinae include some with an additional thiophene unit. The fourth subgroup from 27 retains 14 carbon atoms and produces the "fish poison" tetrahydropyrane found in *Ichthyothere* and the leaves and flowers of *Dahlia coccinea* Cav. An obviously related form of tetrahydropyrane with a ene-diyn-ene (propenyl) end-group rather than a methyl-triyn (propynyl) end-group has been reported from *Clibadium* (Czerson et al., 1979) and the roots of *Dahlia coccinea*.

A number of series of polyacetylenes lacking the methyl-triyn end-group are separately produced from crepenynic acid. One of the simple derivations leads to C_{17} dehydrofalcarinone, which is found in a number of tribes of the family. In spite of its seeming simplicity, dehydrofalcarinone has a significant distribution in the Heliantheae, being rather characteristic of the subtribes Galinsoginae and Helianthinae. There is one anomalous record in *Iva* of the Ambrosiinae.

A C_{16} polyacetylene lacking the methyl-triyn end-group is known from *Dahlia merckii* Lehm., which is the only example of that rare type of polyacetylene in the tribe.

A major group of polyacetylenes lacking the methyl-triyn end-group in the Heliantheae is derived by reduction through C_{14} compounds to various forms with 13 carbon atoms. Among these are the ene-tetrayne-ene group with derived thiophenes and a related group that produces a phenyl unit at the free end of the molecule. The simpler members of the ene-tetrayne-ene series occur in *Guizotia* of the Milleriinae, *Tithonia* of the Helianthinae, *Tridax* of the Galinsoginae, and

Lasthenia of the Baeriinae, but they are most common in the Ecliptinae and the Coreopsidinae. The derived types in the series are concentrated in the Coreopsidinae, but there is one with a phenol unit in *Heliopsis* of the Ecliptinae and some with a thiophene unit in *Lasthenia.*

A derivation of the polyacetylene amides suggested by Bohlmann et al. (1973) is included in the diagram (Figure 23). The amide unit originates from a reaction of the acidified end of the polyacetylene with an isobutyl group from valine peptide. In the Heliantheae, the amides are restricted to members of the subtribe Ecliptinae. Most polyacetylenes are shortened by loss of carbon atoms from the acidified or lower-numbered end of the molecule, but the amides seem unusual by the losses from the usually stable higher-numbered end. Lengths are variable, with both C_{12} and C_{11} in *Acmella* and *Echinacea.* The nonacetylenic amide in *Heliopsis* of the same subtribe seems to have a related derivation as evidenced by the double -CH_2- unit between the units with unsaturated bonds.

Greger (1977) has provided an analysis of the polyacetylenes for the Anthemideae, and a comparison of the Anthemideae and Heliantheae is instructive. Some major pathways seem to differ. The C_{10} series containing dehydromatricaria ester

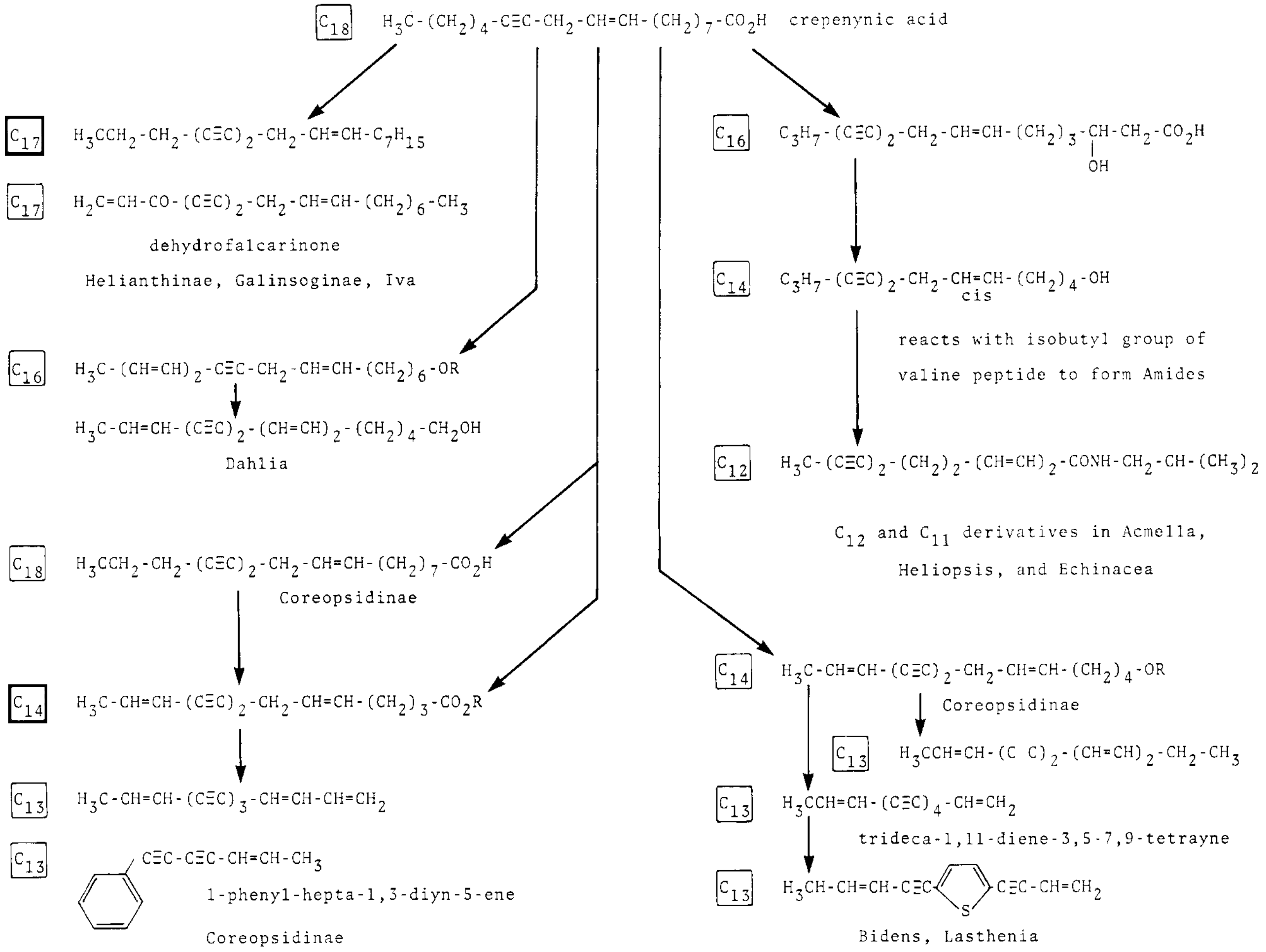


FIGURE 23.—Polyacetylenes of the Heliantheae lacking methyltriyne endgroups showing suggested pathways. (Based on Bolhmann et al., 1973.)

and the series derived from C_{13} triyn-(7, 9, 11)-en-(4) acid occur in the Anthemideae, but not in the Heliantheae. Also in the Anthemideae but not in the Heliantheae are numerous furans and ringenolethers. Present in the Heliantheae but lacking in the Anthemideae are the pentaynene series, the tridecatetrayne series, and the ene-tetrayn-ene series. All the latter involve higher numbers of triple bonds, those capable of giving rise to polythiophenes. As a result, polythiophenes are not found in the Anthemideae.

Furans and ringenolethers are derived in many polyacetylene pathways in the Anthemideae, and polythiophenes are produced in three interrelated pathways in the Heliantheae, examples in which the basic pathways are not as important taxonomically as the enzyme sytems that control the final elaborations on the molecules. In another example, the aromatic polyacetylenes of the Heliantheae involve two different basic pathways and involve different ends of the molecule, but both are almost completely restricted to the Coreopsidinae, where the same enzyme system probably is involved in formation of the phenol unit.

Three other types of chemical data have been mentioned in studies of the Heliantheae. The occurrence of aurone and chalcone types of flavanoids has been noted in the Coreopsidinae and in *Lasthenia* of the Baeriinae, and a relationship between the two groups has been suggested (Bohm, 1977). The two groups also share thiophenes of the ene-tetrayn-ene type. The flavanoid anthocyanins are well known for their importance as flower pigments, and recently the yellow flavonols have been noted for absorption of UV wavelengths in the nectar guide patterns of plants such as *Rudbeckia* and *Gaillardia*. The similarity in UV patterns might have been partial reason for the close relationship given the Helianthinae and Gaillardiinae by Stuessy (1977). These subtribal relationships based on flavanoids are not accepted in the present study, and flavanoids do not seem particularly useful in studies above the genus level.

Cytochrome *c* amino acid sequences have been studied in two species in the family, *Helianthus annuus* L. and *Guizotia abyssinica* Cass., both members of the Heliantheae. The difference of 8 amino acids between the two was a partial basis for raising the Coreopsidinae to tribal rank by Turner and Powell (1977). The conclusion was based on the traditional placement of *Guizotia* in the Coreopsidinae, a position that has proven erroneous.

The amino acid sequences of the more variable but more easily obtained plastocyanins have been analysed for many members of the family, including three genera of the Heliantheae, *Guizotia*, *Helianthus*, and *Rudbeckia* (Boulter et al., 1978). Some heterogeneity is seen in each of the helianthean genera, but there is nothing unique to members of the tribe. The helianthean genera do fall within a general trend shown by members of the subfamily Asteroideae.

The C_4 photosynthetic pathway (Kranz syndrome) has been reviewed for the family by Smith and Turner (1975), and it has been shown to occur in the three helianthean subtribes Coreopsidinae, Flaveriinae, and Pectidinae. The implications of this and other chemical characters reported for the Coreopsidinae are considered further in the discussion of that subtribe.

INSECT CORRELATIONS.—Most members of the Asteraceae produce inflorescences that obviously are able to attract insect pollinators or in some cases birds (Leppik, 1977), and some types of specializations are known that allow pollinators to distinguish individual species (Baagøe, 1977b). Still, extreme specializations toward single-pollinator relationships are not known, and most Asteraceae, including most Heliantheae, remain very facultative in their pollination mechanisms. As a result, studies of specific pollinators furnish little insight into the phylogeny of the Asteraceae.

More significant correlations can be expected with the various types of insects that use the Asteraceae as hosts. No major surveys have been attempted, but many associations have been recorded in various studies and in host indexes. One example is the dipteran genus *Urophora,* whose larvae apparently live almost exclusively in achenes of Asteraceae (Steyskal, 1979). Hosts are known for less than half of the species, and the full range of hosts probably is not known for any. Most of the European species are associated with members of the tribes Cardueae and Anthemideae, which are common in that area. Of the eight American species having host data, two have been recorded from Heliantheae, one from *Borrichia* and one from *Smallanthus*.

Another example of the Heliantheae as hosts involves the Coleoptera. Two genera of the family Bruchidae with an unusual elongate shape, *Dahlibruchus* and *Cosmobruchus*, have been described from *Dahlia* and *Cosmos* respectively (Bridwell, 1931). Both the host genera are in the subtribe Coreopsidinae. Other genera of Bruchidae, for which hosts are known, including one from the lactucean genus *Lapsana*, lack the elongate shape. Bridwell has suggested, "The form in these interesting species is with little doubt due to the shape of the achenes in which they pass their immature stage." Bridwell goes on to correlate the more flattened shape of *Dahlibruchus* with the more flattened shape of the *Dahlia* achenes. It would be instructive to discover a species of Bruchidae that infests the genus *Heterosperma* of the same subtribe, which has great range of achene shapes.

Limits and Relationships of the Tribe

The Heliantheae, as redelimited, consists of approximately 3000 species in about 260 genera. The tribe is concentrated in North and South America, but has a number of pantropical elements and some widely distributed adventives.

Characteristics that are considered basic or primitive in the tribe include the leaves being opposite, with alternate-leaved forms derived. The leaf blades have palmate as well as pinnate venation. The involucre is weakly to strongly subimbricate, with the bracts in many of the advanced subtribes being herbaceous or dimorphic. Receptacles are basically paleaceous, and epaleaceous forms are derived. Both ray and disk flowers usually are present. There is a tendency for suppression of gynoecia, which is expressed in sterile rays, functionally male disk flowers, or rarely dioecism. Flower pigments are mostly yellow. The disk corollas usually have short lobes. The anther thecae are often dark or reddish, and the bases rarely extend below the lower level of the collar. The endothecial cells usually have polarized thickenings on the transverse walls, and radial and laterally polarized forms are derived. The anther appendages usually are ovate and strongly keeled with constricted bases, and the abaxial surface may bear glands or hairs. The style base has hairs in three genera, but it is usually glabrous. The style branches usually have paired stigmatic lines. The achenes are basically prismatic, with numerous compressed or obcompressed forms derived. The achene walls usually are carbonized and striate, with derived nonstriate or rarely noncarbonized forms. In most of the paleaceous subtribes having herbaceous involucral bracts, the achenes seem to have a distinctive slow maturation, with fully mature achenes only in aged heads. The pappus is sometimes of the primitive capillary form with many bristles, or rarely plumose, but more often it is reduced or lacking. The pollen is mostly over 23 μm in diameter with an echinate surface pattern and a helianthean wall structure (Skvarla et al., 1977).

The tribe is placed in the subfamily Asteroideae on the basis of the short disk corolla lobes, the shape of the anther thecae and appendages, the basically paired stigmatic lines, the presence of suppressed gynoecia, the presence of a carbonized achene wall, and the details of pollen structure. Within the subfamily, the Heliantheae are regarded here as parallel to the Eupatorieae, but as more specialized than that tribe on the basis of the heterogamic heads, the presence of suppressed gynoecia, the basically polarized thickenings of the endothecial cells, the constricted bases of the anther appendages, the striate wall of the achenes, the basically polyploid chromosome numbers, and the more complex polyacetylene and sesquiterpene lactone chemistry. The tribe is placed closest to the Inuleae, which seems to differ primarily by the tails on the anthers, the usually flat anther appendage, and the total lack of car-

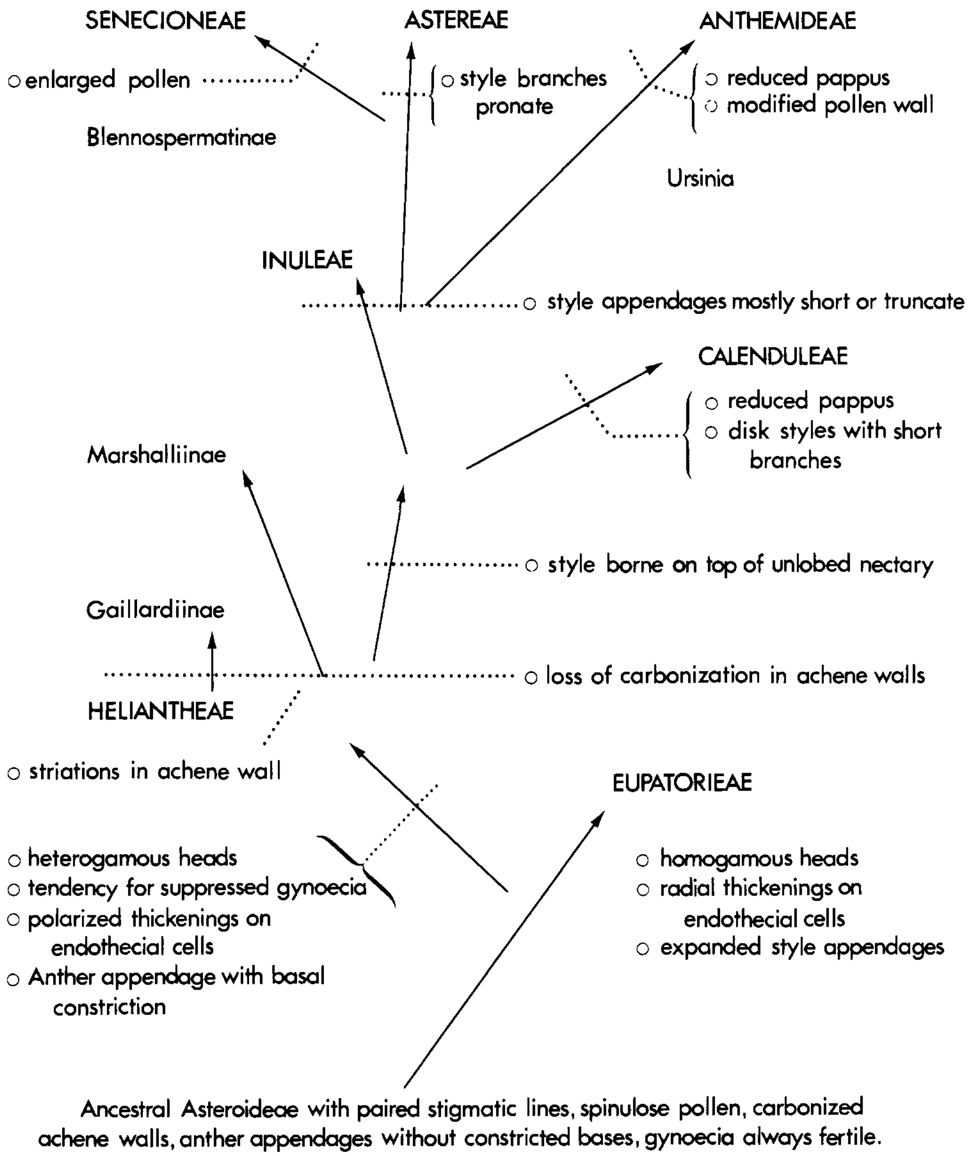


FIGURE 24.—Schematic representation of relationships in the subfamily Asteroideae.

bonization in the achene wall. The Anthemideae, Astereae, and Senecioneae are considered more specialized in structure and chemistry and have their closest relationship to the Inuleae.

The redelimited Heliantheae includes the Ambrosieae Cass., the Coreopsidinae Turner & Powell, the Tageteae Cass., and the Heleniaeae Benth. & Hook. f. These are seen as minor specializations within the general pattern of helianthean evolution. The primary characters of the segregates are often inconstant, and the groups do not seem phyletically more significant or isolated than most other subtribes of the Heliantheae.

A number of genera traditionally placed in the Senecioneae must be included in the Heliantheae. These include *Alepidocline*, *Neurolaena*, and *Schistocarpha* (Robinson and Brettell, 1973b), as well as the genera listed by Nordenstam (1977) as members of a provisional "Arniceae": *Arnica*, *Bartlettia*, *Dimeresia*, *Haploesthes*, *Mallotopus*, *Peucephyllum*, *Psathyrotes*, *Psathyrotopsis*, *Pseudoclappia*, *Raillardella*, and *Whitneya*. The genus *Dyscritothamnus*, originally in the Eupatorieae but more recently shown to include a radiate species (Paray, 1954), is a member of the Heliantheae (Robinson and King, 1977), and also *Lycapsus*, which traditionally has been placed in or near *Alomia* H.B.K. in the Eupatorieae.

The redelimitation of the Heliantheae has resulted in removal or confirmation of removal of some genera from the tribe. *Sheareria* Moore of China, previously placed in the Milleriinae, is a member of the tribe Astereae. It seems related to the majority of genera in that tribe having compressed obovate achenes, but is distinct by the few-flowered heads and the short, subimbricate involucre. The removal of three genera once placed in the Heliantheae has been confirmed, *Microspermum* Lag. to the Eupatorieae (Rzedowski, 1970), *Olivaea* Sch.-Bip. ex Benth. to the Astereae (DeJong and Beaman, 1963), and *Rigiopappus* A. Gray to the Astereae (Robinson and Brettell, 1973c). *Epallage* DC. belongs to the Inuleae (Wild, 1964). In spite of some recent doubts (Jeffrey, 1978), reexamination shows that *Geissolepis* B. L. Robinson, originally of the Galinsoginae, is a member of the Astereae, although it is distinctive and isolated in that tribe (Robinson and Brettell, 1972a).

The impression of phyletic diversity within the Heliantheae seems well established. The present study tends to confirm that the tribe is the most diverse in the family. The measure by which I judge is the need for 35 subtribes in the present treatment. Other tribes with which I have personal experience and where there is comparability are the Eupatorieae with 18 subtribes, the Liabeae with 3 subtribes, the Arctotideae with 2 subtribes, and the Senecioneae with at most 3 subtribes. It should be emphasized that the previous impressions of diversity in the Heliantheae have been based mostly on the extremely obvious nature of many of the characters involved. The comparative uniformity and comparative phyletic insignificance previously assigned to the Eupatorieae were the result of the more subtle nature of its characters.

The order of the subtribes in the present treatment is based on a combination of phyletic, pragmatic, and traditional considerations. Some important general trends seem evident. Most obvious is the isolated position of the Marshalliinae. As indicated under that subtribe, *Marshallia* is outside the main line of evolution in the Heliantheae, and it may ultimately be placed in the closely related Inuleae when the limits of that tribe are more completely understood.

Excluding the Marshalliinae, the subtribes of the Heliantheae can be arranged in a more or less linear series. Combinations of characters place the Ambrosiinae at one extreme of the series with a transition through various groups with separate male and female flowers to members of the tribe such as the Helianthinae, the Galinsoginae, and the Coreopsidinae. With rare exceptions these are all paleaceous. The series continues in the epaleaceous subtribes and reaches its other extreme in the Gaillardiinae, which has the most modified endothecial patterns in the anthers and which lacks carbonization in the achene walls. It is notable that the two extremes in the morphological series also represent extremes in the sequiterpene lactone chemistry: the Ambrosiinae with ambrosanolides and the Gaillardiinae with helenanolides. This more or less linear arrangement of character combinations is seen as a reflection of a predominantly two-directional evolutionary diversification from an ancestral stock more like the central elements of the series.

The helianthean series shows further peculiarities when compared with the supposedly primitive character states in the tribe. High chromosome base numbers and achenes with striations are found randomly through all parts of the series, and thus are presumed to be primitive in the entire series. Probable primitive forms of gynoecial suppression, pleiomorphic achene wall striation, and shrubby to arborescent habit are concentrated in the first group of subtribes, but these are combined with more herbaceous involucres, modified achene shapes, and loss of pappus. In contrast, strongly subimbricate, nonherbaceous involucres, prismatic achenes, and radially symmetrical pappus types are found in the Galinsoginae, which is near the middle of the series, but these are combined with hermaphroditic disk flowers and mostly herbaceous habits. The epaleaceous subtribes are presumably more derived, but many members have prismatic achenes and a number of the subtribes have members with a capillary pappus. Thus, the various parts of the series retain different primitive characters, but no part shows all of the primitive characters combined. The evidence suggests early divergence from extinct ancestral forms.

The present study has indicated more phyletic integrity among the epaleaceous Heliantheae than is generally recognized by recent workers. With the exception of *Geissopappus*, which is a subgroup of *Calea*, the various groups of the "Helenieae" do not find immediate relatives among the conventional Heliantheae, but they represent an extension of the typical element of the tribe through an intergrading series including the Madiinae. This series lacks functionally male disk flowers, mostly lacks dark anthers, and seems to progressively lose paleae, ornamented seed coats, extra thickenings on the endothecial cells, and, finally, the carbonized achene wall. Efforts to integrate some members of the "Helenieae" more closely, such as placing the Gallardiinae near the Helianthinae (Stuessy, 1977) or trying to link *Clappia* and *Pseudoclappia* to members of the paleaceous series through *Varilla* (Turner and Powell, 1977) prove erroneous or extremely dubious. In complete contrast, the various genera from the Senecioneae seem to integrate well: *Schistocarpha* and *Neurolaena* into the conventional Heliantheae, *Haploesthes* into the Flaveriinae, *Pseudoclappia* into the Clappiinae, *Arnica* and its relatives into the Chaenactidinae, and *Psathyrotes* into the Gaillardiinae.

It is worth noting that, in spite of many exceptions, the paleaceous members of the Heliantheae are more concentrated in more tropical areas, whereas the epaleaceous members are mostly temperate or xeric in distribution.

The helianthean series presented in this study agrees in many ways with the traditional treatments of Bentham and Hooker (1873) and Hoffmann (1890–1894). This is partly the unavoidable result of the basic character patterns from which all the treatments are derived. Under the circumstances, it has seemed best to leave all elements of the Heliantheae as close as possible to their traditional places in the series when there are no important reasons to do otherwise.

Not all problems of subtribal sequence are clearly resolved. The Clibadiinae, which shares many characters of the Melampodiinae, is probably close to the Ecliptinae. The Desmanthodiinae, which is superficially similar to the Clibadiinae, has achene-wall and resin-duct characters closest to the Helianthinae and Galinsoginae. There is a reticulating character pattern between the Ecliptinae, Neurolaeninae, Galinsoginae, and Helianthinae. Some of these patterns might result from basic characters, such as achene-wall striations, being suppressed in various groups. In cases of some chemicals or of corolla surfaces, separate origins in different parts of the tribe seem likely. Nevertheless, some character distributions might result from past intergeneric hybridizations. The latter situation would conform to situations now suspected in some Senecioneae (Robinson and Brettell, 1974a) and a few Eupatorieae (Robinson and King, 1977).

A major intent of this study has been the redelimitation and recharacterization of the subtribes of the Heliantheae into distinct phyletic units. I believe the present system furnishes a reliable basis for subtribal assignments of most genera and for comparisons of characters. Some subtribes, such as the Coreopsidinae, Ecliptinae, Galinsoginae, and Helianthinae, which have been poorly defined in the past, now show high internal consistency in many characters and trends. The clear phyletic gaps now seen between most of the subtribes are an extra, but not entirely unexpected, result of the study. They indicate that even at the subtribal level the ancestral stocks have become extinct.

Key to the Subtribes of the Heliantheae

The following key is provided to summarize the most obvious differences between the various subtribes recognized in this study. An attempt has been made to account for some of the exceptional genera by use of parenthetical comments. Nevertheless, it should be noted that many genera, including some that have all the characters of their subtribe, can be keyed more effectively on the basis of their individual characteristics.

1. Achene walls carbonized, without raphides 2
  2. Achenes with five or less ribs or unribbed 3
    3. Plants with involucres usually herbaceous or coriaceous, usually with 2 or more flowers in a head 4
      4. Receptacle with disk usually bearing paleae (lacking paleae in some species of *Calea* and *Clibadium* and in heads with 5 or less flowers); anther thecae often blackened .. 5
        5. Disk achenes prismatic, terete, or compressed, never obcompressed (often with disk achenes sterile); leaves usually simple or divided into narrow lobes; anther appendages with or without glands 6
          6. Disk flowers functionally male, with gynoecia vestigial; veins of disk corolla throat never with fiber sheaths 7
            7. Filaments glabrous; anther thecae not greenish, endothecial cells with thickenings on transverse walls or radially arranged 8
              8. Male and female flowers arranged in separate series in the head or in separate heads 9
                9. Anthers pale, sometimes separate from each other; endothecial cells mostly broader than long, with radial thickenings; plants mostly specialized for wind pollination .... **AMBROSIINAE**
                9. Anthers often dark, always synantherous; endothecial cells quadrate or longer than wide, usually with polarized thickenings . 10
                  10. Leaves alternate, usually closely spirally inserted or rosulate 11
                    11. Small rosulate herbs from Cuba; heads solitary on slender erect peduncles; ray achenes with pappus of radially arranged squamellae or aristae .... **HEPTANTHINAE**
                    11. Coarse rosulate, caulirosulate, or arborescent plants of the northern Andes; heads clustered in terminal or lateral inflorescences; pappus usually absent (usually with 3 squamellae in *Tamania*) .... **ESPELETIINAE**
                  10. Leaves mostly opposite 12
                    12. Disk corolla with distinct resin ducts paired along veins of throat, with yellowish resin .... **DESMANTHODIINAE**
                    12. Disk corollas with resin ducts single along veins of throat, resin either reddish or colorless 13
                      13. Achenes with regular, clear, nonrecessed striations; ray corollas with expanded, strongly trilobed limbs .... **MILLERIINAE**

13. Achenes either without striations or with irregular or recessed striations; limbs or ray corollas mostly bilobed or lacking 14

14. Disk corollas without colored resin in ducts; outer bracts of involucre usually strongly differentiated into spreading foliaceous bracts (lacking in *Ichthyothere*); achenes usually with grooves, costae, or a few partial striations, achenes sometimes enclosed in inner involucral bract .... **MELAMPODIINAE**

14. Disk corollas often with reddish resin in ducts; outer bracts of involucre not strongly differentiated; achenes without evident costae, grooves, or striations, achenes never completely enclosed in involucral bract 15

15. Anthers pale; limb of ray corollas single and expanded or completely lacking; achene glabrous, with regular pattern of isodiametric cells on surface .... **POLYMNIINAE**

15. Anther thecae blackened; ray corollas tubular with 3 or 4 radially arranged apical lobes; achenes usually pubescent; inflorescence with heads often in scorpioid cymes or complex glomerules .... **CLIBADIINAE**

8. Heads with 2 male and 2 female flowers arranged collaterally (small repent herbs from the West Indies) .... **PINILLOSINAE**

7. Filaments densely pubescent below collars; anther thecae greenish, median endothecial cells strongly noduliferous along vertical walls .... **GUARDIOLINAE**

6. Disk flowers hermaphroditic (some genera of Ecliptinae have disk flowers functionally male, but these usually have distinct fiber sheaths along veins of disk corolla throat; also see *Unxia* of the Neurolaeninae which has yellowish anther thecae) 16

16. Achenes without striations 17

17. Anther thecae whitish; pappus lacking; carbonization of achenes in evenly distributed brownish layer; lamina of leaves rather fleshy and deeply lobed (endemic to small Pacific islands off coast of Chile) .... **LYCAPSINAE**

17. Anther thecae usually blackened, sometimes yellowish; pappus often present; carbonization of achenes in unevenly distributed, highly porose, black layer 18

18. Disk achenes usually compressed, ray achenes often broadly triangular or obcompressed, achenes sometimes winged; pappus usually bilaterally symmetrical or lacking, rarely of radially arranged, short, deciduous setae; veins of disk corollas often with

strong fiber sheaths; ducts with colorless resin, ducts in shaft of disk style located outside of veins .... **ECLIPTINAE**

18. Achenes prismatic, never winged; pappus radially arranged or lacking; disk corollas without fibers; ducts often with reddish resin, ducts in shaft of disk style located inside of veins .... **NEUROLAENINAE**

16. Achenes with striations 19
  19. Style branches with continuous stigmatic surface adaxially; achenes of disk flowers compressed 20
    20. Ray flowers fertile, with style; ducts of flower with colorless resin; pappus lacking; basal margins of disk corollas often extended to cover tops of achenes, lower throat of disk corollas not scabrid .... **ZALUZANIINAE**
    20. Ray flowers sterile or lacking, without styles (vestigial style in 1 species of *Helianthopsis*), ray achenes filiform; ducts of flower with yellow resin; pappus usually present and bilaterally symmetrical (lacking in specimens with calvous achenes); basal margins of disk corollas not extended, lower throat of disk corollas distinctly scabrid .... **HELIANTHINAE**
  19. Style branches with paired stigmatic lines; achenes of disk flowers often terete or prismatic 21
    21. Ray flowers sterile 22
      22. Shrubs or small trees with opposite leaves; paleae becoming enlarged with age; ducts with colorless resin; endothecial cells with thickenings polarized on transverse walls; achenes prismatic .... **MONTANOINAE**
      22. Herbs with alternate or basal leaves; paleae not enlarged with age; ducts often with reddish or orange resin; endothecial cells with thickenings radially arranged or polarized on vertical walls; achenes often compressed; receptacles usually highly conical or columnar .... **RUDBECKIINAE**
    21. Ray flowers fertile or lacking 23
      23. Erect or caespitose terrestrial plants; heads not sessile in the axils of leaves on elongate stems; inner surfaces of disk corolla lobes papillose 24
        24. Heads with 5 or more flowers; ray flowers present, with trilobed limb 25
          25. Pappus lacking; ducts single along veins of disk corolla throat, with colorless or orange resin, ducts in shaft of disk style outside of veins; carpopodium symmetrical or slightly asymmetrical .... **MILLERIINAE**
          25. Pappus usually present, with separate segments radially arranged; ducts paired along veins of disk corolla throat, with yellow resin, ducts on shaft of disk style inside of veins; carpopodium strongly asymmetrical,

outer half remaining as isolated sclerified plate at maturity .... **Galinsoginae**

24. Heads with 2 or 3 flowers; ray flowers lacking; pappus a fused replicate ring, deciduous as a unit; acaulescent herbs from the western United States .... **Dimeresiinae**

23. Spreading aquatic plants; heads sessile in axils of leaves on elongate stems; inner surfaces of disk corolla lobes smooth .... **Enhydrinae**

5. Disk achenes obcompressed (sterile and vestigial in a few genera with dissected leaves); leaves often subcompound with ovate or filiform segments; anther appendages always glabrous, often with duct containing reddish resin 26

26. Heads heterogamous or discoid, with tubular disk flowers; involucre usually with strongly differentiated outer series of herbaceous bracts .... **Coreopsidinae**

26. Heads homogamous with bisexual, 5-lobed, ligulate flowers; involucre with coriaceous or woody bracts, without differentiated outer series; plants endemic to Polynesia .... **Fitchiinae**

4. Receptacle usually without paleae on the disk (paleae present among disk flowers in some Madiinae and in *Hymenopappus newberryi*); anther thecae usually pale, sometimes reddish (blackened in *Trichocoryne*) 27

27. Leaves and involucres spotted with distinct, often elongate secretory pits or cavities .... **Pectidinae**

27. Leaves and involucres without secretory pits or cavities 28

28. Involucral bracts in single series, each subtending a flower; ray flowers when present separated from disk by a single series of paleae (rarely with additional paleae on disk); anther thecae often dark reddish; leaves with rather abundant intercellular pectic materials (lacking in vernal annuals) .... **Madiinae**

28. Involucral bracts usually in more than one series; without a single series of paleae inside of ray flowers; anther thecae usually pale, not reddish; leaves without pectic materials 29

29. Achene walls without striations; leaves distinctly petiolate 30

30. Achenes usually rather trigonous, shortly to longly stipitate at the base; disk corollas with 5 lobes .... **Hymenopappinae**

30. Achenes slightly to strongly compressed, not stipitate at the base; disk corollas usually with 4 lobes .... **Peritylinae**

29. Achene walls with striations; leaves with or without petioles 31

31. Endothecial cells short with 3-5 thickenings on transverse walls, thickenings sometimes radially arranged; leaves without distinct petiole; pappus awns or squamae when present without distinct median costa or vascular trace .... **Baeriinae**

31. Endothecial cells short to elongate with 1 or 2 thickenings on transverse walls; leaves with or without distinct petioles; pappus awns or squamae often with distinct median costa or vascular trace .... **Chaenactidinae**

3. Plants with fused, fleshly, slightly winged involucres, with 1 flower in each head; xeromorphic shrubs endemic to southern Baja California .... **Coulterellinae**

2. Achenes with 8–10 ribs; anther appendages glabrous 32

32. Receptacle with paleae on the disk .... **Varillinae**

32. Receptacle without paleae, sometimes with hairs 33

33. Xeromorphic shrubs with alternate leaves, without scarious wings or sheaths at nodes; pappus with numerous capillary bristles in ca. 3 series .... **CLAPPIINAE**

33. Herbs or subshrubs with opposite leaves, with scarious wing or sheath at nodes; pappus lacking or with single series of squamae or bristles 34

34. Erect herbs or subshrubs with heads grouped in axillary or terminal inflorescences .... **FLAVERIINAE**

34. Stoloniferous herbs with heads solitary from axils of leaves .... **JAUMEINAE**

1. Achene walls not carbonized, with raphides 35

35. Receptacle without herbaceous paleae, sometimes with spinelike fimbrillae or with a few bracts between ray and disk flowers; heads with rays present or absent; corollas usually yellow or whitish, with tubes and lobes not long and narrow, throat long; median endothecial cells rather elongate .... **GAILLARDIINAE**

35. Receptacle with herbaceous paleae; heads discoid; corollas lavender or violet, with tubes long and narrow, throat very short; all endothecial cells short; endemic to southeastern United States .... **MARSHALLIINAE**

A Synopsis of the Subtribes of the Heliantheae

The thirty-five subtribes of the Heliantheae are arranged in the following sequence in this treatment. General trends are indicated by the seven major groups. The achene wall type and some notable features are cited for the individual subtribes.

A. Usually paleaceous; usually no pappus; disk flowers male; achenes carbonized.

1. Ambrosiinae: Achenes not striate; often wind-pollinated; male and female flowers often in separate heads; anthers pale, often separate.

2. Espeletiinae: Achenes not striate; leaves alternate, apically in dense clusters or rosettes; often monopodial, often arborescent.

3. Melampodiinae: Achenes usually striate; ray corolla surface papillose, ray achenes often completely enclosed in modified bract.

4. Polymniinae: Achenes not striate; ray corolla surface not papillose, ray achenes not enclosed in bract.

5. Milleriinae: Achenes striate; ray corollas strongly trilobed.

6. Desmanthodiinae: Achenes with or without striations; resin ducts paired in disk corolla, inside veins in style.

7. Clibadiinae: Achenes not striate; ray corollas tubiform; ducts in disk corolla single.

8. Pinillosinae: Achenes not striate; 2 male and 2 female flowers collateral in head.

9. Guardiolinae: Achenes striate; filaments pubescent below collars; endothecial cells with prominent thickenings polarized on vertical walls.

B. Paleaceous; usually no pappus; disk flowers hermaphroditic; achenes carbonized.

10. Enhydrinae: Achenes striate, prismatic; rays fertile; stigmatic lines 2; aquatic herbs.

11. Montanoinae: Achenes striate, prismatic, rays sterile; stigmatic lines 2; trees and shrubs.

12. Rudbeckiinae: Achenes striate, mostly compressed; rays sterile; stigmatic lines 2.

13. Zaluzaniinae: Achenes striate, compressed; rays fertile; stigmatic surface single.

C. Usually paleaceous; usually with pappus; disk flowers usually hermaphroditic; disk achenes prismatic to compressed, carbonized.

14. Heptanthinae: Achenes not striate; disk flowers male; short-stemmed rosulate herbs.

15. Ecliptinae: Achenes not striate, in disk usually compressed; corolla veins often with fiber sheaths; style ducts outside veins in shaft, resin not colored.

16. Helianthinae: Achenes striate, compressed; rays sterile; stigmatic surface single; style ducts outside veins in shaft, resin yellow.

17. Neurolaeninae: Achenes not striate, prismatic; pappus radial; rays fertile; stigmatic lines 2; style ducts inside veins in shaft, resin reddish.

18. Galinsoginae: Achenes striate, prismatic; pappus radial; rays fertile; stigmatic lines 2; style ducts inside veins in shaft, resin yellow.

19. Dimeresiinae: Achenes striate, prismatic; 2 or 3 flowers in head; pappus replicate, deciduous as unit.

D. Paleaceous; usually with pappus; disk flowers usually hermaphroditic; disk achenes obcompressed, carbonized, not striate.
  20. COREOPSIDINAE: Heads heterogamous, with distinct ray and disk flowers; style branches elongate; seed coat not ornamented; no glands on anther appendage.
  21. FITCHIINAE: Heads homogamous, with all flowers ligulate and 5-lobed; style branches short; seed coat not ornamented; no glands on anther appendage.

E. Not paleaceous or secondarily paleaceous on disk; disk flowers hermaphroditic; achenes carbonized, with or without pappus; stigmatic lines 2.
  22. COULTERELLINAE: Achenes striate, prismatic; heads with 1 flower.
  23. PECTIDINAE: Achenes striate, prismatic; leaves and involucre with distinct internal oil glands or cavities.
  24. FLAVERIINAE: Achenes multi-costate; inflorescence terminal or axillary; subshrubs.
  25. VARILLINAE: Achenes multi-costate; ducts single between pairs of veins in corolla throat, resin reddish; paleae present.
  26. CLAPPIINAE: Achenes multi-costate; inflorescence diffuse, with few mostly large heads; ducts sometimes between paired veins; xeromorphic shrubs.
  27. JAUMEINAE: Achenes multi-costate; heads solitary; stoloniferous herbs.
  28. MADIINAE: Achenes not striate; single series of paleae inside rays.
  29. HYMENOPAPPINAE: Achenes not striate, trigonous.
  30. LYCAPSINAE: Achenes not striate, 4-ribbed; leaves spirally inserted, petiolate; disk corollas 4-lobed; paleae present.
  31. PERITYLINAE: Achenes not striate, compressed; leaves opposite, petiolate; disk corollas 4-lobed.
  32. BAERIINAE: Achenes striate, prismatic to compressed; leaves not petiolate; endothecial cells with 3–5 thickenings on transverse walls.
  33. CHAENACTIDINAE: Achenes striate, prismatic to obcompressed; endothecial cells with 1–2 thickenings on transverse walls.

F. Disk mostly without true paleae; disk flowers hermaphroditic; achenes not carbonized, with raphides in wall; pappus radial.
  34. GAILLARDIINAE: Endothecial cells with 1–2 thickenings on transverse walls.

G. Paleaceous; disk flowers hermaphroditic; achenes not carbonized, with raphides in wall; pappus radial with 5 squamae.
  35. MARSHALLIINAE: Heads discoid; anthers slightly tailed; corollas puberulous, with tubes and lobes long and narrow.

Review of the Subtribes of the Heliantheae

The following 35 subtribes include many new segregates that have been validated separately (Robinson, 1978g, 1979a, 1980a). A number of traditional subtribes also are reduced or altered. The most notable examples are the Verbesininae and Zinniinae, which are placed in the Ecliptinae; the Bahiinae, which are placed in the Chaenactidinae; and the Milleriinae, which are completely reinterpreted.

In the generic listings under the subtribes, the accepted genera are marked with an asterisk (*).

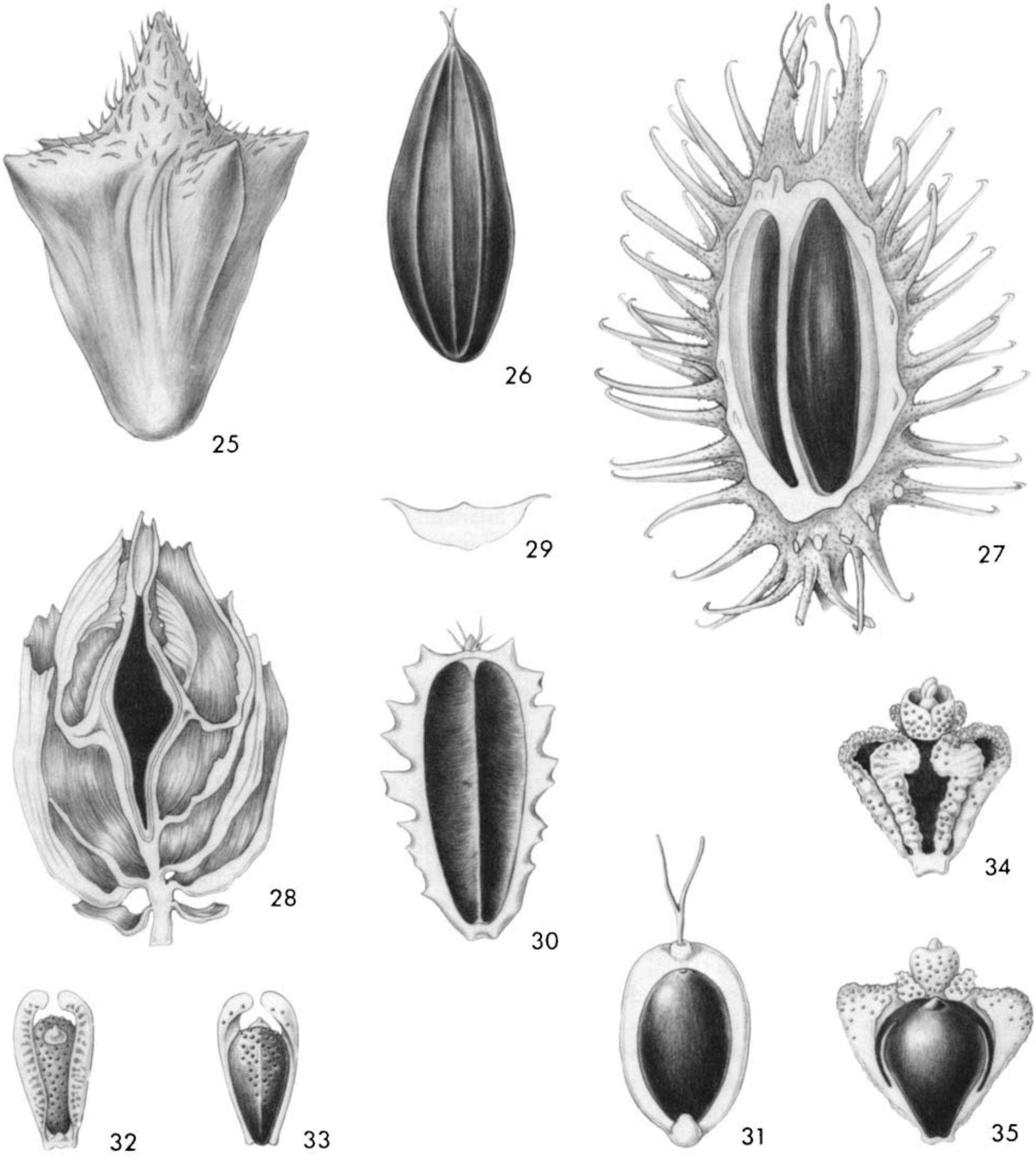
Subtribe 1. AMBROSIINAE

FIGURES 25–35

Subtribe AMBROSIINAE Less., Linnaea, 5:151, 1830.
Tribe AMBROSIEAE Cass., Journ. Phys., 88:191, 1819.
Family AMBROSIACEAE Link, Handbuch, 1:816, 1829.
Family PARTHENIACEAE Link, Handbuch, 1:816, 1829.
Tribe IVEAE Rydb., N. Amer. Fl., 33(4):3, 1922.

**Ambrosia* L. (including *Acanthambrosia* Rydb., *Franseria* Cav., *Gaertneria* Medic., nom./rej., *Hemiambrosia* Delpino), **Dicoria* Torrey & Gray, **Euphrosyne* DC., **Hymenoclea* Torrey & Gray, **Iva* L. (including *Chorisiva* Rydb., *Cyclachaena* Fres., *Leuciva* Rydb., *Oxytenia* Nutt.), **Parthenice* Gray, **Parthenium* L. (including *Villanova* Ortega), **Xanthium* L. (including *Acanthoxanthium* (DC.) Fourreau).

Herbs. Leaves opposite, alternate, or basal. Heads with paleae; involucre herbaceous in ca. 2 series; flowers female or functionally male in same or different heads, when separate the female heads borne below male heads on same plant and often containing 1 flower enclosed in receptacle (2 in *Xanthium*, more in some *Ambrosia*). Ray corollas tubular or with small smooth limbs. Male flowers evenly funnelform with indistinct achene; lobes short, glanduliferous outside, smooth inside; filaments separate or fused to each other; thecae pale, usually separate (synantherous in *Parthenice*



FIGURES 25–35.—Ambrosiinae: 25, *Ambrosia trifida* L., head in fruiting stage, × 12; 26, 27, *Xanthium strumarium* L. (26, achene, × 6; 27, head in partial section containing pair of achenes, × 6); 28, *Hymenoclea salsola* Torr. & Gray, head in fruiting stage in partial section, × 12; 29, 30, *Dicoria canescens* A. Gray, achene, × 12, section and face view; 31, *Euphrosyne parthenifolia* DC., achene, × 24; 32, 33, *Parthenice mollis* A. Gray, ray achene with adjacent paleae, × 12, inside and outside view; 34, 35, *Parthenium hysterophorus* L., ray achene with adjacent paleae, × 12, inside and outside view.

and *Parthenium*); endothecial cells mostly broader than long, with radial thickenings, 4–6 thickenings on transverse walls; appendages without glands, sometimes apiculate or attenuate. Style branches of female flower with 2 stigmatic lines; styles of male flower undivided, with tuft of hairs at tip. Resin ducts with little or no coloration, solitary along veins of male corolla throat. Achenes of female flowers prismatic to obcompressed, sometimes ornamented or forming complexes with adjacent paleae, usually with many uniseriate hairs near tip; walls of achenes carbonized, without striations; cells of seed coat ornamented; pappus of a few short spines or lacking. Pollen 25–30 μm in diameter, often with reduced spinules.

The Ambrosiinae are most notable among the Heliantheae for specializations toward wind pollination. The nonsynantherous condition in the more advanced genera of the subtribe is unique in the family. The subtribe can be characterized by the anther thecae usually lacking black pigment, by the form of the endothecial cells, and by the anther appendages being glabrous and rather thin. Seven of the genera have been examined for chromosomes and all show a base of $X = 18$. Distinctive sesquiterpenes, ambrosanolides, are recorded from *Ambrosia*, *Hymenoclea*, *Iva*, *Parthenice*, *Parthenium*, and *Xanthium*.

The relationship of *Parthenice* and *Parthenium* to the Ambrosiinae was recognized by Bentham, but the two genera were placed technically in the adjacent part of the subtribe Melampodiinae in the Bentham and Hooker system (1873). This was based primarily on the presence of fused anthers and achene-palea complexes in the two genera. Achene-palea complexes are also present in the *Engelmannia* group, which likewise was included in the traditional Melampodiinae by Bentham and Hooker. Stuessy (1973) properly transferred *Parthenice* and *Parthenium* to the Ambrosiinae on the basis of the translucent anthers, the chromosome numbers, and the chemistry, but he allowed for possible relationship to *Engelmannia*. Such relationship was not mentioned in the revision of the tribe by Stuessy (1977), where the *Engelmannia* group was raised to subtribal status. The present treatment places the Engelmanniinae in the Ecliptinae, where the disk corolla shape, the fiber sheaths in the corolla, the black anthers, and the endothecial cells are like those of the *Wedelia* series and totally unlike the Ambrosiinae. The achene-palea complexes in the group are evidently of separate origin.

Many detailed studies of the Ambrosiinae deal with specializations associated with wind pollination in the pollen grains or inflorescence form (Wodehouse, 1928; Payne, 1963, 1964; Skvarla and Larson, 1965; Payne and Skvarla, 1970). The pollen has a foot layer thinner than the adjoining endexine, has cavus areas, has loosely attached exine components on the columellar bases and foot layer, has a rather shallow ektexine, and has lamellations in both apertural and intercolpal areas, all as in other members of the Heliantheae. This is in contrast to pollen in the tribe Anthemideae, where specializations toward wind pollination are also found. Within the Ambrosiinae, *Parthenice*, *Parthenium*, and parts of *Iva* are fully helianthoid in the smaller cavus areas of their grains and in the presence of foramina in the ektexine. Reports of a different pollen form in *Parthenice* have proven erroneous (Bolick and Skvarla, 1976). The more advanced Ambrosiinae, including *Ambrosia*, *Dicoria*, *Euphrosyne*, *Hymenoclea*, *Xanthium*, and typical *Iva*, are nonhelianthoid in the reduction or absence of foramina. Additional specializations in various of the advanced genera include a somewhat thickened, less perforate exine, a second layer of columellae, enlarged vesiculate cavus areas, reduction in spinule length, and shortening of the colpi. Such pollen grains are not found elsewhere in the Heliantheae.

The subtribe shows little relationship to the Melampodiinae as defined in this treatment. The nonstriate achenes of the Ambrosiinae suggest closer relationship to such subtribes as the Clibadiinae and the Ecliptinae.

Subtribe 2. ESPELETIINAE

FIGURES 36–40

Subtribe ESPELETIINAE Cuatr., Phytologia, 35:48, 1976.

**Carramboa* Cuatr., **Coespeletia* Cuatr., **Espele-*

tia Mutis ex H. & B., **Espeletiopsis* Cuatr., **Libanothamnus* Ernst, **Ruilopezia* Cuatr., **Tamania* Cuatr.

Mostly arborescent or shrubby perennials; stems often caulirosula, unbranched or sparingly branched (usually dendroid in *Libanothamnus*). Leaves alternate, rosulate, or subrosulate, vaginate at base (tubular in *Carramboa* and *Libanothamnus*), usually without distinct petioles. Inflorescence terminal (*Libanothamnus*, *Ruilopezia* and *Tamania*) or axillary. Heads with paleae; involucre herbaceous, pluriseriate; flowers female and functionally male in same head. Female flowers in up to 6 series, adaxial surface of rays with short scarcely mamillose cells. Disk corolla lobes 5, short-triangular, hairs of corolla usually blunt or clavate at tip (usually sharp in *Carramboa*); thecae slightly darkened, endothecial cells short, with 2 or 3 thickenings on transverse walls; appendages glabrous. Styles of rays with 2 broad stigmatic lines; styles of male flowers undivided or short-branched, truncate, clavate. Resin ducts without coloration. Achenes of female flowers obovoid, somewhat trigonous to tetragonous, glabrous, walls carbonized, without striations; cells of seed coat irregular, ornamented; pappus lacking (1–3 squamellae in *Tamania*). Pollen ca. 30 μm in diameter.

The Espeletiinae are restricted to rather high elevations in the northern Andes, where they are characteristic of the typical Páramo habitat. The center of diversity and probable center of origin is in Venezuela, with more recent extension into Colombia and northernmost Ecuador.

Most concepts of the group recognize the single genus, *Espeletia*, based on the familiar caulirosula species *E. grandiflora* Humb. & Bonpl. of central Colombia. There are consistent chromosome reports of $X = 19$ for the group (Robinson et al., in press). Cuatrecasas (1976), in his reorganization of the subtribe, emphasized significant variations in habit and correlations with habitat that are not evident in the disarticulated fragments usually found on herbarium sheets.

The genera of the Espeletiinae form a closely related series which is, nevertheless, strongly isolated from other subtribes of the Heliantheae. The group has been placed traditionally in the Melampodiinae and has some similarities to the fruticose genus *Smallanthus* of that subtribe. The Espeletiinae are distinct in the alternate leaves and the unstriated achenes. They also lack the distinct outer series of herbaceous involucral bracts that are found in most Melampodiinae.

The Espeletiinae provides a most striking example of a fundamentally alternate-leaved group in the basically opposite-leaved Heliantheae. The only example of opposite leaves in the subtribe, the bracts on the axillary inflorescences of *Espeletia*, represents a highly specialized condition, being a unique reversal of the common trend toward more alternate leaves in inflorescences and occurring in one of the more specialized genera of the subtribe.

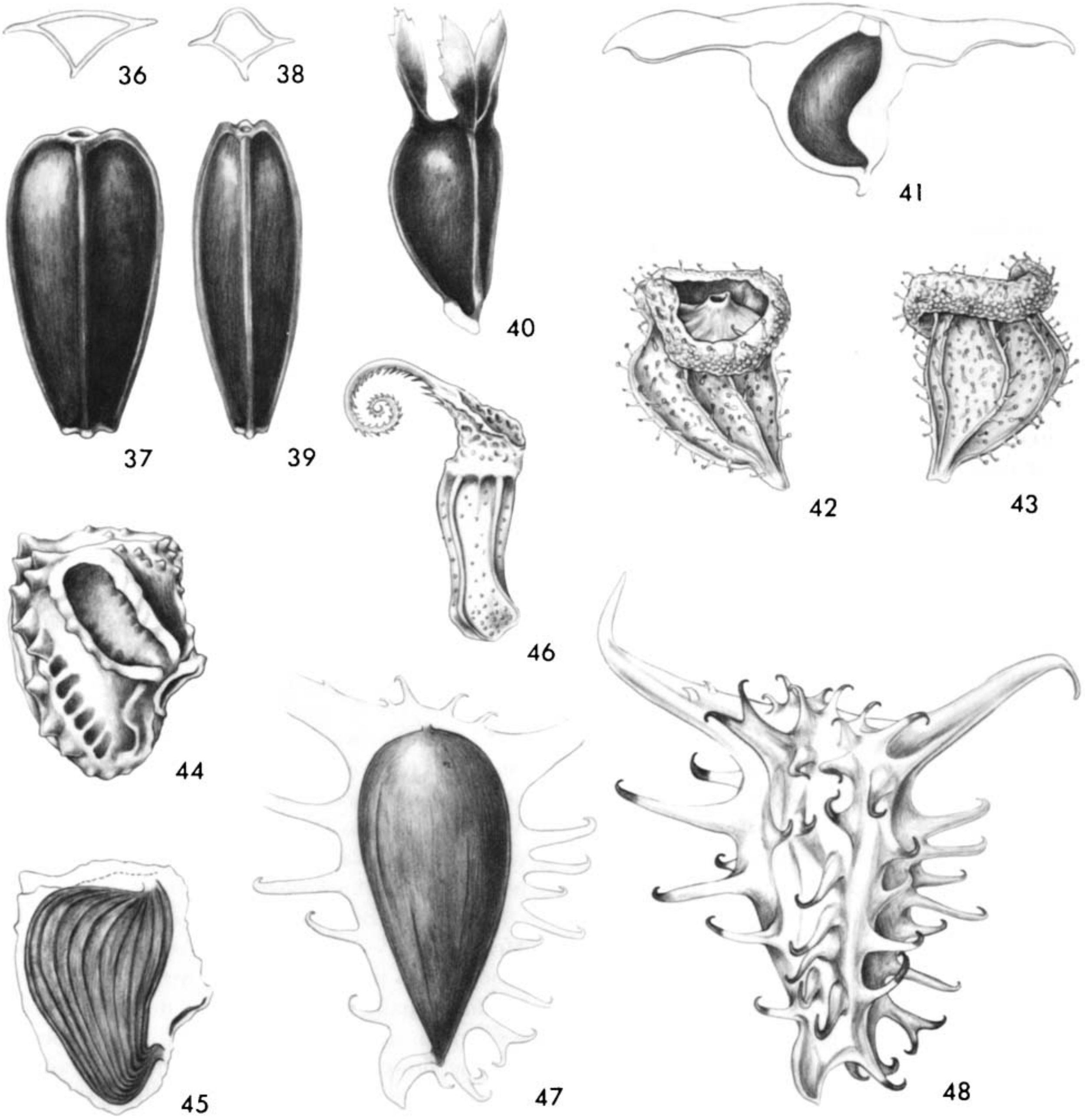
Subtribe 3. MELAMPODIINAE

FIGURES 41–50

Subtribe MELAMPODIINAE Lessing, Linnaea, 5:149, 1830.

**Acanthospermum* Schrank (including *Centrospermum* H.B.K. non Spreng., *Orcya* Vell.), **Ichthyothere* Mart. (including *Latreillea* DC., *Torrentia* Vell.), **Lecocarpus* Decaisne, **Melampodium* L. (including *Alcina* Cav., *Dysodium* Rich. in Pers., *Zarabellia* Cass.), **Smallanthus* Mackenzie in Small.

Herbs, shrubs, or small trees. Leaves opposite. Heads solitary or in terminal or axillary inflorescences, with paleae; involucre herbaceous, pluriseriate, usually with expanded outer series; flowers female or functionally male in same head. Female flowers in 1–3 series; limbs of corollas sometimes reduced, adaxially weakly to strongly papillose, apically bilobed. Disk corolla throat with veins usually narrow (broadened above in *Ichthyothere*); lobes 5, with isodiametric, often papillose cells adaxially; thecae of anthers often darkened; endothecial cells short with usually 2 or 3 thickenings along transverse walls (radial thickenings in some *Melampodium*); anther appendages with or without glands. Styles of rays with stigmatic lines paired; styles of male flowers



FIGURES 36–48.—Espeletiinae-Melampodiinae: 36–39, *Espeletia killippii* Cuatr., outer and inner ray achenes with sections, × 13; 40, *Tamania chardonii* (A. C. Smith) Cuatr., ray achene, × 13; 41–43, *Lecocarpus pinnatifidus* Decaisne, ray achenes enclosed in bract, × 12 (41, section showing form of achene);44, 45, *Melampodium divaricatum* (Rich.) DC., ray achenes enclosed in bract, × 12 (45, section showing form of achene); 46, *Melampodium appendiculatum* B. L. Robins., ray achene enclosed in bract, × 12; 47, 48, *Acanthospermum hispidum* DC., ray achenes enclosed in bract, × 12 (48, section showing form of achene). (Figures 36–40 after Cuatrecasas, unpublished.)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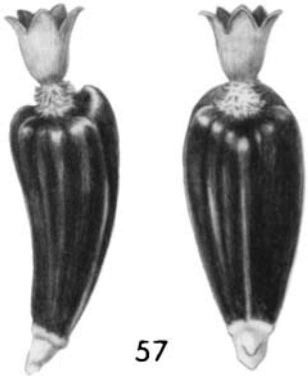
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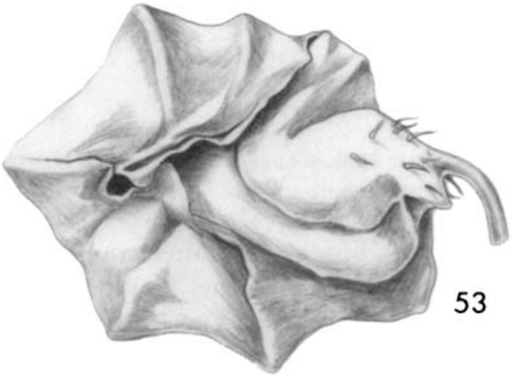
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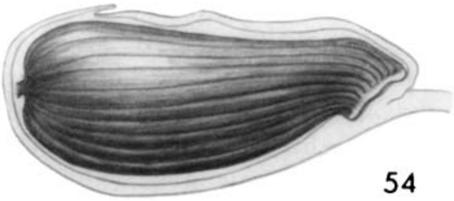
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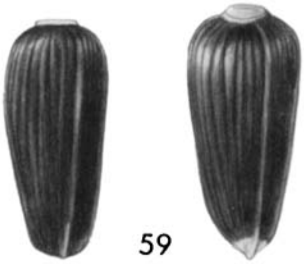
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FIGURES 49–59.—Melampodiinae-Polymniinae-Neurolaeninae-Milleriinae: 49, *Smallanthus uvedalia* (L.) Mackenzie, ray achene, × 8; 50, *Ichthyothere scandens* Blake, ray achene, × 12; 51, *Polymnia canadensis* L., ray achene, × 12; 52, *Unxia camphorata* L. f., ray achene, × 12; 53, 54, *Milleria quinqueflora* L. (53, head at fruiting stage enclosed in involucral bract, × 12; 54, head in section showing mature ray achene, × 12); 55, 56, *Trigonospermum melampodioides* DC., ray achene, cross-section and lateral view, × 17; 57, *Sigesbeckia orientalis* L., disk achenes with corollas, lateral and inside views, × 12; 58, *Rumfordia floribunda* DC., ray achene, × 17; 59, *Guizotia scabra* (Vis.) Chiov., ray and disk achenes, × 17.

not or scarcely divided at tip, with 2 rudimentary stigmatic lines in some *Smallanthus*. Resin ducts without obvious coloration, single along veins of disk corolla throat, outside of veins in shaft of disk style. Achenes of ray flowers often enclosed in subtending involucral bract, slightly compressed, walls carbonized, more or less striate; cells of seed coat slightly to strongly ornamented; pappus absent. Pollen 25–30 μm in diameter.

The Melampodiinae has traditionally included most members of the Heliantheae with suppressed gynoecia in the disk flowers but lacking specializations toward wind pollination. Of the taxa included in the subtribe at various times, many have been excluded in recent studies, *Philoglossa* DC. (Sandwith, 1956), *Dicranocarpus*, *Guardiola*, *Moonia*, *Parthenice*, and *Parthenium* (Stuessy, 1973), *Baltimora*, *Clibadium*, the *Engelmannia* group, *Ichthyothere*, *Rensonia*, and *Schizoptera* (Stuessy, 1977), and the Espeletiinae (Cuatrecasas, 1976). In the present study, the subtribe has been further reduced to a comparatively uniform element in which all members show at least some striations in the achene, and all but *Ichthyothere* have an expanded outer series of involucral bracts.

The striations in the achenes of the subtribe show variations to an extent that contrasts with most other groups of the tribe. In *Acanthospermum*, striations are present only in the form of irregularly placed lines that usually extend only part of the length of the achene. The striations of most other genera are recessed in grooves, but seem otherwise poorly differentiated. Some preparations of *Melampodium* seem to lack striations, and some species of *Ichthyothere* are much less striate that others. One would conclude that the striations of the Melampodiinae are in a more pleiomorphic state than those of most Heliantheae.

A recent article by Czerson et al. (1979) emphasizes the occurrence of the tetrahydropyrane ichthyothereol and the lack of melampolides in both *Clibadium* and *Ichthyothere*. This is contrasted with the condition in *Melampodium* and *Smallanthus* (sic *Polymnia*). While this does not overcome the objections, based on structure, to relating *Ichthyothere* closely to *Clibadium*, it does indicate a greater phyletic gap between *Ichthyothere* and other Melampodiinae.

In the restricted sense, the Melampodiinae is still diverse. The genera *Melampodium* and *Acanthospermum* would be regarded as close relatives by the traditional character of the inner involucral bracts enclosing the ray achenes, but differences in shapes and pubescence of disk corollas, different details of the inside of the lobe tips, and the basically different achene walls suggest otherwise. The distinctions are particularly marked when compared to the basic uniformity seen throughout all major elements of *Melampodium*. All genera retained here in the subtribe seem comparatively remote from each other.

Subtribe 4. POLYMNIINAE

FIGURE 51

Subtribe POLYMNIIAE H. Robinson, Phytologia, 41:43, 1978.

**Polymnia* L. (including *Polymniastrum* Lam.).

Shrubs. Leaves opposite. Inflorescence a terminal cyme. Heads with paleae; flowers female or functionally male in the same head. Female flowers in 1 series; limbs of corollas minute, adaxially nearly smooth, apically unlobed or bilobed. Lobes of disk corollas 5, not papillose inside, with series of multicellular hairs inside along margin, cells of inner surface elongate; thecae of anthers pale; endothecial cells short, with 2 or 3 thickenings along transverse walls; anther appendages with glands abaxially. Styles of rays with prominent pairs of stigmatic lines; styles of male flowers divided at tip, with large coma of hairs abaxially ending below tip, without stigmatic surfaces. Resin ducts colorless, not obvious, single along veins of disk corolla throat, marginal in lobes, apparently outside of veins in shaft of disk style. Achenes of ray flowers somewhat obcompressed, walls carbonized, without striations, with distinct thin layer of sclerids, cells of surface subquadrate in regular pattern; cells of seed coat mostly elongate, weakly ornamented; pappus absent. Pollen 25–27 μm in diameter.

The subtribe contains only two species of *Polym-*

nia that are endemic to eastern North America. The genus is notable for the lack of a differentiated series of outer involucral bracts, the nearly smooth upper surface of the rays, the elongate cells on the inside surface of the disk corolla lobes, the pale anther thecae, the small regular cells on the surface of the achenes, and the lack of striations in the achene wall. These furnish a significant contrast to genera of the Melampodiinae with which *Polymnia* has previously been associated. *Smallanthus*, a mostly tropical genus often included in *Polymnia*, remains in the Melampodiinae.

There is actually no assurance that *Polymnia* is closely related to the Melampodiinae with which it shares the lack of pappus and the functionally male disk flowers. At the beginning of this study, *Unxia* was regarded as a member of the Polymniiae, sharing most of the essential characters of the subtribe. Examination of two rarer species of *Unxia*, however, has shown definite relationship to the genus *Calea* and the Neurolaeninae, a group in which there is no other example of suppressed gynoecia in the disk flowers, and where a pappus is usually present (Robinson, 1980b). *Polymnia* does not share the features of the Neurolaeninae seen in *Unxia*, but like *Unxia*, it might have its closest relationship to genera having hermaphroditic disk flowers.

Subtribe 5. MILLERIINAE

FIGURES 53–59

Subtribe MILLERIINAE Benth. & Hook. f., Gen. Pl., 2:190, 1873.

**Axiniphyllum* Benth., **Guizotia* Cass., nom. cons. (including *Ramtilla* DC. ex Wight, *Veslingia* Vis.), **Milleria* L., **Rumfordia* DC., **Sigesbeckia* L. (including *Limnogenneton* Sch.-Bip. ex Walp., *Minyranthes* Turcz., *Sckuhria* Moench., nom. rej., non *Schkuhria* Roth, *Trimeranthes* (Cass.) Cass.), **Trigonospermum* Less.

Herbs with opposite leaves. Heads in terminal usually subcymose inflorescences, with paleae. Ray flowers female; limbs of corollas papillose adaxially, strongly trilobed apically. Disk flowers functionally male or hermaphroditic; lobes weakly to strongly papillose inside; anther thecae blackened; endothecial cells short, with 2 or 3 thickenings on transverse walls; anther appendages usually without glands (with glands in *Guizotia* and *Milleria*). Style branches of rays and hermaphroditic disk flowers with paired stigmatic lines. Resin ducts without colored resin (distinctly colored in *Guizotia*), ducts solitary along veins of disk corolla throat, inside of veins in shaft of disk style. Achenes terete to trigonous, with carbonized walls, with distinct striations; cells of seed coat irregular or interlocking, with ornate walls; pappus absent. Pollen 30–40 μm in diameter.

The Milleriinae has been traditionally characterized by heads with few flowers, but that concept is rejected here. Various genera are excluded, *Sheareria* to the tribe Astereae, *Delilia* and *Tetranthus* to the Ecliptinae, *Ichthyothere* to the Melampodiinae, *Clibadium*, *Lantanopsis*, and *Riencourtia* to the Clibadiinae, *Desmanthodium* and *Stachycephalum* to the Desmanthodiinae, and *Pinillosa* to the Pinillosinae. The genus *Milleria* itself shows relationships to the group of genera including *Rumfordia*, and the subtribal name is applied to the group in this treatment.

At least part of the present subtribal grouping has support from other studies. The presence of two highly differentiated series of involucral bracts with one of the series strongly glanduliferous has caused *Rumfordia* and *Sigesbeckia* to be placed together in traditional systems. The studies of McVaugh and Laskowski (1972) and Turner (1978a) indicate the relationship of *Trigonospermum* to *Sigesbeckia*, and the generic position of some species has been disputed. The tie between *Rumfordia* and *Axiniphyllum* is mentioned by Sanders (1977) and Turner (1978b).

The position of *Guizotia* is less certain. The genus has been placed in the Coreopsidinae by traditional systems and by Stuessy (1977). Baagøe (1974) transferred the genus to the Verbesininae, but later agreed with Stuessy (Baagøe, 1977a). The more definitive concept of the Coreopsidinae in this study excludes *Guizotia*. The placement of

Guizotia in the Milleriinae, however, is based mostly on the close approximation of technical characters and is made in spite of differences in habit, the strictly yellow rather than whitish flower color, and the colored resin in the corolla ducts. The genus is unusual in the Heliantheae by its restriction to the African region and its uncertain relationship to anything in the Western Hemisphere. *Sigesbeckia* also extends its range into the Eastern Hemisphere, but it seems to represent a separate, more recent introduction of the typical element of the subtribe into that area.

Guizotia and *Helianthus*, in which amino acid sequences of the cytochrome *c* are known, are subtribally distinct, but they are clearly in the same paleaceous series of the tribe. The differences of 8 amino acids (Boulter et al., 1972) indicate considerable instability in the molecule in the tribe. All speculations regarding the Coreopsidinae based on *Guizotia* cytochrome *c* (Turner and Powell, 1977) must be rejected since the genus is not a member of that subtribe.

Various authors such as Stuessy (1977) and Turner (1978a) relate the *Rumfordia–Sigesbeckia* series to the Melampodiinae. Relationship to *Melampodium* is possible, but it seems best to hold these genera with strongly 3-lobed rays in a separate subtribe for which the name Milleriinae is available.

Subtribe 6. DESMANTHODIINAE

FIGURES 60–65

Subtribe DESMANTHODIINAE H. Robinson, Phytologia, 41:40, 1978.

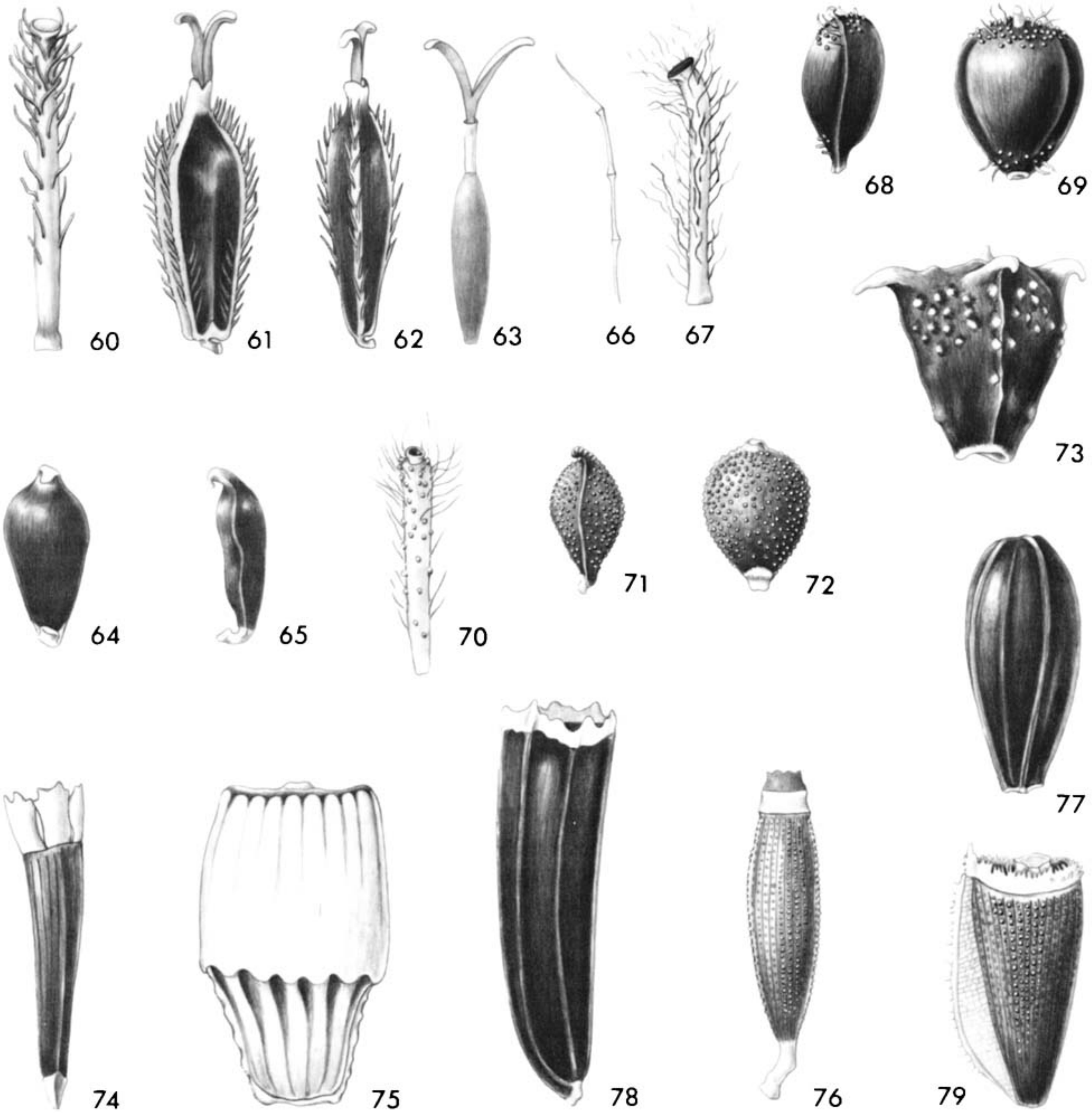
**Desmanthodium* Benth., **Stachycephalum* Sch.-Bip. ex Benth.

Subshrubs or shrubs with opposite leaves. Inflorescence with scorpioid cymes or syncephala. Heads with few flowers, heterogamous, with small involucral bracts in 1–2 series, with paleae. Ray flowers female; corolla limb lacking or with adaxial papillae and a trilobate tip. Disk flowers functionally male; corolla lobes and sometimes throat papillose inside; lobes oblong-ovate, with blunt uniseriate-celled hairs outside; thecae of anthers pale; endothecial cells with radial thickenings or with 3–5 thickenings on transverse walls; anther appendage sometimes glanduliferous. Branches of ray style with paired stigmatic lines, disk style undivided and without stigmatic surface. Resin ducts yellowish, paired along veins of disk corolla throat, along margin and sometimes midline of lobes, ducts inside of veins in disk style. Achenes of rays obovate and obcompressed, walls carbonized, with or without striations; cells of seed coat not ornamented?; pappus absent. Pollen ca. 25 μm in diameter.

Since the habits and the traditional characters of *Desmanthodium* and *Stachycephalum* are similar, their close relationship has never been questioned. Nevertheless, a number of basic differences are obvious, including the condensed inflorescence, the vesicle surrounding the ray flower, the minute tubular ray corolla, the usually radial thickenings of the endothecial cells, and the distinct striations in the achene in *Desmanthodium*, all in contrast to *Stachycephalum*. The well-developed yellowish resin ducts with the pairs along the veins of the corolla throat and the papillosity inside the disk corolla throats in species of both genera tend to confirm the relationship between the genera. The habits and the structure of the heads suggest relationship to the Clibadiinae, and the Desmanthodiinae are positioned accordingly here, but the hairs of the corollas are different and the achenes of *Desmanthodium* are striate. The color and arrangement of resin ducts might indicate ties to the Helianthinae and Galinsoginae, and the group should be checked for dehydrofalcarinone polyacetylenes.

The exact nature of the vesicle around the ray achene in *Desmanthodium* is not obvious. It is usually referred to as a palea, but it is positioned directly inside the subtending involucral bract, rather than alternating as it should be. The hairs on its surface are like those on the unenclosed disk achenes, and it seems the vesicle might be a special outer layer of the achene, rather than a palea.

The subtribe is strictly neotropical, centering in Central America. *Desmanthodium* extends into



FIGURES 60–79.—Desmanthodiinae-Clibadiinae-Pinillosinae-Guardiolinae-Enhydrinae-Montanoinae-Rudbeckiinae: 60–63, *Desmanthodium perfoliatum* Benth. (60, disk achene, × 17; 61, 62, ray florets in envelope, × 12; 63, ray floret without envelope, × 12); 64, 65, *Stachycephalum argentinum* Griseb., ray achenes, lateral and face views, × 12; 66–69, *Clibadium surinamense* L. (66, hair from achene, × 85; 67, disk achene, × 17; 68, 69, ray achenes, lateral and face views, × 12); 70–72, *Lantanopsis hispidula* Wright ex Griseb. (70, disk achene, × 17; 71, 72, ray achenes, lateral and face views, × 12); 73, *Pinillosa berteri* (Spreng.) Urb., ray achene, × 12; 74, *Guardiola pappifera* P. G. Wilson, ray achene, × 5; 75, *Guardiola mexicana* H. & B., ray achene, × 12; 76, *Enhydra sessillis* DC., achene, × 17; 77, *Montanoa tomentosa* DC., disk achene, × 12; 78, *Rudbeckia laciniata* L., disk achene, × 12; 79, *Ratibida columnifera* (Nutt.) Woot. & Standl., disk achene, × 17.

northern South America, whereas *Stachycephalum* is disjunct between Mexico and southern South America.

Subtribe 7. CLIBADIINAE

FIGURES 66–72

Subtribe CLIBADIINAE H. Robinson, Phytologia, 41:39, 1978.

**Clibadium* L. (including *Ballieria* Aubl., *Orsinia* Bertol. ex DC., *Oswaldia* Cass., *Trixis* Sw. non L.), **Lantanopsis* Wright ex Griseb., **Riencourtia* Cass. (including *Pontesia* Vell.).

Herbs and shrubs with opposite leaves. Inflorescence strongly cymose, often scorpioid. Heads heterogamous, with small herbaceous involucral bracts in few series; with paleae (lacking on disk in some *Clibadium*). Ray flowers female, up to 26 in 1-many series; corolla tubiform with 3 or 4 subequal disciform lobes. Disk flowers functionally male, 1–22; corolla without fiber-sheaths in throat; lobes slightly to strongly mamillose inside; hairs on outer surface of lobes uniseriate-celled, with elongate, papillose penultimate cells and short, apiculate, smooth apical cell; anther thecae and appendages blackened; endothecial cells short with 2–4 thickenings on transverse walls; appendage sometimes glanduliferous. Branches of ray style with paired stigmatic lines, disk style undivided and lacking stigmatic surface. Resin ducts somewhat reddish, ducts solitary along veins of disk corolla throat. Ray achenes obovate, subterete or angular to slightly obcompressed, often with prominent apical neck or stalk, densely pubescent with hairs or glands, walls carbonized, without striations; cells of seed coat elongate or irregular with ornamented walls; pappus absent. Disk achenes with long hairs. Pollen 23–30 μm in diameter.

The subtribe is distributed throughout the Neotropical region. *Clibadium* is widely distributed, but with only one species in eastern Brazil; *Lantanopsis* is West Indian, and *Riencourtia* is mostly Brasilian extending north to Venezuela. The group is marked by the strongly cymose inflorescence, the disciform ray corollas, the penicillate tuft of distinctive hairs that is often well developed on the tips of the disk corollas, and the dense pubescence of the achenes of most species. A sigmoid twist is seen at the apex of the ray achene in *Lantanopsis* and some *Clibadium* species. The black anthers and nonstriate achene walls are reminiscent of the Ecliptinae, but the characteristically male disk flowers with undivided styles and the common presence of reddish resin justify a separate subtribal status. The lack of a pappus and the reduced rays result in a placement here nearer to the Ambrosiinae than the Ecliptinae.

Some other genera have been placed close to *Clibadium* in various treatments. *Desmanthodium* is similar in habit and form of the heads, but has differently arranged ducts in the disk corolla with yellowish resin, the anthers are pale, and the hairs of the corolla lobes are totally different with blunt tips and evenly spaced septations. *Delilea* has some resemblance in habit and reduction of the male flowers, but the male corolla has well-developed fiber sheaths along the veins of the throat, the style is divided, and the sterile achene is glabrous. The inflorescence is also actually subumbellate rather than strongly cymose, unlike the Clibadiinae. The presence of the fiber sheaths indicates that *Delilea* is a member of the Ecliptinae.

Ichthyothere was first placed in the same subtribe with *Clibadium* by Stuessy (1977), but the two genera are juxtaposed in traditional systems and generally are considered close relatives. The idea is reinforced by the occurrence of the fish poisons or tetrahydropyranes in both genera. Nevertheless, *Ichthyothere* lacks the inflorescence form, disk corolla form and pubescence, and achene pubescence characteristic of the Clibadiinae. In addition, the achene is striate and the veins of the disk corolla throat are expanded above in unique manner in *Ichthyothere*. The genus is returned to the Melampodiinae in the present treatment and is not considered a close relative of the Clibadiinae.

The different basic arrangements of functionally male and female flowers in the members of the Clibadiinae seem worthy of detailed study.

Subtribe 8. PINILLOSINAE

FIGURE 73

Subtribe PINILLOSINAE H. Robinson, Phytologia, 41:42, 1978.

**Pinillosa* Ossa ex DC., **Koehneola* Urb.?

Minute, repent herbs. Leaves opposite, with distinct petioles; lamina suborbicular, palmately veined. Heads solitary on long peduncles; involucral bracts 4, herbaceous; 2 female flowers and 2 male flowers borne collaterally, male flowers inside of smaller involucral bracts. Corolla of female flower obsolete. Corolla of male flower with elongate tube and lobes, with very short throat; lobes densely and strongly papillose inside; anther thecae blackened; endothecial cells subquadrate to broader than long, with radial thickenings; anther appendages obsolete. Style branches of female flowers large, with paired stigmatic lines; style branches of male flowers large, with expanded, patelliform tips, densely papillose, without stigmatic surface. Resin ducts not evident. Achenes of female flowers prismatic, 4-lobed, walls carbonized, without striations; cells of seed coat not ornamented; pappus absent. Pollen ca. 25 µm in diameter.

The subtribe, as represented by *Pinillosa* of Cuba and Hispaniola, is distinct among the Heliantheae by a number of characters, including the repent habit, the collateral male and female flowers of strikingly different forms, the obsolete appendage of the anther, the radial thickenings of the endothecial cells, the expanded tips of the male style branches, and the 4-lobed achenes. *Koehneola* of Cuba, of which only the description has been seen, may be related to *Pinillosa* having a similar repent habit, heads with 4 involucral bracts and 2 each of 2 types of flowers collaterally arranged, deeply lobed disk corollas and an achene without a true pappus. In described features, the latter genus differs by the presence of a deeply bifid female corolla, less differentiated styles in the male flowers, and incompletely suppressed gynoecium in the male flowers, and the presence of a broad appendage on the anther.

Pinillosa is one of a group of West Indian genera of reduced habit and solitary, long-pedunculate heads that traditionally is placed in the Milleriinae. Others of the group are the Cuban genera *Heptanthus* and *Tetraperone*, which have a rosulate habit and have more numerous ray and disk flowers in the head; and *Tetranthus* of Hispaniola and the Bahamas, with 4 hermaphroditic flowers in the head, simple achene wall structure, and fused stigmatic surfaces. The first two are placed in a separate subtribe, Heptanthinae, and the last is placed in the Ecliptinae.

The intensely blackened anther thecae and the nonstriate achene wall of *Pinillosa* might indicate that it is close to the Ecliptinae. Because of the similarities in appearance and geography, it is possible that *Pinillosa* is actually closely related to *Tetranthus*, but the many differences in detail make this doubtful.

Subtribe 9. GUARDIOLINAE

FIGURES 74, 75

Subtribe GUARDIOLINAE H. Robinson, Phytologia, 41:41, 1978.

* *Guardiola* Cerv. ex Humb. & Bonpl. (including *Tulocarpus* Hook. & Arn.).

Subshrubs with opposite leaves, glabrous or subglabrous; leaf blades simple. Inflorescence terminal. Heads often aggregated, heterogamous, with involucral bracts subequal in 1–2 series, with paleae. Ray flowers female; corolla limb white, adaxially papillose. Disk flowers functionally male; corolla with elongate tube, deeply 5-lobed; lobes on inner surface smooth below and strongly papillose above; filaments densely pilose below the collar; thecae of anthers blackish green; median endothecial cells strongly noduliferous along vertical walls; anther appendage with 1 or 2 large glands abaxially. Branches of ray style large, with paired stigmatic lines; branches of disk style elongate, sharply and densely papillose on outer surface, sometimes with obsolete pairs of stigmatic lines on lower inside surface. Resin ducts reddish, ducts numerous in involucral bracts; ducts indistinct in throat of disk corolla, often prominent in lobes; ducts not evident in styles. Achenes of rays slightly obcompressed, strongly indurated, walls carbonized, with distinct striations; cells of seed coat slightly distorted, with prominent irregular thickenings on walls; pappus absent (with crown of 5 subquadrate indurate squamae in *G. pappifera* Wilson). Pollen 30–35 μm in diameter.

Guardiola usually has been placed in the Melampodiinae because of the suppressed gynoecia of the disk flowers. Stuessy (1973) transferred the genus to the Coreopsidinae, which it resembles in habit and details of the involucre. Initial doubts regarding Stuessy's placement derive from the presence of glands on the anther appendages in *Guardiola* and the apparent lack of glands on the anther appendages of the Coreopsidinae (Robinson and Brettell, 1973a). On further analysis, *Guardiola* shows distinct striations in the achene wall and strongly ornamented cells of the seed coat, characters also absent in the Coreopsidinae. The scarcely flattened ray achenes further indicate that the divergence between *Guardiola* and the Coreopsidinae occurred before the latter gained any of its characteristic features.

The glands on the anther appendages of *Guardiola* are distinct and massive, unlike the usual biseriate, capitate glands on other Heliantheae. In the specimens showing colored resin ducts in the disk corolla lobes, the ducts are inside the veins and do not join where they terminate at the top of the throat. In the species I have sampled, there is no variation in the dense pubescence of the anther filaments or in the prominent thickenings along the vertical walls of the endothecial cells.

The single genus of the subtribe is restricted to Mexico.

Subtribe 10. ENHYDRINAE

FIGURE 76

Subtribe ENHYDRINAE H. Robinson, Phytologia, 41:398, 1979.

**Enhydra* Lour. (including *Cryphiospermum* P. Beauv., *Hingtsha* Roxb., *Meyera* Schreb., *Sobreyra* Ruiz & Pav., *Sobrya* Pers., *Tetraotis* Reinw., *Wahlenbergia* Schum., non Schrad., non Blume).

Aquatic herbs with opposite leaves. Inflorescence of sessile axillary heads. Heads heterogamous, with herbaceous involucral bracts in few series, with paleae. Ray flowers female; limbs of corollas minute, smooth adaxially. Disk flowers hermaphroditic; corolla lobes slightly longer than wide, smooth on inner surface, outer surface nearly glabrous; thecae of anthers slightly darkened, endothecial cells short with single thickenings on transverse walls; anther appendages ovate, with glands abaxially. Style branches with paired stigmatic lines, with short blunt papillose appendages. Ducts of disk corollas often with reddish resin, ducts solitary along veins of throat, continued along margins of lobes; ducts of style inside the veins. Achenes prismatic or terete, short- to long-stipitate at base, walls carbonized, with striations; cells of seed coat inornate; small upper callus present, pappus absent. Pollen ca. 27–35 μm in diameter.

The single genus *Enhydra*, has a form reminiscent of some Ecliptinae, but the striate subterete achenes are completely foreign to that subtribe. The reddish resin that sometimes is present in the disk corollas and the ducts inside of the veins of the style suggest a relationship to the Neurolaeninae, but the striate achenes and the lack of pappus favor placement in the tribal scheme nearer the Montanoinae. The aquatic specialization of the Enhydrinae seems distinctive.

Enhydra occurs at lower elevations in tropical and subtropical parts of both hemispheres.

Subtribe 11. MONTANOINAE

FIGURE 77

Subtribe MONTANOINAE H. Robinson, Phytologia, 41:42, 1978.

**Montanoa* Cerv. in Llave & Lex. (including *Eriocoma* H.B.K., non Nutt., *Montagnaea* DC., *Uhdea* Kunth).

Shrubs and small trees with opposite leaves; leaves distinctly petiolate, blades trinervate and often lobed. Inflorescence corymbose-paniculate. Heads with ray and disk flowers, with small herbaceous involucral bracts in 2–3 series; paleae present and accrescent with age. Ray flowers sterile; limb of corolla long, papillose on upper surface. Disk flowers hermaphroditic; corolla densely scabrid outside; lobes short- to long-triangular, with stomates on outer surface, papillose inside; anther thecae blackened; endothecial cells short, with 2 or 3 thickenings on transverse walls; anther appendage ovate, with glands and hairs abaxially. Branches of style with paired stigmatic lines, appendage tapering. Resin ducts without evident color. Disk achenes quadrangular obpyramidal, walls carbonized, with striations, surface of wall woody; cells of seed coat weakly ornamented; pappus absent. Pollen ca. 25–35 μm in diameter.

The position of the Montanoinae in the present subtribal sequence is based primarily on the bisexual disk flowers having uncompressed, epappose achenes. Previous treatments have associated *Montanoa* with various other genera with sterile ray flowers, genera placed here in the Helianthinae and Ecliptinae. *Rojasianthe* of the latter subtribe is of interest because it is the only other genus in the tribe with paleae markedly enlarged with age, but the presence of a pappus and the specialized form of disk corolla make close relationship to *Montanoa* doubtful. Mature achenes of *Rojasianthe* have not been seen, but there seem to be no striations in the wall. The achenes in *Montanoa* are more like those in the Melampodiinae and Milleriinae, but the scarcely lobed sterile rays and the hermaphroditic disk flowers preclude inclusion of the genus in either group.

The genus *Montanoa* occurs in Mexico, Central America, and northern South America.

Subtribe 12. RUDBECKIINAE

FIGURES 78, 79

Subtribe RUDBECKIINAE H. Robinson, Phytologia, 41:43, 1978.

**Dracopis* Cass., **Ratibida* Raf., **Rudbeckia* L. (including *Heliophthalmum* Raf., *Lepachys* Raf., *Obeliscotheca* Adans., *Peramibus* Raf.).

Plants herbaceous with alternate leaves. Inflorescence with scapose solitary heads or sparsely branched. Heads with highly conical or columnar receptacles, with ray and disk flowers, involucral bracts herbaceous in ca. 2 series, with paleae. Ray flowers sterile; limb of corolla prominent, papillose on upper surface. Disk flowers hermaphroditic; lobes short, triangular, papillose on inner surface; anther thecae blackened; endothecial cells subquadrate, with thickenings radial or on vertical walls; anther appendage ovate, with cluster of stout glands abaxially. Branches of style with paired stigmatic lines; appendage short to long-tapering, with dense brush of long papillae. Resin partially reddish; ducts of disk corolla throat solitary along veins. Disk achenes compressed to subquadrangular, walls carbonized, with striations; cells of seed coat not or slightly ornamented; pappus absent or with two aristate projections. Pollen ca. 23–27 μm in diameter.

The Rudbeckiinae is an exclusively North American group previously placed in the broadly interpreted Verbesininae of Bentham and Hooker (1873) and in the more narrowly interpreted Helianthinae of Stuessy (1977). Similarities in habit and in some details such as sterile rays and the shape of the *Ratibida* achene do suggest a relationship to elements from the traditional Verbesininae, which are placed here in the Ecliptinae. The Rudbeckiinae differ from these genera and all Ecliptinae by the striate achenes, the radial or vertical arrangements of thickenings in the endothecial cells, the distinctive cluster of stout, cylindrical glands on the anther appendages, and the common occurrence of prominent reddish resin in the ducts of the disk corolla throat.

The Rudbeckiinae, as delimited here, seems to be an entirely natural group in spite of the more truncated style branches and more compressed achenes of *Ratibida* and the vertically rather than radially arranged endothecial thickenings in *Dracopis*. *Echinacea*, which is usually regarded as a close relative of *Rudbeckia*, has nonstriate achenes, lacks the cluster of distinctive glands on the anther appendage, has single thickenings on the transverse walls of the endothecial cells, and has a single, fused stigmatic surface on each style branch. *Echinacea* is evidently not particularly close to the Rudbeckiinae, and it conforms in all essential details to the present interpretation of the Ecliptinae.

Subtribe 13. ZALUZANIINAE

FIGURES 80-83

Subtribe ZALUZANIINAE H. Robinson, Phytologia, 41:44, 1978.

**Chromolepis* Benth., **Hybridella* Cass. (including *Chiliophyllum* DC., nom. rej., non Philippi), **Zaluzania* Pers. (including *Chrysophania* Kunth ex Less., *Ferdinanda* Lag.).

Herbs or shrubs with alternate or basal leaves, blades often lobed or dissected. Inflorescence with few to many heads in corymbose panicles, or heads solitary on peduncles from basal rosette. Heads heterogamous; receptacle convex or shortly conical; involucre herbaceous in ca. 2 series; paleae present. Ray flowers female (substerile in *Zaluzania grayana* B. L. Robins. & Greenm.); limb of corolla prominent, papillose on upper surface, bilobed or obscurely trilobed at tip. Disk flowers hermaphroditic; corolla outer surface often covered with dense pubescence of blunt or gland-tipped hairs, base often with extended margin covering top of achene; lobes short, papillosity on inner surfaces rather abruptly demarcated at base; anther thecae blackened; endothecial cells with 2-4 thickenings on transverse walls; anther appendages ovate, with or without glands abaxially. Style branches with single, fused stigmatic surface inside. Resin ducts not colored, solitary and sometimes prominent along veins of disk corolla throat. Achenes slightly compressed, walls carbonized, with striations; cells of seed coat not ornamented, without sinuous walls; pappus absent. Pollen 25-30 μm in diameter.

In Stuessy's revised system of the tribe (1977), *Zaluzania* is placed in the Neurolaeninae, while *Chromolepis*, in spite of its fertile rays, is placed in the Helianthinae. Actually, the striate achenes and fused stigmatic surfaces of the Zaluzaniinae are suggestive of the latter subtribe. Differences in the rays, the lack of the distinctive resin ducts, and the lack of the characteristic scabrous bases of the corolla throats clearly distinguish the Zaluzaniinae from the Helianthinae. Also, the achenes are fundamentally epappose in the Zaluzaniinae, a condition permitting the unique expanded corolla base in *Zaluzania*, whereas the Helianthinae are basically pappose with intermittent calvous forms.

The fused stigmatic surface of the style branches and the fertile rays furnish technical distinctions from various other epappose subtribes having hermaphroditic disk flowers. Alternate leaves are consistent in known members of the Zaluzaniinae as in the Rudbeckiinae, but the character also is found in other subtribes, especially among genera from more temperate areas.

The subtribe is native to the southwestern United States and adjacent Mexico. A South American species previously placed in *Zaluzania* is the basis of the genus *Kingianthus* of the subtribe Ecliptinae (Robinson, 1978b).

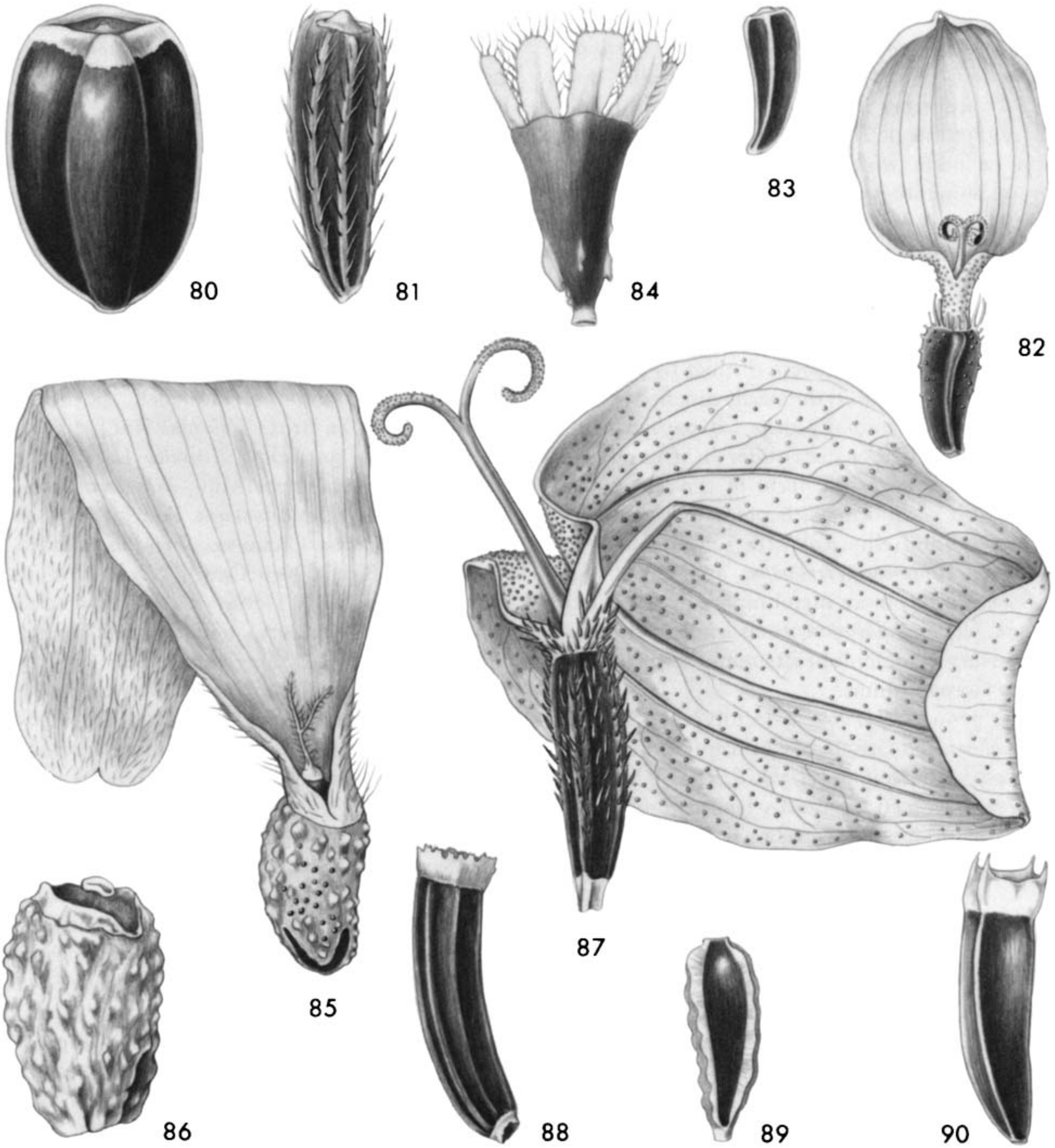
Subtribe 14. HEPTANTHINAE

FIGURE 84

Subtribe HEPTANTHINAE H. Robinson, Phytologia, 41:41, 1978.

**Heptanthus* Griseb., **Tetraperone* Urb.

Plants rosuliform with short erect stems, leaves distinctly petiolate. Heads solitary on long peduncles; with ray and disk flowers; involucre herbaceous in ca. 2 series; paleae few or lacking. Ray flowers female; limb of corolla papillose above, bilobed at tip. Disk flowers functionally male; corolla with short lobes, lobes slightly papillose on inner surface; anther thecae slightly blackened; endothecial cells short, with thickenings of inner cells sometimes radial, inner walls often strongly ornamented; anther appendage without



FIGURES 80–90.—Zaluzaniinae-Heptanthinae-Ecliptinae: 80, 81, *Chromolepis heterophylla* Benth. (80, ray achene, × 12; 81, disk achene, × 12); 82, 83, *Zaluzania angustata* (Lag.) Sch.-Bip. (82, ray floret, × 12; 83, disk achene, × 12); 84, *Heptanthus cochlearifolius* Griseb., ray achene, × 17; 85, 86, *Heliopsis buphthalmoides* (Jacq.) Dunal (85, ray floret with persistent corolla, × 12; 86, disk achene, × 17); 87, 88, *Zinnia grandiflora* Nutt. (87, ray floret with persistent corolla, × 8; 88, disk achene, × 12); 89, *Sanvitalia aubertii* A. Gray, disk achene, × 12; 90, *Borrichia frutescens* (L.) DC., disk achene, × 12.

glands. Style branches of rays with paired stigmatic lines; style of disk flowers distinctly branched, densely long-papillose. Resin ducts mostly indistinct (reddish and distinct in involucre and paleae of *Tetraperone*). Ray achenes polygonal or terete, with brownish carbonization, not striate, sometimes winged; cells of seed coat rather subquadrate, strongly ornamented; pappus of radially disposed squamellae or aristae; disk achenes linear, inornate. Pollen 25–35 μm in diameter.

The Heptanthinae is regarded here as a natural group of two Cuban genera distinct by the small erect rosuliform habit, the sterile disk flowers, and the prominent, radially disposed pappus of the ray achenes. The genera differ in a number of features, including the form of the leaf blades, which are cordiform with palmate venation in *Heptanthus* and elliptical with subpinnate venation in *Tetraperone. Heptanthus* apparently lacks paleae and has more membranaceous involucral bracts, whereas *Tetraperone* has some thin paleae and firmer involucral bracts reminiscent of those in the Coreopsidinae.

The genus *Heptanthus* is lectotypified here by *H. cochlearifolius* Griseb. My concept of the species is based on the isotype *Wright 2819* (US). Material of *Tetraperone* seen has mostly lacked corollas, but remnants of one disk corolla were found tangled in the bracts of a dried head.

Subtribe 15. ECLIPTINAE

FIGURES 85–129

Subtribe ECLIPTINAE Lessing, Linnaea, 6:153, 1831.
Subtribe ZINNIINAE Benth. & Hook., Gen. Pl., 2:193, 1873.
Subtribe VERBESININAE Benth. & Hook., Gen. Pl., 2:193, 1873.
Subtribe ENGELMANNIINAE Stuessy, Biol. Chem. Compositae, 645, 1977 [1978].

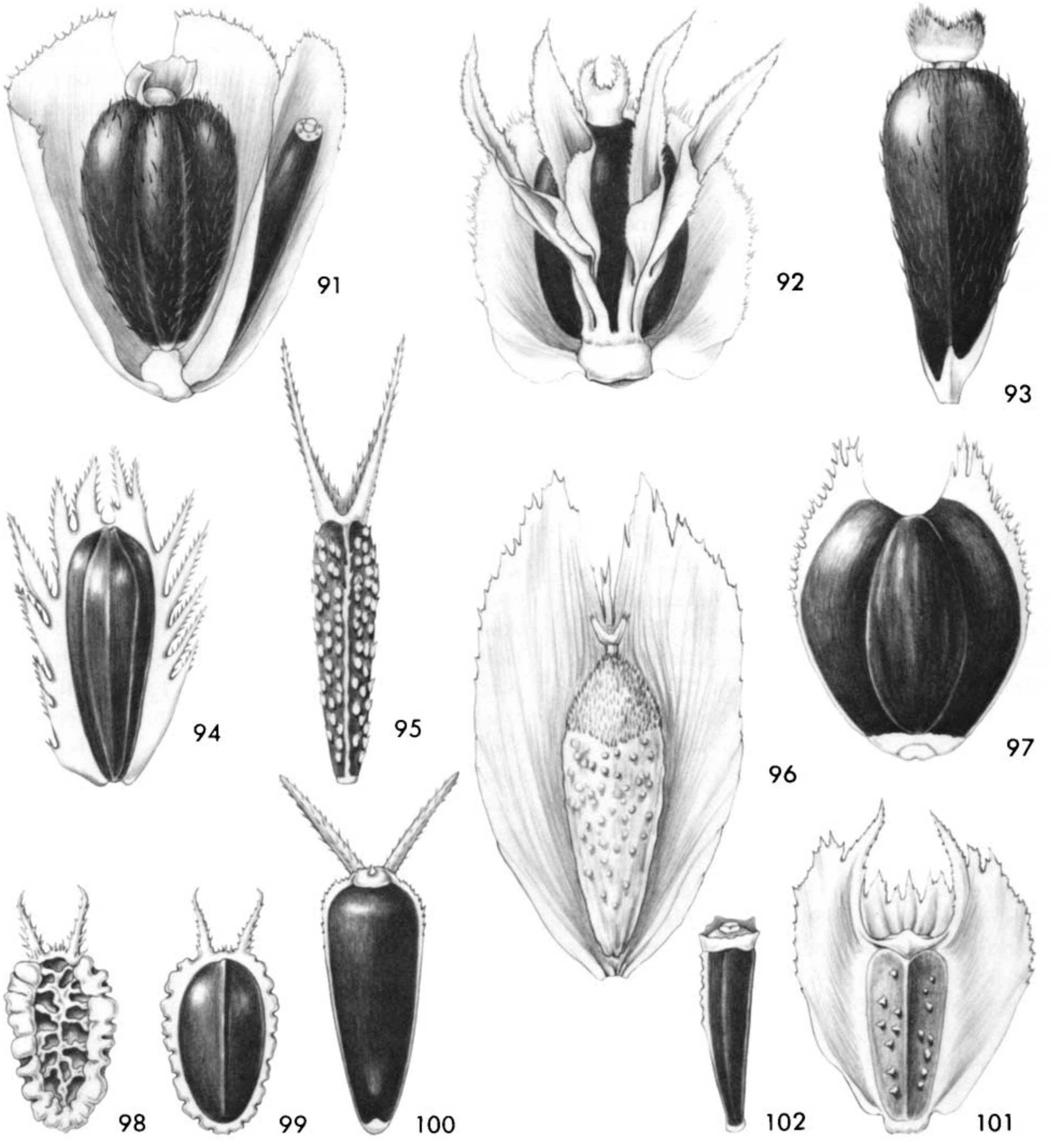
**Acmella* Rich. ex Pers. (including *Colobogyne* Gagnep., *Pyrethrum* Medic., non Zinn.), **Ancistrophora* A. Gray, **Angelphytum* Barroso, **Aspilia* Thou. (including *Anomostephium* DC., *Coronocarpus* Schum., *Dipterotheca* Sch.-Bip., *Gymnolomia* H.B.K., *Harpephora* Endl., *Wirtgenia* Sch.-Bip.), **Balsamorhiza* Hook., **Baltimora* L. (including *Fougeria* Moench., *Fougerouxia* Cass., *Scolospermum* Less.), **Berlandiera* DC., **Blainvillea* Cass. (including *Eisenmannia* Sch.-Bip., nom. nud.), **Borrichia* Adans. (including *Adelmannia* Reichb., *Diomedea* Cass., *Helicta* Cass., *Trimetra* Moc. & Sesse ex DC.), **Calyptocarpus* Less. (including *Blainvillea* subg. *Oligogyne* (DC.) Baker, *Galophthalmum* Nees & Mart.), **Chrysogonum* L. (including *Cargilla* Adans., *Diotostephus* Cass.), **Delilia* Spreng. (including *Desmocephalum* Hook. f., *Elvira* Cass., *Meratia* Cass., non Loisel., *Micrococecia* Hook. f.), **Dimerostemma* Cass. (including *Serpaea* Gardn.), **Dugesia* A. Gray, **Echinacea* Moench. (including *Brauneria* Neck. ex Britt., *Helichroa* Raf.), **Eclipta* L., nom. cons. (including *Abasaloa* La Llave & Lex. ?, *Eupatoriophalacron* Mill., *Micrelium* Forsk., *Paleista* Raf.), **Eleutheranthera* Poiteau ex Bosc (including *Euxenia* Chamisso, *Fingalia* Schrank, *Kegelia* Sch.-Bip., *Ogiera* Cass.), **Encelia* Adans. (including *Pallasia* L'Hérit. ex Ait., non Scop., non L. f., non Klotzsch., non *Pallassia* Houtt.), **Enceliopsis* A. Nels., **Engelmannia* Torr. & Gray, **Exomiocarpon* Lawalrée, **Fenixia* Merrill, **Flourensia* DC., **Geraea* Torr. & Gray, **Helianthella* Torr. & Gray, **Heliopsis* Pers.(including *Andrieuxia* DC., *Helepta* Raf., *Kallias* Cass.), **Hoffmanniella* Schlect., **Kingianthus* H. Robins., **Lasianthaea* DC. (including *Telesia* Raf.), **Leptocarpha* DC., **Lindheimera* Gray & Engl., **Lipochaeta* DC. (including *Aphanopappus* Endl., *Microchaeta* Nutt., *Schizophyllum* Nutt., non Fries), **Lundellianthus* H. Robins., **Macraea* Hook. f. (including *Trigonopterum* Steetz ex Anderss.), **Melanthera* Rohrb. (including *Echinocephalum* Gardn., *Lipotriche* R. Br., *Psathurochaeta* DC., *Wuerschmittia* Sch.-Bip. ex Walp.), **Monactis* H.B.K. (including *Astemma* Less., *Monopholis* Blake), **Otopappus* Benth. (including *Notoptera* Urb.), **Oxycarpha* Blake, **Oyedaea* DC., **Perymeniopsis* H. Robins., **Perymenium* Schrad., **Philactis* Schrad., **Phoebanthus* Blake, **Plagiolophus* Greenm., **Podachaenium* Benth. ex Oerst. (including *Dicalymma* Lem., *Cosmophyllum* Koch), **Podanthus* Lag., nom. cons., non *Podanthes* Haw., **Rensonia* Blake, **Rojasianthe* Standl. & Steyerm., **Salmea* DC., nom. cons., non *Salmia*

Cav. (including *Fornicaria* Raf., *Hopkirkia* Spreng.), **Salmeopsis Benth.,* **Sanvitalia* Gualt. ex Lam. (including *Anaitis* DC., *Lorentea* Orteg., non Lag.), **Schizoptera* Turcz., **Silphium* L., **Sphagneticola* Hoffm. ?, **Spilanthes* Jacq., **Steiractinia* Blake, **Synedrella* Gaertn., nom. cons. (including *Ucacou* Adans.), **Synedrellopsis* Hieron. & Kuntze, **Tetranthus* Swartz, **Verbesina* L. (including *Achaenopodium* Brandeg., *Actinomeris* Nutt., *Altamirania* Greenm., *Chaenocephalus* Griseb., *Ditrichum* Cass., nom. rej., non Hampe, *Hamulium* Cass., *Hingstonia* Raf., *Ochronelis* Raf., *Phaethusa* Gaertn., *Platypteris* H.B.K., *Ridan* Adans., nom. rej., *Saubinetia* Remy, *Tepion* Adans., *Ximenesia* Cav.), **Vigethia* Weber, **Wedelia* Jacq., nom. cons., non Loefl. (including *Menotriche* Steetz, *Niebuhria* Neck. ex Britt., non Scop., non DC., *Pascalia* Orteg., *Stemmodontia* Cass., *Thelechitonia* Cuatr., *Trichostemma* Cass., non *Trichostema* L., *Trichostephium* Cass.), **Wollastonia* DC. ex Decaisne, **Wulffia* Neck. ex Cass. (including *Chatiakella* Cass., *Chylodia* Rich. ex Cass., non *Chilodia* R. Br., *Tilesia* Meyer), **Wyethia* Nutt. (including *Alarconia* DC., *Melarhiza* Kellogg, nom. provis.), **Zexmenia* La Llave & Lex., **Zinnia* L., nom. cons. (including *Crassina* Scepin, *Diplothrix* DC., *Lepia* Hill, nom. rej., *Mendezia* DC., *Sanvitaliopsis* Sch.-Bip. ex Benth., *Tragoceras* H.B.K.).

Annual or perennial herbs, shrubs, or small trees. Leaves opposite, alternate or basal, with or without distinct petioles. Inflorescence of solitary heads on long peduncles or in panicles, axillary or terminal. Heads usually heterogamous; involucre herbaceous in 2–4 series, sometimes with scarious inner series; paleae present. Ray flowers female or sterile, rarely absent; limb of corolla papillose above, bilobed or obscurely trilobed at tip. Disk flowers hermaphroditic or sometimes functionally male; fibrous sheaths often present along veins of throat, rarely fibers in lobes or between veins; lobes usually short (long in *Rojasianthe*), slightly to strongly papillose inside, often more papillose or with hairlike papillae adaxially near margin, lobes often densely scabrous outside, sometimes with glands; anther thecae usually black (pale in *Encelia* group and some *Verbesina*); endothecial cells with 1–3 thickenings on transverse walls; appendages ovate, with or without glands abaxially. Styles distinctly branched, branches rarely with glands abaxially; stigmatic surface fused or divided into a pair of lines. Ducts of corollas without colored resin (traces of reddish resin in *Perymenium* and *Echinacea*), ducts solitary along veins of disk corolla throat, ducts of style shaft, where evident, outside of veins, usually outside of veins in branches. Achenes of fertile rays usually broadly triangular to obcompressed, disk achenes compressed or quadrangular; walls carbonized, without striations; cells of seed coat slightly irregular, walls not strongly sinuous, usually ornamented on tangential surfaces; pappus often with 2 aristae, sometimes with squamellae, a circle of short deciduous setae, or lacking. Pollen mostly 25–35 μm in diameter.

The Ecliptinae initially seems rather amorphous, but it is regarded here as natural, being comparable phyletically to such subtribes as the Ambrosiinae, Galinsoginae, Helianthinae, Pectidinae, and Gaillardiinae. All members have blackened, nonstriate achenes and lack well-developed patterns of colored resin in the ducts of their corollas. The anthers tend to be strongly blackened. Many of the members have fibers along the veins of the disk corollas, a feature not seen elsewhere in the Heliantheae. Where known, the polyacetylenes lack any of the special epoxides or ketones found in some other subtribes. Ambrosanolides and helenanolides are lacking. The subtribe contains the only three genera of the tribe from which amides have been reported, *Acmella*, *Echinacea*, and *Heliopsis* (Bohlmann et al., 1973). The only members of the Heliantheae known to have glands on the abaxial surface of the style branches are also in the Ecliptinae, *Podachaenium* (Robinson, 1978c), *Zexmenia mikanioides* (Britt.) Blake (Anderson et al., 1979), and species of *Dimerostemma*. In the last case glands occur on both the branches and the upper shaft of the style.

The diversity of the group has led to many separate subtribes being established. The name "Ecliptinae" has priority in the present combined



FIGURES 91–102.—Ecliptinae: 91, *Chrysogonum virginianum* L., ray and disk achenes in bract complex, × 12; 92, *Engelmannia pinnatifida* Torr. & Gray, ray achene in bract complex, × 8; 93, *Wedelia calycina* L. C. Rich., disk achene, × 8; 94, 95, *Synedrella nodiflora* (L.) Gaertn. (94, ray achene, × 12; 95, disk achene, × 12); 96, *Rensonia salvadorica* Blake, ray achene, × 12; 97, *Schizoptera peduncularis* (Benth.) Blake, ray achene, × 12; 98, 99, *Synedrellopsis grisebachii* Hieron. & O. Kuntze, achenes showing variation, × 12; 100, *Calyptocarpus vialis* Less., ray achene, × 12; 101, 102, *Lundellianthus guatemalensis* (J. D. Smith) Rindos (101, ray achene, × 12; 102, disk achene, × 12).

concept. Stuessy (1977) accepted a narrower concept which included *Wedelia* and many related genera that had previously been placed in four different subtribes. The Stuessy grouping was generally defined by a herbaceous habit and carpellate ray florets. The name "Verbesininae," which was used for the typical subtribe of the Heliantheae by Bentham and Hooker (1873), was retained by Stuessy for a more artificial group generally defined as shrubby with neuter ray florets. Stuessy also established the subtribe Engelmanniinae for a group of North American genera with achene complexes that were once placed in the Melampodiinae, and he recognized the traditional Zinniinae in which the ray corollas are usually fused to the achenes and are persistent at maturity.

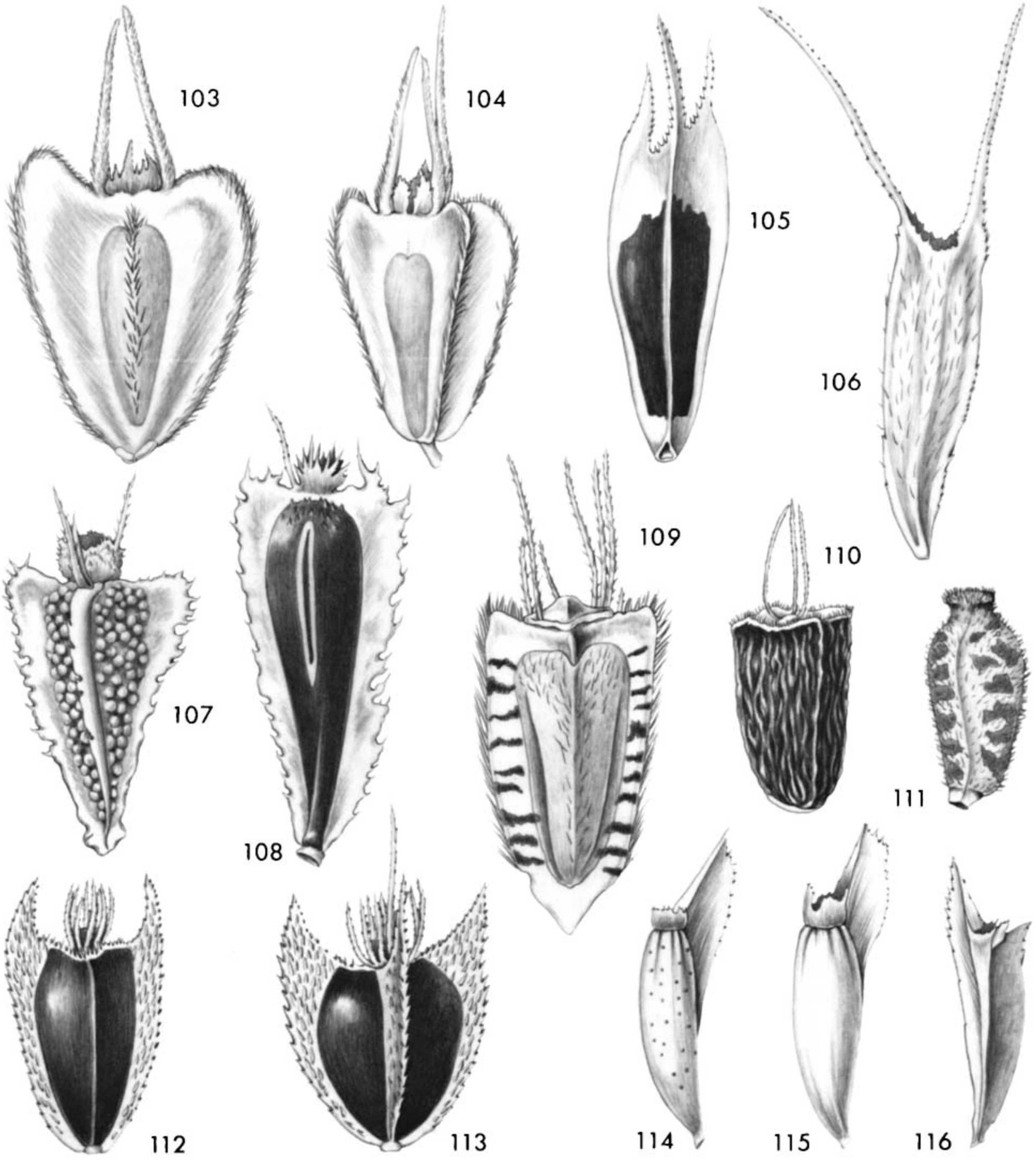
The present concept of the Ecliptinae is not strictly a combination of Stuessy's four subtribes. Some genera placed in the Ecliptinae by Stuessy, such as *Enhydra* and *Garcilassa*, and all but one of those in his group 1 of the Verbesininae are excluded here. Some genera placed elsewhere by Stuessy, such as *Delilea* (Milleriinae) and the *Encelia* group (Helianthinae), are included here.

There are significant subgroupings within the Ecliptinae. Regarding the typical element, *Eclipta* itself is distinctive by the filiform paleae, but in habit and various details of styles and disk achenes it is similar to *Wedelia*, with which it shares the specific flavanoid wedelolactone (Hegnauer, 1977). In the group related to *Eclipta* and *Wedelia*, the ray achenes, when fertile, characteristically are trigonous to broadly obcompressed, in contrast with the more compressed or quadrangular achenes of the disk. The stigmatic lines of the group are separated in pairs. As an additional character, many of the genera have disk corollas of identical, narrowly funnelform shape with short, externally scabrid lobes and fibers or fiber-sheaths along the veins of the throat. This has been seen in American species of *Aspilia* and in *Berlandiera*, *Calyptocarpus*, *Chrysogonum*, *Delilea*, *Engelmannia*, *Exomiocarpon*, *Fenixia*, *Hoffmanniella*, *Lasianthaea*, *Lindheimera*, *Lundellianthus*, *Oyedaea*, *Rensonia*, *Schizoptera*, *Silphium*, *Steiractinia*, *Synedrella*, *Synedrellopsis*, *Vigethia*, *Wedelia*, *Wollastonia*, and *Zexmenia*. This extremely natural group includes genera placed by Bentham and Hooker (1873) and by Hoffman (1890-1894) in the Milleriinae, the Melampodiinae, and Verbesininae, and the Coreopsidinae. Fiber development reaches its extreme in *Rensonia*, with broad sheaths along the margins of the lobes, and there are many auxillary fiber strands in the lower parts of the corolla in *Synedrellopsis*. In the *Wedelia* group, the paleae usually have broad, blunt, and often colored tips, a striking contrast to those of the peripherally related *Eclipta*. In accepting the recent resurrection of *Lasianthaea* (Becker, 1976), it should be noted that both it and *Zexmenia* are in the relationship of *Wedelia*. Rindos (1980) furnishes significant insights into generic limits in this group. *Baltimora* also seems properly placed here (Stuessy, 1977), even though no fibers have been seen in the corollas. The genera of Stuessy's subtribe Engelmanniinae are distinctive in the achene complexes in their ray flowers, but they all fall within the present series. They have disk corollas essentially identical to those of *Wedelia* in shape, pubescence and, except for *Dugesia*, in presence of fiber-sheaths. The broadly margined ray achenes are approached in form in such genera as *Schizoptera*, *Synedrella*, and *Synedrellopsis*.

Dugesia is one of the two genera of the Heliantheae from which eremophiline sesqueterpene lactones have been reported (Bohlmann and Zdero, 1976). The presence of this class of compounds, until recently known only from the Senecioneae, must be rechecked.

The genera *Balsomorhiza*, *Helianthella*, and *Wyethia* are coarse alternate-leaved herbs with sterile rays and with fibers usually forming sheaths along the veins of the disk corolla throats, but they are distinct from the previous group by the fused stigmatic surface on the style branches. Although lacking fibers and showing prominent resin in the style branches, *Echinacea* also seems to belong in this group.

Borrichia is the remaining genus where fibers have been seen in the corolla. The opposite leaves, elongate lobes of the disk corollas, and fused



FIGURES 103–116.—Ecliptinae: 103, 104, *Zexmenia serrata* La Llave (103, disk achene, × 12; 104, ray achene, × 12); 105, 106, *Lasianthaea fruticosa* (L.) Becker, ray and disk achenes, × 12; 107, 108, *Perymeniopsis ovalifolia* (A. Gray) H. Robins., disk achenes, × 12; 109, *Steiractinia mollis* Blake, disk achene, × 12; 110, *Melanthera aspera* (Jacq.) Small, disk achene, × 12; 111, *Eleutheranthera ruderalis* (Swartz) Sch.-Bip., disk achene, × 12; 112, 113, *Perymenium grande* Hemsl. (112, disk achene, × 12; 113, ray achene, × 12); 114–116, *Otopappus verbesinoides* Benth. (114, 115, disk achenes, × 12; 116, ray achene, × 12).

stigmatic surfaces seem to preclude inclusion of the genus in either of the preceding groups, but the distinctive disk corollas and the deciduous ray corollas seem to exclude it from the *Zinnia* relationship where it was placed by Stuessy (1977). *Borrichia* also has distinctive septate hairs on the backs of the style branches.

I am convinced that the traditional Zinniinae, even without *Borrichia*, is an unnatural group. The strongly petiolate *Philactis* and *Heliopsis* seem close to each other, but not close to *Zinnia* or *Sanvitalia*. All the Zinniinae share the basic characters of the Ecliptinae, and some genera such as *Helianthella* and some specimens of *Zexmenia*, not in the traditional Zinniinae, seem to have ray corollas fused to the achenes.

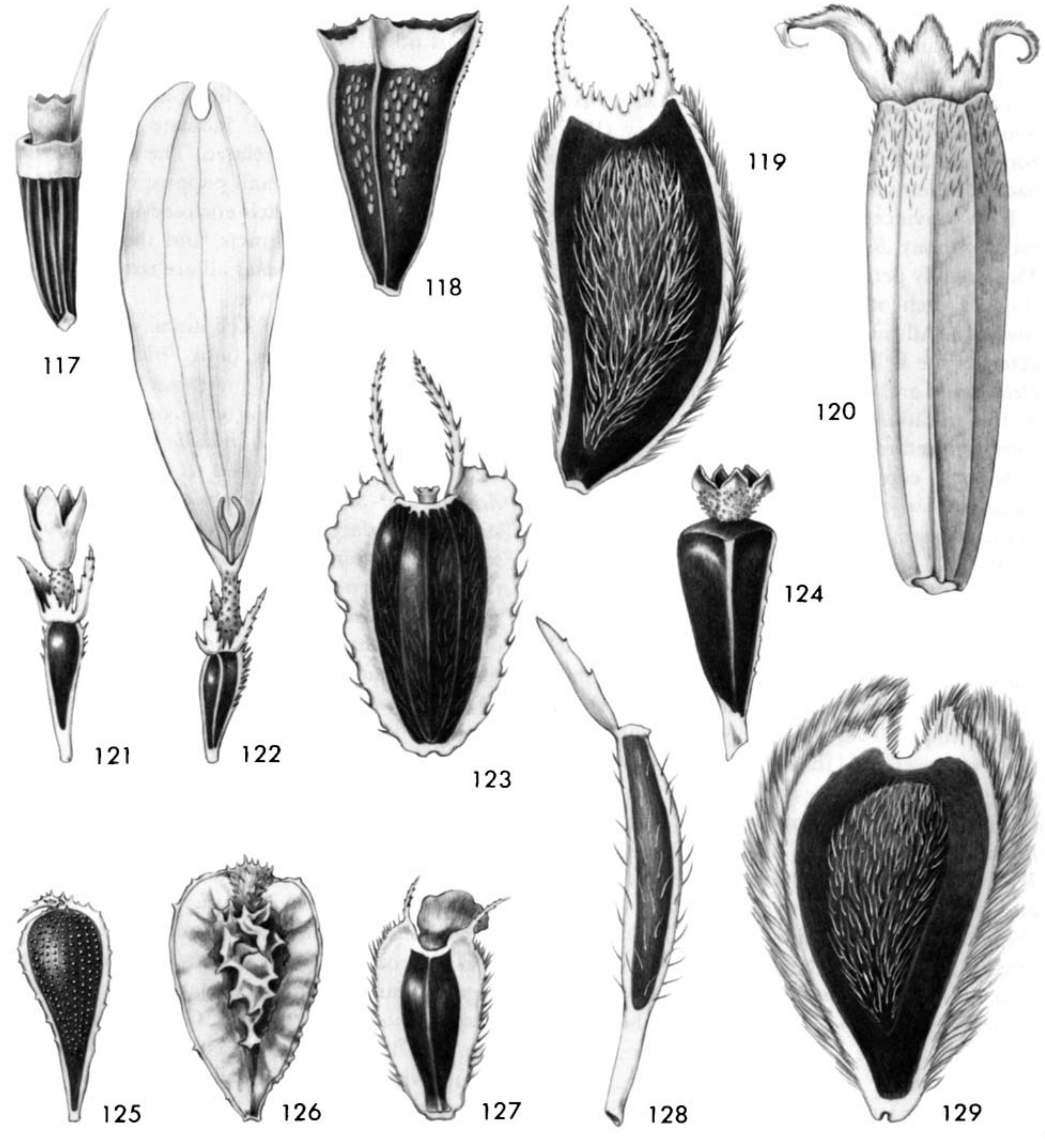
A radial capillary pappus in the Heliantheae usually is associated with subtribes having prismatic achenes, but four genera of the Ecliptinae have short deciduous bristles arranged more or less radially: *Melanthera*, *Perymenium*, *Rojasianthe*, and *Steiractinia*. A transitional situation to the biaristate condition is seen in *Perymeniopsis*, which has clusters of setae at the outer and inner limits of the pappus and has squamellae inserted at a slightly higher level between. Various differences between genera and the existence of a transitional genus indicate that the genera with such a radial capillary pappus do not form a natural group. *Melanthera* seems closely related to the epappose *Wulffia*, which also lacks fibers in the disk corollas, and is clearly related to the partially pappose *Wollastonia* (Fosberg and Sachet, 1980) of the *Wedelia* group in which corolla fibers occur. Even *Perymenium* and *Steiractinia* may not be so closely related as sometimes thought, since the former lacks fibers in the disk corolla which are present in the latter.

The best example of a dioecious member of the tribe is *Podanthus* of Chile, which seems closely related to the heterogamous genus *Leptocarpha* of the same area. These genera, along with *Macraea* of the Galapagos and *Podachaenium* of Mexico and Central America, are notable for the slender bases of their achenes.

The small, repent *Tetranthus* of the West Indies has been placed previously in the Milleriinae with various other West Indian genera having small stature and few-flowered heads. Of the other genera, *Pinillosa* shares the habit and four flowers in the heads, but details indicate that the two genera are not closely related. The achenes with nonstriate walls, the small pappus, the four hermaphroditic flowers each enclosed in one of the convolute involucral bracts, and the fused stigmatic surface in *Tetranthus* all are readily accommodated in the Ecliptinae.

Among the genera of Ecliptinae with strongly compressed disk achenes, both *Verbesina* and *Plagiolophus* have broad wings, but the narrow-necked achene of the latter suggests that is is closer in relationship to *Wedelia* than *Verbesina*. Genera more closely related to *Verbesina* include *Acmella* and *Salmea*, which seem to have fused stigmatic surfaces on the style branches, but in some more robust specimens there is slight separation of stigmatic lines. *Acmella*, which until recently has usually been placed in the synonymy of *Spilanthes*, has resin ducts of the style branches inside of somewhat broadened veins. In contrast *Spilanthes urens* Jacq., the type species of *Spilanthes*, has the ducts outside the unbroadened veins throughout the shaft and branches of the style, as in most Ecliptinae. It is notable that the three heliantheanean genera containing amides, *Acmella*, *Echinacea*, and *Heliopsis*, while all members of the Ecliptinae, do not seem particularly closely related to each other within the subtribe. Only in *Acmella* are the amides acetylenic.

One group of genera near *Verbesina* having stigmatic surfaces unquestionably fused includes *Encelia*, *Enceliopsis*, *Flourensia*, *Geraea*, and *Phoebanthus*. The first four of these seem to form a natural group, with characteristically pale anther thecae and sterile rays. Although the group of four genera is distinctive, every one of its characters is duplicated elsewhere among the closely related genera of the Ecliptinae. Even pale anther thecae are common in some Mexican species of *Verbesina*. The *Encelia* group often has been placed close to members of the *Helianthus* group, especially *Simsia*, and the group was retained in the Helian-



FIGURES 117–129.—Ecliptinae: 117, *Oxycarpha saedaefolia* Blake, achene, × 12; 118, *Echinacea atrorubens* Nutt., disk achene, × 12; 119, *Helianthella uniflora* (Nutt.) Torr. & Gray, disk achene, × 8; 120, *Wyethia helenioides* (DC.) Nutt., disk achene, × 12; 121, 122, *Podachaenium eminens* (Lag.) Sch.-Bip., ray and disk achenes, × 12; 123, *Verbesina virginica* L., disk achene, × 12; 124, *Podanthus mitiqui* Lindl., achene from female plant, × 12; 125, 126, *Macraea laricifolia* Hook.f., disk achenes, × 12; 127, *Spilanthes urens* Jacq., disk achene, × 12; 128, *Monactis pallatangensis* (Hieron.) H. Robins., disk achene, × 12; 129, *Encelia canescens* Lam., disk achene, × 12.

thinae in the recent treatment by Stuessy (1977), where the Verbesininae were given separate subtribal status. The lack of colored resin in the corollas, the nonstriate achenes, the lack of scabrosity on the lower throat of the disk corollas, and the apparent lack of dehydrofalcarinone polyacetylenes mark the *Encelia* group as Ecliptinae rather than Helianthinae.

The genera *Monactis* and *Kingianthus* of Ecuador and Peru are distinguished from most other Ecliptinae by alternate leaves and prismatic or terete achenes. The two genera seem transitional to the subtribe Neurolaeninae, but they differ from the latter by the pappus, when present, being asymmetrical, and by the complete lack of colored resin.

No material of *Sphagneticola* Hoffm. of Rio de Janeiro, Brasil, has been seen in this study. Hoffmann (1900) originally assigned the genus to the Coreopsidinae, but commented on the "*facie Wedeliae.*" Neither the description nor a type photograph show any basis for placement in the Coreopsidinae, but the habit, the mention of "*Antherae nigrae*," and the description of the achenes as "*vix compressa juniora obscure 2-4-costata, apice corona humilis fimbriata coronata, basi in stipitem achaenio proprio dimidio breviorum contracta*" indicate a probable place in the Ecliptinae.

The Ecliptinae occurs predominantly in the Western Hemisphere, where it is well represented in both the Nearctic and Neotropical regions. A number of separate elements such as *Acmella* and *Wollastonia* occur naturally in the Eastern Hemisphere.

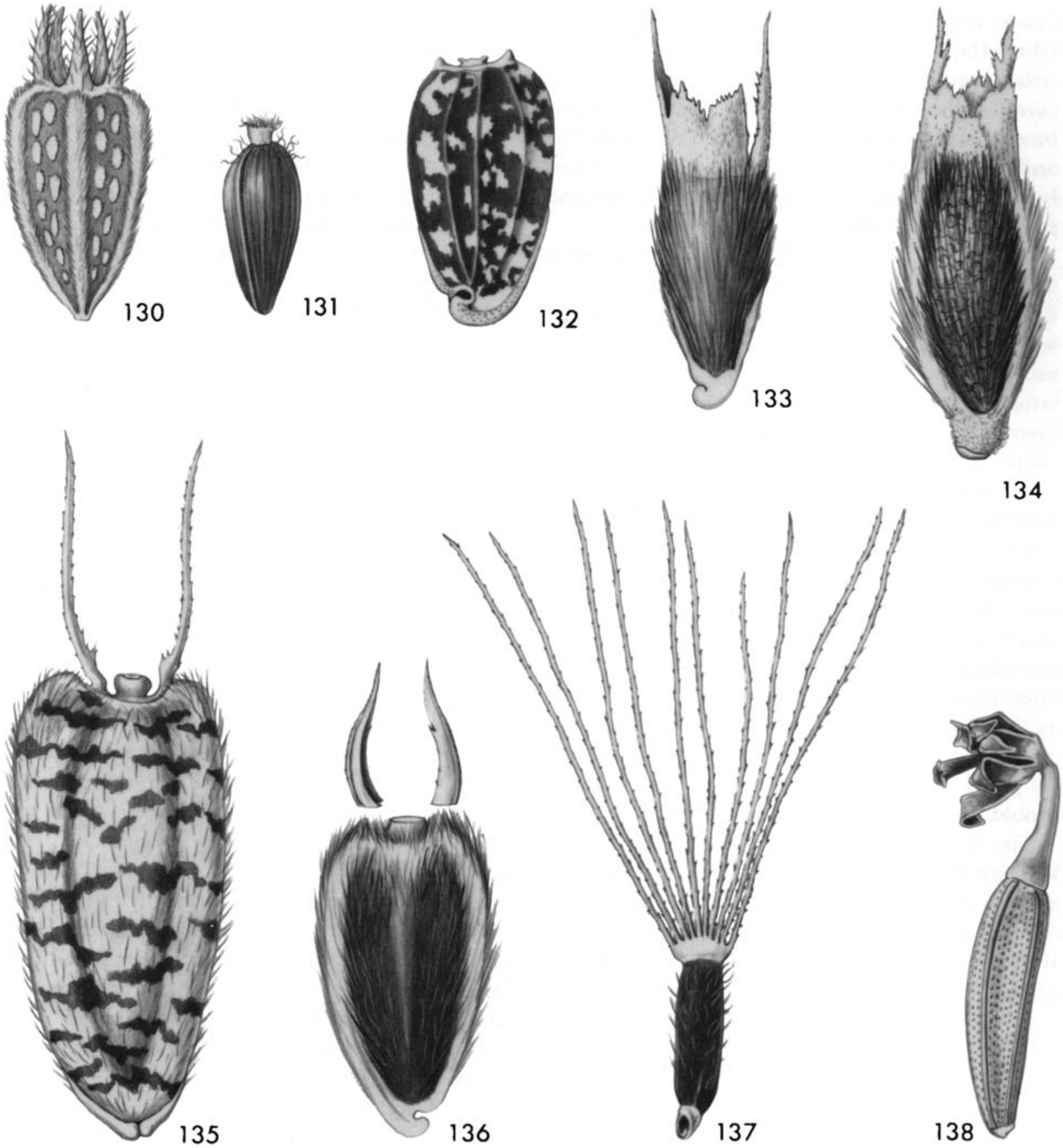
Subtribe 16. HELIANTHINAE

FIGURES 130–136

Subtribe HELIANTHINAE Dumort., Fl. Belg. Prodr., 71, 1827.
Subtribe LAGASCEINAE Benth. & Hook., Gen. Pl., 2:190, 1873.

**Agiabampoa* Rose ex Hoffm., **Aldama* La Llave & Lex., **Alvordia* Brandeg., **Garcilassa* Poepp. & Endl., **Helianthopsis* H. Robins., **Helianthus* L. (including *Discomela* Raf., *Echinomeria* Nutt., *Harpalium* Cass., *Linsecomia* Buckl), **Heliomeris* Nutt., * *Iostephane* Benth., **Lagascea* Cav., nom. cons. (including *Calhounia* A. Nels., *Nocca* Cav.), **Pappobolus* Blake, **Prionocarpus* Blake, **Rhysolepsis* Blake, **Scalesia* Arn. (including *Zemisne* Degener & Sherff), **Sclerocarpus* Jacq., **Simsia* Pers. (including *Armania* Bertol. ex DC., *Barratia* Gray & Engl.), **Stuessya* Turner & Davies, **Syncretocarpus* Blake, **Tithonia* Desf. (including *Mirasolia* (Sch.-Bip.) Benth. & Hook.), **Viguiera* H.B.K. (including *Bahiopsis* Kellogg, *Haplocalymma* Blake, *Hymenostephium* Benth., *Leighia* Cass.).

Annual or perennial herbs, rarely shrubs. Leaves opposite or alternate. Inflorescence with heads solitary or sparsely to densely clustered (single-flowered heads enclosed in secondary heads in *Lagascea*). Heads usually with ray and disk flowers, sometimes discoid; involucre with herbaceous bracts in ca. 2 series (more series in some *Viguiera*, fused into single tube in *Lagascea*); paleae usually present (absent in *Lagascea*), usually strongly conduplicate. Ray flowers sterile; limb of corolla with papillose upper surface, tip bilobed or obscurely trilobed. Disk flowers hermaphroditic; corolla throat narrowly cylindrical, base of throat rounded or bulging with scabrid outer surface; lobes usually slightly longer than wide, triangular, usually papillose on inner surface; anther thecae black; endothecial cells subquadrate or short-oblong, with 1 or 2 thickenings on transverse walls; connective sometimes with glands; anther appendage often with glands or hairs. Style branches of disk flowers sometimes laterally compressed, with single narrow stigmatic surface. Ducts with prominent yellowish resin (pale resin in *Agiabampoa*); ducts single or paired along veins of disk corolla throat, 2–6 ducts in shaft of style outside of veins, usually outside veins in style branches but sometimes inside or on both sides. Ray achenes sterile, sometimes enclosed in involucral bracts (*Sclerocarpus, Aldama*); disk achenes compressed (terete in *Lagascea*), walls carbonized, with distinct striations; carpopodium of two short, rounded, opposing lobes; cells of seed coat not or weakly ornamented; pappus usually of 2 aristae, often with



FIGURES 130–138.—Helianthinae-Neurolaeninae: 130, 131, *Lagascea mollis* Cav. (130, single head from cluster showing involucre, × 12; 131, the single achene from the head, × 12); 132, *Scalesia affinis* Hook. f., disk achene, × 12; 133, *Viguiera dentata* (Cav.) Spreng., disk achene, × 12; 134, *Syncretocarpus sericeus* (DC.) Blake, disk achene, × 8; 135, *Simsia sanguinea* A. Gray, disk achene, × 12; 136, *Helianthus annuus* L., disk achene, × 12; 137, *Neurolaena lobata* (L.) R. Br., disk achene, × 17; 138, *Staurochlamys burchellii* Baker, disk achene, × 12.

squamellae, sometimes absent. Pollen 27–35 μm in diameter.

The subtribe is almost entirely Nearctic and Neotropical in distribution, with the genera centered in Mexico and the United States. A few species are widely adventive or cultivated. One species of *Sclerocarpus* apparently is native in Africa.

The Helianthinae is one of the most concisely characterized subtribes in the present treatment. All members have sterile rays, single stigmatic surfaces on the style branches of the disk flowers, ducts outside of the veins in the styles, and striations in the walls of the achenes. Also, the resin in the ducts is yellowish in all members except the slightly anomalous *Agiabampoa.*

The present concept has very little in common with the traditional broadly and erratically delimited typical subtribe that has been called variously Helianthinae or Verbesininae. The narrower interpretation of the Helianthinae by Stuessy (1977) is an improvement, but remains very unnatural, since it includes such genera as *Balsamorhiza*, *Encelia*, *Rudbeckia*, and *Tetragonotheca*, while excluding *Alvordia*, *Agiabampoa*, *Lagascea*, *Garcilassa*, *Scalesia*, *Aldama*, and *Sclerocarpus*. Of the latter series, here placed in the Helianthinae, *Garcilassa* simply never seems to have been critically examined before, and Eliasson (1974) has already discussed the relationship of *Scalesia* of the Galapagos. *Lagascea* and the related *Agiabampoa* and *Alvordia* (Stuessy, 1976, 1978) are unusual in the subtribe only by specializations toward compound heads and by the presence of resin ducts inside the veins of the style branches. *Aldama* has recently been resegregated from *Sclerocarpus* (Feddema, 1971), but both share all characters of the subtribe Helianthinae and must be rather closely related.

The *Encelia* group is excluded here, although its members closely resemble some genera of the Helianthinae such as *Simsia.* The traditional treatments prior to the study by Blake (1913) did not separate *Simsia* and *Encelia* generically. The *Encelia* group has sterile rays, single stigmatic surfaces on the style branches, and chromosome numbers often $n = 17$, as in the Helianthinae. However, the *Encelia* group has colorless ducts, lacks dehydrofalcarinone, lacks scabrosity on the base of the disk corolla throat, and has nonstriate achene walls, all of which indicate a position in the Ecliptinae. The aristae of the achenes even seem different in basic structure, being more of an extension of the body of the achene, and not a sharply defined or deciduous structure as in the Helianthinae.

The Helianthinae seems to be more closely related to the Galinsoginae. The two subtribes share similar systems of resin ducts, striate achene walls, and polyacetylene chemistry. Both have dehydrofalcarinone, which has been reported elsewhere in the tribe only in *Iva* of the Ambrosiinae (Bohlmann et al., 1973), and both seem to lack the thiophenes that are common in other subtribes such as the Ecliptinae and Rudbeckiinae. The Helianthinae are readily distinguished from the Galinsoginae by the sterile rays, the basically compressed achenes and bilateral pappus, and the single stigmatic surface on the style branches. In the Helianthinae, the carpopodium is a short beaklike pair of lobes that seem to bite the achene free at the base as it matures, and there is no structure that approaches the specialized, asymmetric, sclerified plate that is characteristic of the Galinsoginae. As a final distinction, the resin ducts of the styles usually are completely outside of the veins in the Helianthinae and usually are completely inside the veins or collateral with them in the Galinsoginae. In rare cases such as *Lagascea* and *Tridax*, members of both subtribes achieve an intermediate condition, with ducts outside the veins in the style shaft and inside the veins in the branches.

Most members of the Helianthinae differ from the Galinsoginae by having solitary resin ducts along the veins of the disk corolla throat. There is a tendency for multiple ducts in the style and paired ducts in the corolla throat in the *Hymenostephium* and *Haplocalymma* parts of *Viguiera.* Supplementary resin ducts reach their extreme in species like *V. sylvatica* Klatt of Costa Rica and in the related genus *Garcilassa.*

Most members of the subtribe, including the genus *Viguiera*, have a chromosome number of $X = 17$. Recently, the genus *Heliomeris* has been resurrected from the synonymy of *Viguiera* for a series of species having $X = 8$ (Yates and Heiser, 1979). *Heliomeris* of the western United States and northern Mexico is scarcely distinct in any other way. The exappendiculate style branches differ from those of typical *Viguiera*, but many species presently retained in *Viguiera* have exappendiculate styles. It is therefore significant that *Heliomeris* has a unique pattern of resin ducts in the styles: the ducts are prominent in, but restricted to, the branches. The termination of the duct is usually abrupt, and no ducts are evident in the shaft of the style. It is also notable that the chromosome number is $n = 17$, the style is long-appendiculate, and the duct is not restricted to the style branches in *Viguiera porteri* (A. Gray) Blake, a species of the southeastern United States that was placed in *Viguiera* sect. *Heliomeris* by Blake (1918).

Subtribe 17. NEUROLAENINAE

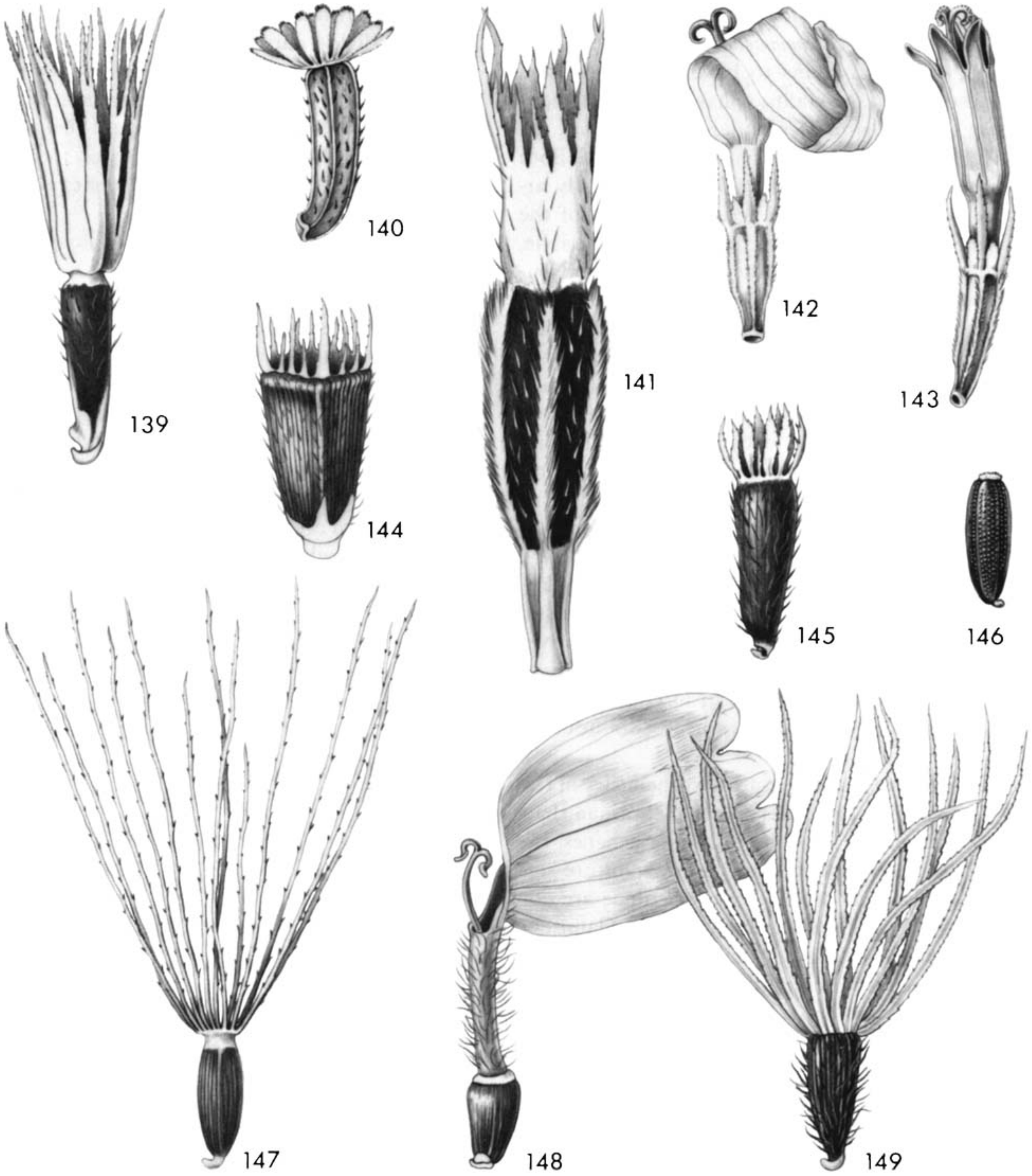
FIGURES 52, 137–143

Subtribe NEUROLAENINAE (Rydb.) Stuessy, Turner & Powell, Biol. Chem. Compositae, 645, 1977 [1978].
Tribe NEUROLAENEAE Rydb., N. Amer. Fl., 34(4):303, 1927.

**Brasilia* Barroso, **Calea* L. (including *Amphicalea* (DC.) Gardn., *Caleacte* R. Br., nom. provis., *Calebrachys* Cass., *Geissopappus* Benth., *Leontophthalmum* Willd., *Meyeria* DC., *Mocinna* Lag.), **Greenmaniella* Sharp, **Neurolaena* R. Br., **Staurochlamys* Baker, **Tetrachyron* Schlect., **Tyleropappus* Greenm., **Unxia* L. f. (including *Greenmania* Hieron., *Pronacron* Cass.).

Perennial herbs or shrubs; leaves alternate, opposite, or whorled. Inflorescence usually terminal, usually paniculate, sometimes reduced to single head. Heads heterogamous or discoid; involucre of partially herbaceous to completely coriaceous bracts, often in 4 or more series; paleae usually present. Ray flowers female; upper surfaces of limb with oblong scarcely mamillose cells, usually distinctly trilobed at tip (reduced and unlobed in some *Unxia*). Disk flowers usually hermaphroditic, functionally male in *Unxia*; corolla lobes short (in some *Neurolaena*) or long (in *Calea* group and some *Neurolaena*), cells of inner surface oblong and scarcely bulging; anther thecae black (in *Neurolaena* and *Staurochlamys*) or yellow (in *Brasilia*, *Calea*, *Tyleropappus* and *Unxia*); endothecial cells with 1–3 thickenings on transverse walls; anther appendage ovate, with or without glands abaxially. Branches of styles with paired stigmatic lines. Ducts of corollas usually with prominent reddish resin (lacking in typical *Neurolaena*), ducts solitary along veins of disk corolla throat, along margins in lobes, ducts in shaft of style inside of veins. Achenes prismatic, walls carbonized, without striations; cells of seed coat weakly ornamented; pappus radially symmetrical, usually of numerous bristles or squamellae (lacking in *Unxia*). Pollen 25–35 μm in diameter (to 55 μm in *Calea belemii* H. Robins.).

Traditionally *Neurolaena* has been placed with the genus *Schistocarpha* in the tribe Senecioneae, apparently being excluded from the Heliantheae because of its well-developed pappus of numerous capillary bristles. The paleae in the two genera are in conflict with the epaleaceous condition of the true Senecioneae and are not homologous to the form of chaff found in the often associated Liabeae. Such paleae were undoubtedly a factor in the unexplained creation of a separate tribe by Rydberg (1927). In transferring the two genera to the Heliantheae, Robinson and Brettell (1973b) first noted basic differences in the achene wall that could indicate that *Neurolaena* and *Schistocarpha* were not each other's closest relatives. In formally adopting the subtribe in the Heliantheae, Stuessy (1977) included an assortment of genera in addition to *Neurolaena* and *Schistocarpha*, genera as diverse as *Bebbia*, *Clappia*, *Dyscritothamnus*, *Greenmaniella*, *Varilla*, and *Zaluzania*. The group parallelled in part the artificial grouping included at the same time by Turner and Powell (1977) in their Varillinae. Though many similar genera are included by Stuessy, *Tridax* is left in the Galinsoginae, perhaps because of its more herbaceous habit.



FIGURES 139–149.—Neurolaeninae-Galinsoginae: 139, *Calea jamaicensis* L., disk achene, × 12; 140, *Calea (Geissopappus) caleoides* (DC.) H. Robins., disk achene, × 12; 141, *Brasilia sickii* Barroso, achene, × 12; 142, 143, *Tetrachyron orizabensis* Sch.-Bip. ex Klatt. (142, ray achene, × 12; 143, disk achene, × 12); 144, *Tetragonotheca texana* Gray × Engelm., achene, × 12; 145, *Galinsoga quadriradiata* R. & P., disk achene, × 17; 146, *Jaegeria hirta* (Lag.) Less., disk achene, × 24; 147, *Schistocarpha eupatorioides* (Fenzl) O. Kuntze, disk achene, × 17; 148, 149, *Alloispermum caracasanum* (H.B.K.) H. Robins (148, ray achene, × 8; 149, disk achene, × 12).

Of the genera included by Stuessy (1977), only *Neurolaena* and *Greenmaniella* are retained here. Most confusion seems to have involved genera placed here in the Galinsoginae such as *Schistocarpha*, *Bebbia*, *Dyscritothamnus*, and *Alloispermum*, the last resurrected from the synonymy of *Calea*. Both subtribes share prismatic achenes, a radially arranged pappus, colored resin, a position of the resin duct inside the veins in the shaft of the style, and usually a subimbricate involucre. The Neurolaeninae differ by the resin being reddish, the ducts being solitary along the veins of the disk corolla throat, the ducts being marginal in the corolla lobes, by the nearly smooth adaxial surfaces of the corollas, by the generally longer lobes of the disk corollas, and by the achenes lacking striations. The two subtribes share a similar asymmetric form of carpopodium on the achene, but in the Neurolaeninae, the inner cushion has firmer cells that don't collapse at maturity. Chemically the Neurolaeninae lack the dehydrofalcarinone polyacetylenes that are characteristic of the Galinsoginae, but have thymol derivatives in both *Neurolaena* and *Calea*. Thymol derivatives are not presently known from any other paleaceous subtribe in the Heliantheae (Robinson et al., 1978).

The achene wall structure and chemistry of the Neurolaeninae are closer to the Ecliptinae than the Galinsoginae, but the prismatic achenes, radial pappus, and frequent reddish resin are signifciant distinctions. The Neurolaeninae are not so obviously a natural subtribe as the Galinsoginae. *Staurochlamys* is particularly distinct in its lack of a subimbricate involucre. *Neurolaena* also is distinct from the *Calea* group by its capillary pappus, dark anther thecae, alternate leaves, and the inconsistent presence of reddish resin.

In the course of this study, the genus *Calea* has been redelimited. *Alloispermum* has been resurrected from synonymy and placed in the Galinsoginae (Robinson, 1978d), and *C. skutchii* Blake has been transferred to *Podachaenium* in the Ecliptinae (Robinson, 1978c).

Tetrachyron is held separate from *Calea*, but it is similar to that genus in the position of the style ducts, the prismatic achenes without striations, and the radial (4-parted) pappus. Characters that make placement in the Neurolaeninae uncertain are the lack of complete differentiation of the inner surface of the carpopodium and the sometimes double ducts along the veins of the disk corolla throat. The genus has been monographed by Wussow and Urbatsch (1979).

Some membes of the *Calea* group show reduction in paleae or suppression of disk flower gynoecia. Epaleaceous species of *Calea* were treated as a separate genus *Geissopappus* by Bentham and placed in the tribe Helenieae in Bentham and Hooker (1873). The genus *Unxia* also has paleae of reduced size, but it is most notable for the functionally male disk flowers. The styles of the disk flowers are completely sterile, lacking either branches or stigmatic papillae. The reductions in the two genera are totally independent of similar reductions elsewhere in the Heliantheae.

The subtribe is restricted to the Neotropical region.

Subtribe 18. GALINSOGINAE

FIGURES 144–152

Subtribe GALINSOGINAE Benth. & Hook., Gen. Pl., 2:198, 1873.

**Alepidocline* Blake, **Alloispermum* Willd. (including *Allocarpus* H.B.K., *Calydermos* Lag.), **Aphanactis* Wedd., **Bebbia* Greene, **Cuchumatanea* Seid. & Beaman, **Cymophora* B. L. Robins., **Dyscritothamnus* B. L. Robins., **Faxonia* Brandeg., **Galinsoga* Ruiz & Pavon (including *Adventina* Raf., *Stemmatella* Wedd. ex Benth. & Hook., *Stenocarpha* Blake, *Vargasia* DC., non Bertol. ex Spreng., *Vasargia* Steud., *Vigolina* Poir., *Wiborgia* Roth, nom. rej., non Thunb.), **Jaegeria* H.B.K. (including *Aganippea* Sesse & Moc. ex DC., *Heliogenes* Benth., *Macella* Koch), **Oteiza* La Llave, **Sabazia* Cass. (including *Baziasa* Steud., *Tricarpha* Longpre), **Schistocarpha* Less. (including *Neilreichia* Fenzl, *Zycona* O. Kuntze), **Selloa* H.B.K., nom. cons., non Spreng. (including *Feaea* Spreng., *Feaella* Blake), **Tetragonotheca* L. (including *Bikera*

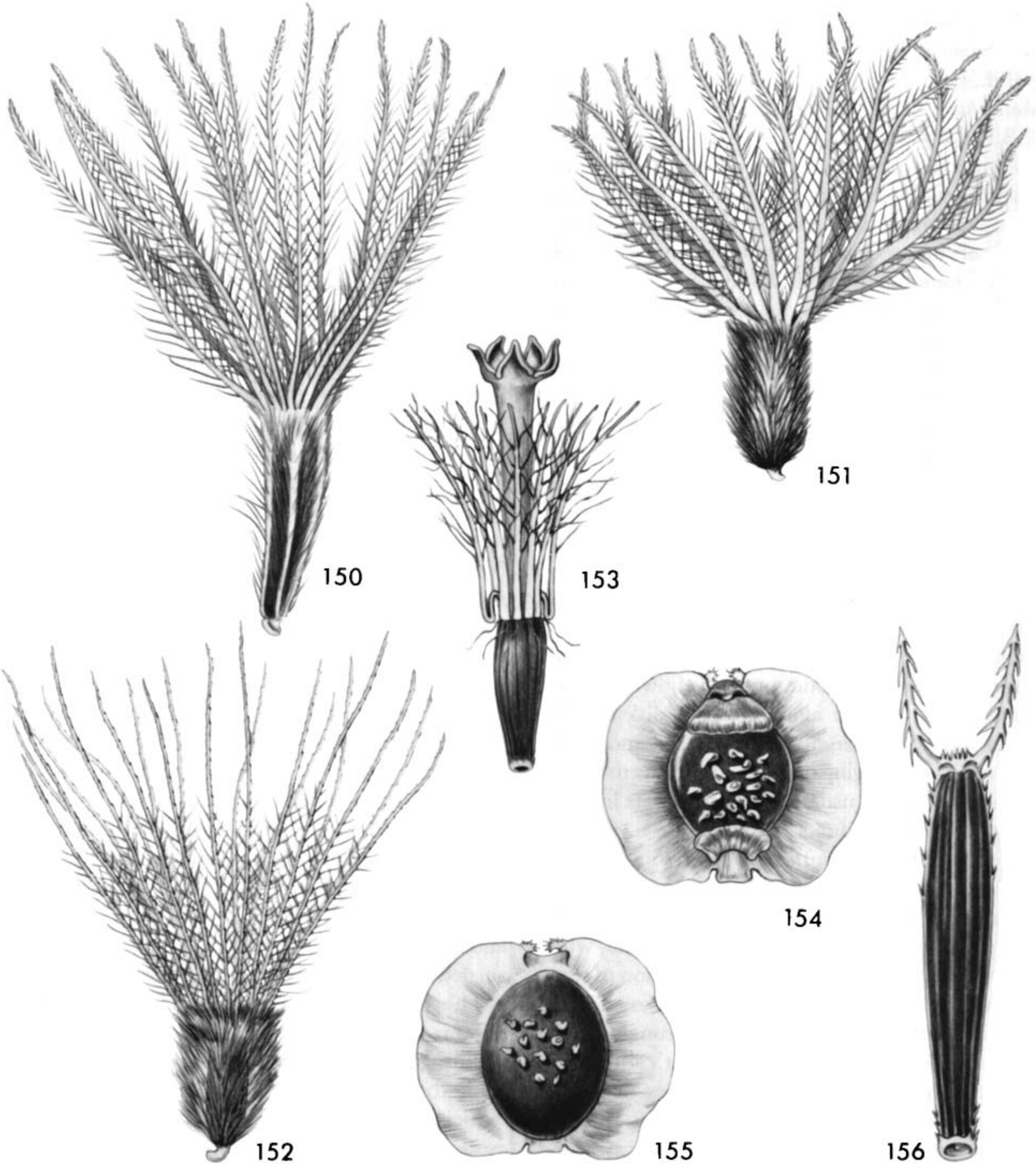
Adans., *Gonotheca* Raf., *Halea* Torr. & Gray, *Tetragonosperma* Scheele), **Tridax* L. (including *Balbisia* Willd., nom. rej., non Cav., *Bartolina* Adans., *Carphostephium* Cass., *Mandonia* Wedd., *Ptilostephium* H.B.K., *Sogalgina* Cass.).

Annual or perennial herbs, occasionally shrubs. Leaves usually opposite, sometimes in basal rosette. Heads one to few on short to long peduncles, or in corymbose usually terminal panicles. Heads usually heterogamous; involucre usually subimbricate, bracts in 2-5 series, coriaceous or sometimes herbaceous; paleae present (rare in *Alepidocline*), sometimes deeply trifid (in *Faxonia*, some *Sabazia*, some *Schistocarpha*). Ray flowers female; limb of corolla papillose on upper surface, usually white, usually trilobed at tip. Disk flowers hermaphroditic; lobes of corolla short-triangular, mamillose or papillose on inner surface; anther thecae rather pale to slightly darkened; endothecial cells subquadrate or oblong, with 1-3 thickenings on transverse walls (thickenings on vertical walls in a few *Tridax*); anther appendages ovate, with or without glands. Style branches with stigmatic lines paired. Ducts with yellowish resin, ducts usually paired along veins of disk corolla throat, on inner side of veins in lobes and often remote from margin, ducts from adjacent lobes not fused at sinus; usually with two ducts in style inside of veins (4 ducts collateral to 4 veins in style shaft of *Oteiza*, *Schistocarpha*, and some *Tridax*; 4 ducts outside of 2 veins in *Tridax brachylepis* Hemsl.). Achenes prismatic, walls carbonized, with striations; carpopodium asymmetrical, with hardened plate on outer side, with cushion of soft, collapsing cells on inner side; cells of seed coat irregular with sinuous walls, often strongly ornamented; apex of achene with distinct callus usually bearing radially disposed bristles or squamellae (plumose bristles in *Bebbia* and *Tridax*), pappus sometimes lacking (lacking on ray achenes and present in disk in *Alloispermum*, *Faxonia*, and some *Sabazia*). Pollen 23-35 μm in diameter (smaller and apparently nonfunctional in *Faxonia*).

The subtribe was established by Bentham and Hooker (1873) for members of the Heliantheae having a terete or prismatic achene bearing numerous pappus elements. The listing of genera included some extraneous genera such as *Balduina*, *Dubautia*, and *Marshallia*, while close relatives of *Galinsoga* such as *Jaegeria* and *Sabazia* were excluded. The only member of the Neurolaeninae included was *Calea*, but the genus *Neurolaena* itself was excluded from the tribe. An improved concept is evident in the recent publications of Stuessy (1977) and Canne (1978), but the definition remains imprecise. In his key to subtribes, Stuessy emphasizes the conical receptacle and usually translucent anthers, characters that are, at best, unreliable. Steussy includes *Spilanthes* of the Ecliptinae and *Isocarpha* of the tribe Eupatorieae, but excludes *Bebbia* and *Schistocarpha* which are placed in his extremely artificial subtribe Neurolaeninae. Most recently, natural limits have been recognized between Galinsoginae and the Neurolaeninae (Robinson, 1979b), and *Schistocarpha* has been transferred to the former, while the typical element of *Calea* has been transferred to the Neurolaeninae.

The Galinsoginae is regarded here as a totally natural group of Neotropical genera which is represented in the Eastern Hemisphere only by adventive species of *Galinsoga* and *Tridax*. The subtribe shares many characters with the Neurolaeninae, but it seems most closely related to the Helianthinae with the characters discussed under that subtribe. The extensive development of ducts in the flowers of both subtribes with yellow resin and dehydrofalcarinone polyacetylenes is regarded as particularly significant.

The prismatic achenes, radially symmetrical pappus, and often subimbricate involucre of the Galinsoginae conform with states held in this study to be primitive in the tribe. In contrast, the reduced, often annual habit of the plants seems more derived. The low chromosome numbers in the group, where base numbers over $X = 10$ are lacking, may be a reflection of the trend toward the short-lived perennial or annual habit, but it could be a relict of the $X = 10$ that is believed to be basic for the subfamily Asteroideae (Robinson, et al., in press). The distinctive, shrubby *Dyscri-*



FIGURES 150–156.—Galinsoginae-Dimeresiinae-Coreopsidinae: 150, *Bebbia juncea* (Benth.) Greene, achene, × 12; 151, *Tridax procumbens* L., disk achene, × 12; 152, *Dyscritothamnus filifolius* B. L. Robins., achene, × 8; 153, *Dimeresia howellii* A. Gray., achene, × 12; 154, 155, *Coreopsis lanceolata* L., disk achenes, × 12 (154, inner surface; 155, outer surface); 156, *Bidens pilosa* L., disk achene, × 7.

tothamnus with its achenes densely covered with "zwillingshaare" is the most divergent element in the subtribe, and may represent a more ancestral habit. A chromosome report for the latter would be very instructive.

Limited observations of the surfaces of the ovule indicate potentially useful variations in the subtribe. The cells are irregularly shaped and annulately ornamented in *Schistocarpha*, in at least one *Tridax*, and to a lesser extent in *Sabazia liebmannii* Klatt. The cells in the equivalent layer in *Alloispermum* and *Sabazia acoma* (Blake) Longpre have nearly straight walls and no annulate ornamentation. The cells of *Selloa* are irregular in shape and mostly inornate. In *Galinsoga filiformis* Hemsl., the cells are elongate with closely sinuous walls, and the cells seen in *Jaegeria* are elongate with nonsinuous inornate walls.

Through the kindness of Drs. Ornduff and Strother at the University of California at Berkeley, it has been possible to make a microscopic examination of the sparing material of *Faxonia pusilla* Brandeg., an endemic of southern Baja California which is known only from the type specimen. The immature but well-formed achenes lack carbonization, but they show the correlated punctations in a striated pattern characteristic of the Galinsoginae. The carpopodium of the ray achenes, the double or even triple resin ducts along the veins of the disk corolla throat, and the ducts inside the veins of the style seem to confirm this placement. The trifid paleae of the receptacle and the pappus restricted to the disk achenes find their equal in various other genera of the subtribe. The ray corollas of *Faxonia* are not tubular as represented by Brandegee (1894), but are mostly reduced to a filiform limb. The leaves are long-petiolate and mostly narrow-bladed, as originally described.

Some unique features of *Faxonia* tend to indicate an apomictic condition. No stigmatic papillae have been seen on either the ray or disk styles, and the anthers are very reduced and unopened with thin-walled, mostly slightly distorted pollen. The apparently nonfunctional pollen grains are unique in their size, usually ca. 15 μm in diameter, although sometimes varying to ca. 20 μm. Grains smaller than 23 μm have been noted otherwise in the Asteraceae only in the tribe Eupatorieae. The seemingly defective nature of *Faxonia* might suggest a hybrid origin, but sources for such a hybrid are not obvious and recent origin is not likely. *Faxonia* seems to be an extremely reduced ephemeral. I suspect a greatly reduced chromosome number with some loss of essential genetic material. The genus must have persisted for a considerable time strictly through apomixis.

Subtribe 19. DIMERESIINAE

FIGURE 153

Subtribe DIMERESIINAE H. Robinson, Phytologia, 41:40, 1978.

**Dimeresia* A. Gray (including *Ereminula* Greene).

Annual herbs with leaves in sessile rosette, petioles scarcely distinct. Heads aggregated in a sessile cluster, discoid; involucre of 2 or 3 herbaceous bracts; paleae absent. Flowers 2 or 3 per head, disciform, hermaphroditic; corolla reddish; throat narrowly cylindrical, sparsely glanduliferous outside; lobes 5, ovate, strongly papillose inside, glabrous outside; anther thecae pale; median endothecial cells elongate, elliptical, with single thickenings at ends; anther appendages ovate, with glands abaxially. Base of style with distinct node; style branches with paired stigmatic lines, with papillae abaxially nearly to base. Resin ducts not evident, without colored resin. Achenes terete, walls carbonized and appearing castaneous, with striations represented by regular grooves; carpopodium indistinct; cells of seed coat with strongly sinuous walls, slightly ornamented on surfaces; pappus deciduous as a unit, segments united at base, basal sheath of pappus folded back on itself, segments densely fringed above with hairlike cells. Pollen ca. 30 μm in diameter.

The subtribe contains a single species, *Dimeresia howellii* A. Gray, from the western United States. The plants are easily distinguished by the few-flowered heads aggregated into a sessile cluster in a basal rosette of leaves. The basally fused pappus, which falls as a unit, also is distinctive.

Gray (1886) described the anthers as "caudato-sagittatae" at the base and placed the genus in the Inuleae, where it remained in the treatment by Hoffmann (1890–1894). Actually, the anthers are scarcely longer at the base than many other members of the Heliantheae, and the tips are not caudate. The carbonized and striate achenes confirm the helianthean nature of the genus.

The lack of paleae is correlated with the reduced number of flowers in the head, and its does not seem to reflect a position near the epaleaceous series of subtribes in the Heliantheae. The achene walls of *Dimeresia* lack the knoblike thickenings in the carbonization that are present in most epaleaceous subtribes. The combination of achene wall structure, strongly papillose corolla lobes, and pappus indicates a position near the Helianthinae and Galinsoginae, and the terete achenes, paired stigmatic lines, and reduced annual habit are most like the latter. The lack of distinct resin ducts and the obsolete carpopodium furnish a technical basis for distinction of the Dimeresiinae, but numerous other subtle details such as the difference in endothecial cells and texture of the pappus suggest greater phyletic distance from the Galinsoginae and possible independent development of the reduced habit.

Subtribe 20. COREOPSIDINAE

FIGURES 154–161

Subtribe COREOPSIDINAE Less., Linnaea, 5:153, 1830.
Family COREOPSIDACEAE Link, Handbuch, 1:768, 1829.
Subtribe PETROBIINAE Benth. & Hook., Gen. Pl., 2:192, 1873.
Tribe COREOPSIDEAE Turner & Powell, Biol. Chem. Compositae, 724, 1977 [1978].

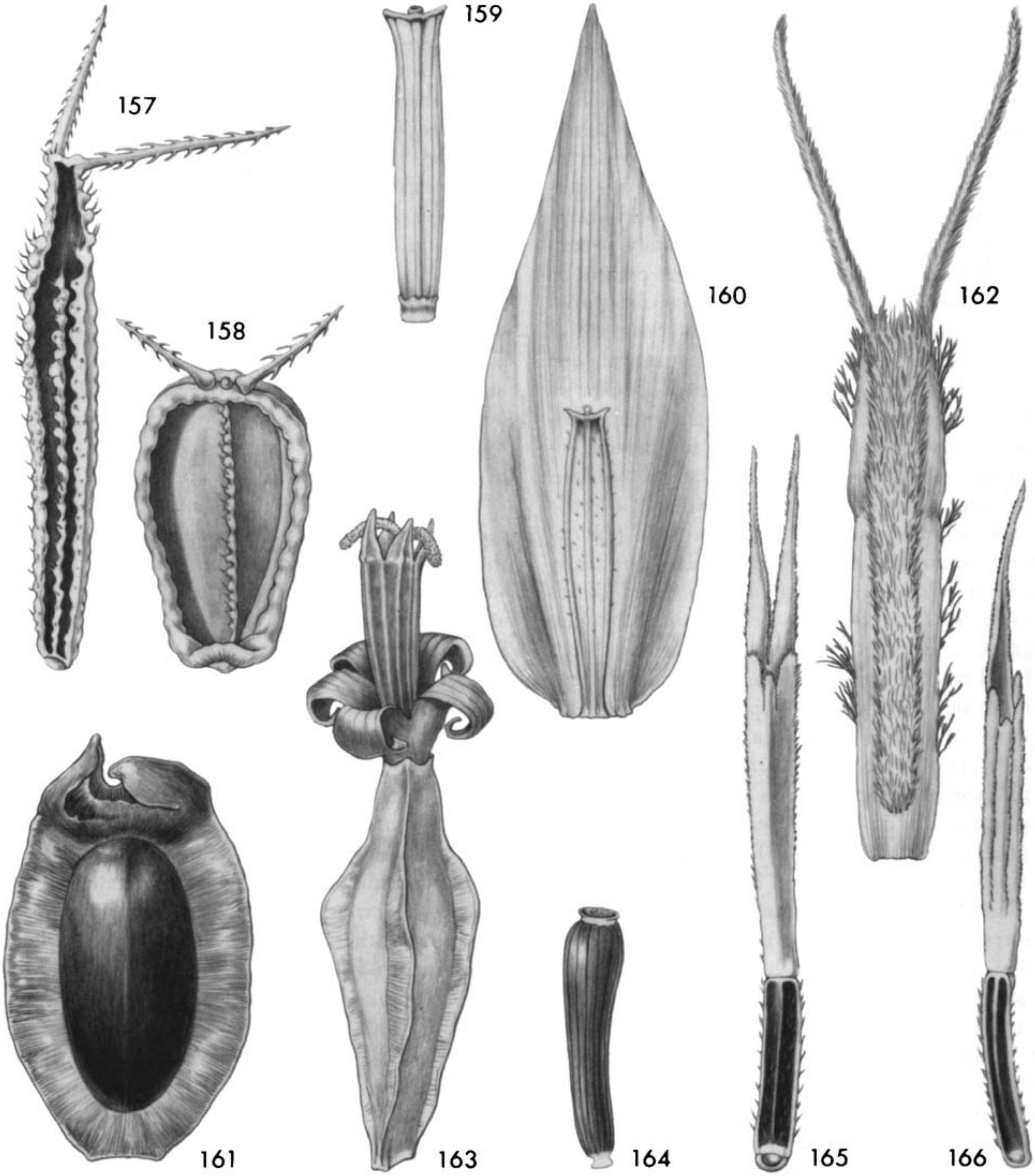
**Bidens* L. (including *Campylotheca* Cass., *Delucia* DC., *Diodonta* Nutt., *Kerneria* Moench.), **Chrysanthellum* Rich. (including *Adenospermum* Hook. & Arn., *Chrysanthellina* Cass., *Collaea* Spreng., non DC., *Neuractis* Cass., *Sebastiania* Bertol.), **Coreocarpus* Benth. (including *Acoma* Benth.), **Coreopsis* L. (including *Agarista* DC., non Don, *Anacis* Schrank, *Calliopsis* Reichb., *Chrysomelea* Tausch, *Chrysostemma* Less., *Coreopsoides* Moench., *Diplosastera* Tausch, *Electra* DC., non Panzer, *Epilepsis* Benth., *Leachia* Cass., *Selleophytum* Urb.), **Cosmos* Cav. (including *Adenolepsis* Less.), **Cyathomone* Blake, **Dahlia* Cav. (including *Georgina* Willd.), **Dicranocarpus* A. Gray, **Ericentrodea* Blake & Sherff, **Eryngiophyllum* Greenm., **Glossocardia* Cass., **Glossogyne* Cass. (including *Diodontium* F. Muell., *Gynactis* Cass.), **Goldmanella* Greenm.? (including *Goldmania* Greenm., non Rose ex Micheli), **Guerreroia* Merr., **Henricksonia* Turner, **Heterosperma* Cav. (including *Microdonta* Nutt.), **Hidalgoa* La Llave & Lex., **Isostigma* Less., **Megalodonta* Greene, **Microlecane* Sch.-Bip., **Moonia* Arn. (including *Pentalepsis* F. Muell.), **Narvalina* Cass. (including *Needhamia* Cass., non Scop.), **Oparanthus* Sherff, **Petrobium* R. Br. (including *Laxmannia* Forst. & Forst., nom. rej., non R. Br.), **Thelesperma* Less. (including *Cosmidium* Nutt.).

Annual and perennial herbs, shrubs, and small trees. Leaves usually opposite, usually with dissected blades (alternate with asymmetrical, simple blades in *Goldmanella*). Heads usually in lax, corymbose or cymose panicles often solitary on long peduncles, not or rarely congested. Heads usually heterogamous, gynoecia sometimes suppressed in ray flowers or in disk flowers, plants tending to be dioecious in *Petrobium*; involucre usually with distinct outer series differing in structure and color; paleae present, scarious, not conduplicate. Flowers usually yellow, sometimes purple, reddish, or whitish. Rays usually present and female, sometimes sterile or lacking; limb of corollas papillose on upper surface, often prominently trilobed at apex. Disk flowers usually hermaphroditic, sometimes functionally male (*Dicranocarpus*, *Hidalgoa*, *Moonia*); corolla lobes slightly to distinctly longer than wide, cells of inner surface short, smooth to mamillose or papillose, outer surface often with short, sharp hairs or spicules; filaments usually smooth, lower part hirsute in *Cosmos*; anther thecae usually slightly to strongly darkened; endothecial cells short, usually with 2–4 thickenings on transverse walls (radially thickened in *Dahlia*); anther appendage usually ovate (very short and truncate in *Hidalgoa*), without glands, often with central duct containing colored resin. Styles usually branched, disk styles unbranched in some genera (such as *Dicranocarpus* and *Hidalgoa*), branches of fertile styles with stigmatic lines usually paired, sometimes with lines indistinct or fused. Ducts commonly with reddish resin; ducts usually prominent in inner involucral bracts, often present in paleae and achenes; ducts of disk corolla throat usually paired along veins, usually outside of veins in styles (apparently inside in unbranched disk style of *Dicranocarpus*); isolated pocket of colored resin often prominent in anther appendage. Achenes of both ray and disk flowers obcompressed, sometimes winged on lateral margins (*Coreopsis*, *Heterosperma*), achenes when all fertile sometimes dimorphic or heteromorphic (*Heterosperma*, some *Bidens*) walls carbonized, basically without striations (broad, uncarbonized bands present in some *Bidens*), carbonization showing additional pattern of knoblike thickenings; cells of seed coat not ornamented, with straight somewhat thickened walls; pappus usually present, often of a pair of lobes or aristae lateral to the corolla, rarely polysetose (*Ericentrodea*) or bearing 4 paleaceous squamellae (on disk achenes of *Henricksonia*), aristate forms often strongly retrorsely barbellate (many *Bidens*). Pollen 25–35 μm in diameter.

The Coreopsidinae and the Fitchiinae form a natural group that is widely distributed pantropically. No other element of the tribe is as well represented in the Eastern Hemisphere. The number of genera on isolated islands suggests that the wide distribution is correlated with superiority of long-range dispersal mechanisms; probably it is not indicative of greater age for the group.

The Coreopsidinae and Fitchiinae can be distinguished as a group from all other subtribes of the Heliantheae by the obcompressed achenes of both the ray and disk flowers. Some problems are possible in placing genera with sterile disk achenes, but some other characters are available. The habit with opposed dissected leaves, the numerous prominent resin ducts in the inner involucral bracts, and the differentiated outer involucre usually provide a distinctive appearance. Ducts in the anther appendages and achenes with prominent reddish resin are not known in any other subtribe. The frequent presence of a reddish duct and complete lack of glands on the anther appendages of the Coreopsidinae has been noted by Robinson and Brettell (1973a). The stigmatic surface in the subtribe seems ancestrally separated into a pair of lines though these are not distinct in some of the members. The carbonization in the achene wall is basically nonstriate, although a specialized form of broad banding has been seen in *Bidens*, which may or may not be homologous to striations seen in other subtribes of the Heliantheae.

The Coreopsidinae traditionally have contained a large core of closely related genera, but the actual limits have been unnatural because of some extraneous genera that have been included as well as some relatives that have been excluded. Some improvements are seen in the recent survey by Stuessy (1977); the changes in that study can be evaluated as follows. An extraneous element that includes *Calyptocarpus* and *Synedrella*, having obcompressed ray achenes but prismatic disk achenes, is correctly transferred to the Ecliptinae by Stuessy. *Guizotia*, which was transferred to the Verbesininae by Baagøe (1974), was returned to the Coreopsidinae by Stuessy. The terete, striate achenes, the ornamented seed coats, and the glanduliferous anther appendages all dictate against inclusion of *Guizotia*, and that genus is placed in the Milleriinae in this study. Of the genera included in the Coreopsidinae for the first time by Steussy (1973, 1977), *Dicranocarpus* of the western United States and Mexico, *Moonia* of the Indian Ocean region, and *Petrobium* of St. Helena are unquestionably related, but *Jaumea*, *Guardiola*, *Staurochlamys*, and *Venegasia* are not. *Jaumea* is placed here in the Jaumeinae and *Venegasia* in the Chaenactidinae. *Guardiola* differs from the Coreopsidinae by the strongly annulate, elongate cells of the seed coat, the striate achenes, and the distinctive form of large gland at the base of the



FIGURES 157–166.—Coreopsidinae-Fitchiinae-Coulterellinae-Pectidinae: 157, 158, *Heterosperma pinnatum* Cav., achenes, × 12 (157, central achene; 158, outer achene); 159, 160, *Dahlia coccinea* Cav. (159, disk achene, × 6; 160, disk achene with palea, × 6); 161, *Hidalgoa ternata* La Llave & Lex., ray achene, × 8; 162, *Fitchia nutans* Hook. f., achene, × 6; 163, 164, *Coulterella capitata* Vasey & Rose (163, head with fused involucre and flower, × 12; 164, the single achene from the head, × 12); 165, 166, *Tagetes subulata* Cerv. ex La Llave & Lex., achenes, × 8.

anther appendages. *Guardiola* has nodular thickenings on the lateral walls of the subquadrate median endothecial cells, a precise pattern not duplicated elsewhere in the tribe. *Guardiola* is placed here in a separate subtribe Guardiolinae. *Staurochlamys* is rejected from the Coreopsidinae because of the glands on the anther appendages, the prismatic rather than obcompressed achenes, and the totally dissimilar differentiated outer involucral bracts. The genus is placed in the Neurolaeninae in this study.

Certain features of the monotypic *Goldmanella* of Central America have caused both Stuessy and myself to place the genus in the Coreopsidinae. There are numerous resin ducts in the involucral bracts, and the achenes are slightly broadened. Still, the alternate leaves with broad, simple, asymmetrical blades and the subimbricate involucre make the genus thoroughly anomalous in the subtribe.

Turner and Powell (1977) have proposed a tribe Coreopsideae containing various elements included in the Coreopsidinae by Stuessy as well as *Fitchia* and elements such as *Jaumea* from the Jaumeinae. It was a second instance where these authors proposed a group including both paleaceous and epaleaceous genera. Their treatment is not supported by the evidence in this study. Part of the difficulty arises from the failure of Turner and Powell to either describe their tribe or to indicate any of its points of difference from the Heliantheae or even the Senecioneae. One of their reasons for recognizing a separate tribe apparently was the differences of eight amino acids in the sequences of the cytochrome *c* of *Helianthus* and *Guizotia*. This is not really relevant, since *Guizotia* is not a member of the Coreopsidinae.

No amino acid sequences of either cytochrome *c* or plastocyanin have been determined for any member of the Coreopsidinae as presently delimited, but a number of other types of chemical data are available.

In reference to the flower color of the Asteraceae, Cronquist (1955) stated "that the yellow pigments are partly plastid-borne carotinoids and partly water-soluble anthoxanthins chemically allied to the anthocyanins, and that several yellow pigments including both carotinoids and anthoxanthins may be present in a single flower." The particular group of anthoxanthins of interest in the 1955 paper were the anthochlors or aurone and chalcone flavonoids. According to Cronquist, anthochlors had been found in nearly 200 species of the Coreopsidinae, and except for several species of *Baeria* (*Lasthenia*) they were not known elsewhere in the family. Cronquist cited Gertz (1938), Geissman (1941a,b, 1942), and Geissman and Heaton (1943, 1944). The presence of anthochlors in other families seemed possible. Regarding the anthochlors, Cronquist said, "Within the Compositae, their very wide distribution in and usual restriction to the Coreopsidinae furnish further evidence of the naturalness of that subtribe."

Much refinement has occurred in the knowledge of anthochlors since 1955. Three papers in the Symposium on the Biology and Chemistry of the Compositae mentioned the compounds (Harborne, 1977; Heywood et al., 1977; and Bohm, 1977), and an extensive study has been published by Crawford and Stuessy (1981). Both types of anthochlors prove to occur in both subfamilies, with the phloroglucinol-based anthochlors in the Cardueae (*Carthamus*), Eupatorieae (*Chromolaena*) and Inuleae (*Gnaphalium*, *Helichrysum*) and resorcinol-based anthochlors in the Lactuceae (*Calycoseris*, *Malacothrix*, *Pyrrhopappus*) and the Heliantheae. In the Heliantheae, anthochlors occur in two epaleaceous genera, *Lasthenia* and *Syntrichopappus*, and in four genera of the Helianthinae, *Helianthus*, *Simsia*, *Tithonia* and *Viguiera*, in addition to various genera that have been placed in the Coreopsidinae. In the Crawford and Stuessy (1981) study, all 25 genera tested that are placed in the Coreopsidinae by both Stuessy (1977) and the present treatment proved to have anthochlors. It is notable that two genera not recognized here as members of the subtribe, *Guardiola* and *Venegasia*, lack anthochlors. The genera *Staurochlamys* and *Guizotia*, included in the Coreopsidinae by Stuessy (1977) but placed in the Neurolaeninae and Milleriinae respectively in the present treatment, apparently have anthochlors. The mutual occurrence of anthochlors in the Coreopsidinae and in *Lasthenia* is paralleled by the apparent restriction of thiophene forms of the ene-tetrayne-ene polyacetylenes to these same two groups in the Heliantheae. For this reason Bohm (1977) safely concluded: "... on the basis of anthochlor and acetylene chemistry *Lasthenia* would be judged to lie closer to Coreopsidinae than to Senecioneae...." There seems to be no basis, however, for Harborne's (1977) comment, "Recent work ... has indicated that *Lasthenia* and *Syntrichopappus* (Helenieae) could well be accommodated on morphological grounds in the Coreopsidinae (Heliantheae) ...."

The Coreopsidinae seem to have a greater diversity of polyacetylenes than any other subtribe of the Heliantheae. Involved are both of the major pentaynene and ene-tetrayne-ene pathways with various derived thiophenes. Aromatic endgroups are present in the acetylenes of many Coreopsidinae, formed on either end of the molecule. Such aromatic acetylenes are found elsewhere in the tribe only in *Heliopsis* of the Ecliptinae. Unique aromatic thiophenes are found in *Coreopsis* and *Bidens*. Rarer types of polyacetylenes found in *Dahlia* include a tetrahydropyrane like that in *Ichthyothere* and the only examples in the Heliantheae of C_{16} acetylenes lacking methyltriyne endgroups.

The Kranz syndrome or C_4-phostosynthetic pathway provides more efficient use of ambient CO_2 at higher temperature and higher light intensity than the common C_3 pathway, and it seems to confer advantages to some plants in hot or exposed environments. Occurrence of the character is somewhat erratic among higher plants. The pathway was orginally discovered in sugar cane, and it is found in various other grasses including part but not all of the genus *Panicum*. In the chenopodiaceous genus *Atriplex*, a species with the C_4 pathway forms hybrids with a species lacking the trait. The distribution of the syndrome in the Asteraceae has been reviewed by Smith and Turner (1975) using isotope ratios of CO_2 from combustion of fragments of herbarium material. Tests of various Astereae and Heliantheae revealed C_4 ratios in five genera of the Coreopsidinae, *Chrysanthellum*, *Eryngiophyllum*, *Glossocardia*, *Glossogyne*, and *Isostigma*, four of 12 species tested of *Flaveria* in the Flaveriinae, and in one genus, *Pectis*, of the Pectidinae. The lack of any special relationships between the three subtribes, and the numerous members of all three subtribes that lack the Kranz syndrome, indicate that the syndrome is independently derived in each group. Even within the groups where the character is probably monophyletic, there may be reversions or complications from hybridization.

Subtribe 21. FITCHIINAE

FIGURE 162

Subtribe FITCHIINAE Carlquist, Univ. Calif. Publ. Bot., 29:5, 1957.

**Fitchia* Hook. f.

Shrubs or trees, glabrous except in leaf axils. Leaves opposite, with distinct petioles; blades simple, entire or with one to several teeth. Heads campanulate, terminal, solitary or rarely in groups of two or three; peduncle recurved; heads homogamous; involucre multiseriate, subimbricate, bracts coriaceous to woody; paleae present, not conduplicate. Flowers hermaphroditic; corollas ligulate with 5 narrow lobes; adaxial surface of lobes mostly smooth, tips with laciniate crests outside, each lobe with 3 or more veins; anther thecae pale; endothecial cells short, with 2 or 3 thickenings on transverse walls; anther appendages lanceolate, nearly flat, without glands. Style branches short, with continuous stigmatic surface. Ducts or secretory canals numerous in involucre, paleae, and flowers, resin not obviously colored; ducts of achene numerous, accompanying and slightly interior to veins, usually not reaching base or tip of achene, short ducts often present in awns (absent in *F. speciosa* Cheeseman); ducts of flowers usually paired along and slightly outside of veins below sinuses, usually single along marginal veins of lobes; ducts present in anther connectives; incomplete ducts of style positioned outside of veins. Achenes broadly obcompressed, walls carbonized, without striations, numerous subsidiary veins present, style veins continuous with median veins of inner and outer surface; cells of seed coat not ornamented; pappus of two awns borne laterally, vein usually present in awn; pubescence and teeth of body and awns of achene antrorse. Pollen 40–70 μm in diameter.

The subtribe contains the single distinctive Polynesian genus *Fitchia*. The genus is unquestionably related to the Coreopsidinae with which it shares the characteristically obcompressed achenes. In both structure and geography, the Coreopsidinae seem a likely ancestor to the Fitchiinae.

The specialized homogamous ligulate heads of *Fitchia* resemble those of the Lactuceae (Cichorieae), and the genus was placed in that tribe by Bentham and Hooker (1873) and Hoffman (1890–1894). Drake del Castillo (1898) did not agree, placing the genus in the Mutisieae. Stebbins (1953) rejected the genus from the Lactuceae and suggested a position in the Mutisieae or Heliantheae. The proper relationship and distinct subtribal status of *Fitchia* were established by Carlquist (1957) in his detailed taxonomic and anatomical study of the genus.

Subtribe 22. COULTERELLINAE

FIGURES 163, 164

Subtribe COULTERELLINAE H. Robinson, Phytologia, 41:40, 1978.

**Coulterella* Vasey & Rose.

Brittle, succulent shrubs, with glabrous stems and leaves, lower leaves opposite. Heads aggregated in corymbose to subumbellate terminal inflorescences; involucre fused into utriculiform, low-winged cyathium, fleshy, becoming corky at maturity; flowers 1, rarely 2, paleae absent. Flowers discoid, hermaphroditic; corollas greenish-yellow, 10-nerved; throat short; lobes elongate, smooth, with strong marginal and median nerves; anther thecae pale; endothecial cells oblong, with 1 or 2 thickenings on transverse walls; anther appendages minutely glanduliferous. Style branches papillose on complete abaxial surface, stigmatic lines paired. Ducts not distinct, without obvious colored resin. Achenes prismatic, walls carbonized, with distinct striations; cells of seed coat elongate, with lateral walls slightly ornamented; pappus absent. Pollen ca. 40 μm in diameter.

The single genus *Coulterella* contains one species, *C. capitata* Vasey & Rose, growing mostly on beaches around La Paz Bay and on nearby islands in southern Baja California. As represented in the colored photograph in the paper by Moran (1970), the branches of *Coulterella* have a crassulaceous aspect. Because of the single-flowered heads, the genus was originally placed close to *Lagascea* in the subtribe Lagasceinae. The general similarity of *Coulterella* to the Flaveriinae and rejection from the proximity of *Lagascea* was first reported by Stuessy (1976), and additional support for such a treatment has been obtained from chemical evidence (Robinson et al., 1978). Simple thiophenes are found in *Coulterella*, and polythiophenes are present in the Flaveriinae and Pectidinae. Thiophenes are not known in *Lagascea* or other members of the subtribe Helianthinae to which it is related. Also, *Lagascea* and other Helianthinae contain dehydrofalcarinone, which is not found in *Coulterella* or the related subtribes Flaveriinae and Pectidinae.

In spite of the similarity of *Coulterella* to groups such as the Flaveriinae, a separate subtribal status is required. The achenes of *Coulterella* lack the numerous costae and the extra knoblike thickenings in the carbonization that are present in the Flaveriinae and Clappiinae. The corollas differ by their short throats and long lobes. Carlquist (1957) noted that the median and lateral bundles of the lobes all terminate freely in the lobe tips, and that all 10 veins continue separately into the achenes instead of being joined at the top of the achenes as in other genera. Carlquist also found that secretory ducts or canals such as are found in *Lagascea* were lacking.

Of the related subtribes, the Pectidinae, which has noncostate, striate achenes, seems most similar to *Coulterella*. It is notable that the Pectidinae also have examples of fused involucres. The involucres of *Coulterella* might be interpreted to have a slight glandular development at the top, but the distinct type of gland characteristic of the Pectidinae is lacking. The specialized floral anatomy of *Coulterella* is not found in the Pectidinae.

Subtribe 23. PECTIDINAE

FIGURES 165–167

Subtribe PECTIDINAE Less., Linnaea, 5:134, 1830.
Tribe TAGETEAE Cass., Journ. Phys., 88:162, 1819.
Subtribe TAGETINAE Less., Linnaea, 6:253, 1831.

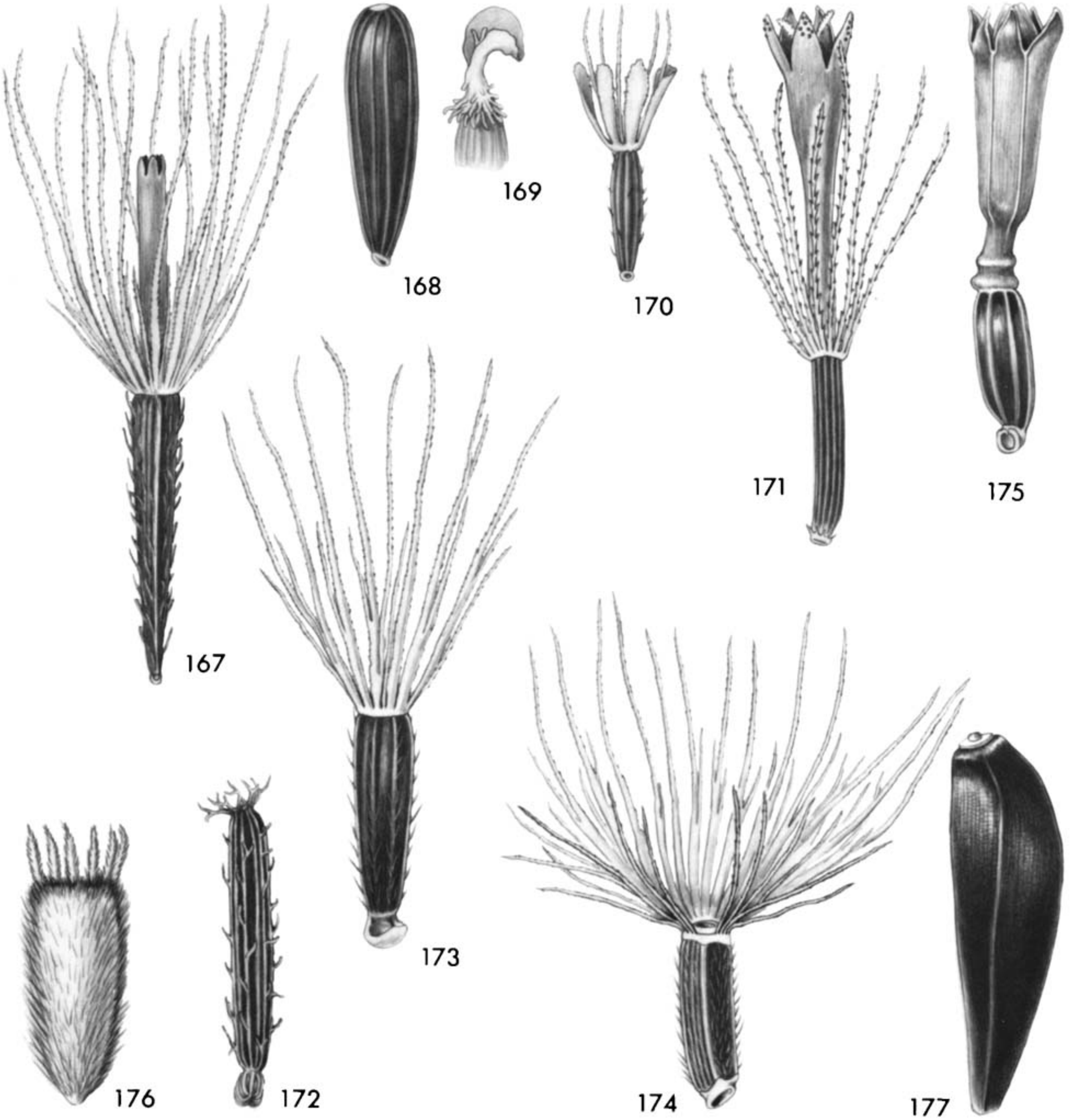
**Adenopappus* Benth., **Adenophyllum* Pers. (including *Clomanocoma* Cass., *Lebetina* Cass., *Schlechtendalia* Willd., nom. rej., non Less.), **Chrysactinia* A. Gray, **Dyssodia* Cav. (including *Boebera* Willd., *Boeberastrum* (A. Gray) Rydb., *Rosilla* Less., *Syncephalantha* Bartl.), * *Gymnolaena* (DC.) Rydb., **Harnackia* Urb., **Hydropectis* Rydb., **Hymenatherum* Cass. (including *Aciphyllaea* (DC.) A. Gray, *Comaclinium* Scheidw. & Planch., *Dysodiopsis* (A. Gray) Rydb., *Gnaphalopsis* DC., *Lowellia* A. Gray., *Thymophylla* Lag.), **Lescaillea* Griseb., **Leucactinia* Rydb., **Nicolletia* A. Gray, **Pectis* L. (including *Cheilodiscus* Triana, *Chthonia* Cass., *Cryptopetalon* Cass., *Helioreos* Raf., *Lorentea* Lag., non Orteg., *Pectidium* Less., *Pectidopsis* DC., *Seala* Adans., *Stammarium* Willd. ex DC. in syn.), **Porophyllum* Guett. (including *Kleinia* Jacq., non Mill.), **Schizotrichia* Benth., **Strotheria* Turner (including *Graciela* Rzed.), **Tagetes* L. (including *Diglossus* Cass., *Enalcida* Cass., *Solenotheca* Nutt.), **Urbinella* Greenm., **Vilobia* Stroth.

Annual or perennial herbs, subshrubs, or shrubs, with opposite or alternate leaves. Inflorescence usually diffuse, with heads solitary and peduncled or aggregated (forming compound heads in two species of *Dyssodia*). Leaves and involucres with prominent, often swollen, pellucid glandular spots or cavities. Heads usually heterogamous; involucre uniseriate or with a few subtending bractlets, bracts free or fused; paleae absent. Rays when present female; corolla limb papillose on upper surface. Disk flowers hermaphroditic (achenes of disk sterile in 1 species of *Pectis*); corollas usually glabrous or with minutely clavate small hairs, distinctly capitate hairs present in *Pectis*; lobes usually short, inner surface usually papillose, papillae evenly distributed or concentrated near margins, papillae sometimes hairlike, fringe of hairlike papillae also sometimes present inside of veins in corolla throat; anther thecae pale; median endothecial cells short to laxly elongate, end walls with 0–2 thickenings; anther appendage without glands. Style branches with paired stigmatic lines. Ducts without or with small amounts of colored resin; ducts along veins of corolla throat single; ducts in shaft of style outside of veins. Achenes cylindrical or prismatic, walls carbonized, with striations; cells of seed coat weakly ornamented; pappus in 0–3 series, of various setae, squamellae, or laciniate fused elements, sometimes lacking. Pollen 25–40 μm in diameter.

The subtribe is widely distributed in the Neotropical region from Mexico southward to Argentina. Two species of *Tagetes* are widely cultivated as ornamentals.

The Pectidinae have been readily distinguished in the past because of their general aspect and their characteristic secretory cavities. The cavities produce numerous monoterpenes which seem to discourage insect attack. Sesquiterpene lactones, which are common anti-herbivore compounds in other groups of Heliantheae, seem to be absent in the Pectidinae. Because the subtribe seems rather distinctive, it sometimes has been given tribal rank (Strother, 1977). The actual differences of the group are minor, however, compared to those of some other subtribes in the Heliantheae.

The Pectidinae contains two subgroups, each recognized at the subtribal level by Strother (1977). The first group, containing only the genus *Pectis*, is defined by Strother as having leaves always opposite and simple with bristly cilia at the base, having ray florets borne on the bases of the subtending bracts rather than on the receptacle, and having anther appendages and the



FIGURES 167–177.—Pectidinae-Flaveriinae-Clappiinae-Jaumeinae-Varillinae-Madiinae: 167, *Pectis sessiliflora* (DC.) Sch.-Bip., achene, × 12; 168, 169, *Flaveria trinervia* (Spreng.) C. Mohr (168, achene, × 17; 169, top of ray achene with corolla, × 17); 170, *Sartwellia mexicana* A. Gray, disk achene, × 17; 171, *Haplöesthes greggii* A. Gray, disk achene, × 17; 172, *Varilla mexicana* A. Gray, achene, × 17; 173, *Clappia suaedaefolia* A. Gray, achene, × 12; 174, *Pseudoclappia arenaria* Rydb., achene, × 8; 175, *Jaumea carnosa* (Less.) A. Gray., achene, × 12; 176, *Blepharipappus scaber* Hook., achene, × 12; 177, *Madia glomerata* Hook., ray achene, × 12.

style branches short. The remaining genera, the Tagetinae, are distinguished by Strother as having leaves opposite, alternate, or both, mostly pinnately parted, with simple blades rarely having bristly cilia at the base, having all florets being borne on the receptacle, and having the anther appendages lance-ovate and the style branches elongate. The carpopodium in *Pectis* is nearly symmetrical, while those of other genera are distinctly asymmetrical. Baagøe (1977a) reports a smoother senecionoid ligule surface in *Pectis* compared to a more papillose helianthoid type in *Tagetes*, *Nicolletia*, and *Schizotrichia*. Both types occur in *Chrysactinia*, however. The C_4 photosynthetic pathway is characteristic of *Pectis*, where Smith and Turner (1975) have examined 20 species, and apparently is restricted to that genus; twelve genera of the Tagetinae, *Adenophyllum*, *Chrysactinia*, *Dyssodia*, *Gymnolaena*, *Hymenatherum*, *Leucactinia*, *Nicolletia*, *Porophyllum*, *Schizotrichia*, *Strotheria*, *Tagetes*, and *Urbinella* were tested by Smith and Turner with negative results.

Colored resin has been seen in small amounts in the disk corollas of *Adenopappus* and *Nicolletia*. Papillosity of the inner surface of the disk corolla lobes varies. Limited sampling indicates that there is none in *Pectis*, *Gymnolaena*, and *Schizotrichia eupatorioides* Benth. Papillosity covers the complete inner surface in *Tagetes*, *Chrysactinia*, *Hymenatherum*, *Leucactinia*, and *Porophyllum*. Papillae are restricted to the edges of the lobes in various genera including *Nicolletia* and in the Peruvian species *Dyssodia lopez-mirandae* Cabrera which Strother (1969) would place in *Schizotrichia*.

The present study recognizes *Vilobia* Strother (1968) and the segregates *Adenophyllum* and *Hymenatherum* from *Dyssodia* at the generic level. In reversing a previous judgment (Robinson, 1973), *Vilobia* is distinguished from *Tagetes* on the basis of a laciniate pappus-type not equalled among the numerous variations found in the latter genus. Nevertheless, the two genera are almost certainly very closely related. The segregates of *Dyssodia* were not given generic rank by Strother (1977), but they were considered sufficiently distinct to be treated individually. Strother's schematic diagram of relationships among the "Tageteae" clearly suggests that the subgenera of *Dyssodia* are not each other's closest relatives.

Keil (1978) has reported sterile achenes in the disk flowers of *Pectis linifolia* L. var. *hirtella* Blake, representing a further isolated occurrence of this character in the Heliantheae.

Subtribe 24. FLAVERIINAE

FIGURES 168–171

Subtribe FLAVERIINAE Less., Synopsis, 235, 1832.

**Flaveria* Juss. (including *Brotera* Spreng. in Schrad., non Cav., *Dilepis* Suess. & Merxm., *Neuenbergia* Willd., *Vermifuga* Ruiz & Pav.), **Haploesthes* A. Gray, **Sartwellia* A. Gray.

Herbs or subshrubs, glabrous or slightly puberulous. Leaves opposite, united by narrow scarious wing across node. Inflorescence terminal in laxly corymbose panicle or in dense cyme, or axillary. Heads heterogamous; involucre with bracts thinly to thickly herbaceous, in ca. 2 series, subequal; paleae absent. Ray flowers female; limb of corollas mostly smooth. Disk flowers hermaphroditic; corolla lobes short, mostly smooth, with cells often enlarged, outer surface usually glabrous (puberulous with moniliform uniseriate hairs below in *Flaveria trinervia* (Spreng.) C. Mohr); anther thecae pale; endothecial cells short, with 2–4 thickenings on transverse walls; anther appendage oblong, without glands. Style branches short, truncate, with paired stigmatic lines. Ducts usually without obvious colored resin (some reddish resin seen in *Flaveria linearis* Lag.); ducts of disk corolla throat solitary along veins, ducts of lobes marginal. Ducts possibly present outside of veins in style shaft, ducts present inside veins in style branches. Achenes prismatic, with numerous ribs, walls carbonized with regular pattern of extra thickenings often nearly outlining cells of adjacent layer, striations lacking; carpopodium distinct with many rows of small cells, asymmetrical to nearly symmetrical; cells of seed coat elongate, with regular pattern of alternating thickenings restricted to lateral walls; pappus absent in *Flaveria* (a small crown or squamellae in 2 species), of bristle-tipped squamellae in *Sartwellia*, of capillary bristles in *Haploesthes*. Pollen 25–27 µm in diameter.

The subtribe is widely distributed in the drier and more open habitats in tropical and subtropical America. One species of *Flaveria* occurs in Australia, and two other species have been introduced into Asia and Africa.

The present concept of the Flaveriinae follows that of Turner and Johnston (1961) and Turner and Powell (1977). The close relationship of the three genera seems to be confirmed by the structure of the many-ribbed or multicostate achenes, and by the cellular details of the seed coat. The variation in the pappus in the subtribe has resulted in the traditional placement of the genera in two different tribes, *Flaveria* and *Sartwellia* in the Helenieae and *Haploesthes* in the Senecioneae. Regarding pappus variation in the subtribe, it is notable that an obsolete pappus occurs in 2 species of *Flaveria* (Powell, 1978).

The polyacetylenes of the Flaveriinae include a number of highly derived forms of the pentaynene series. Tri-thiophenes are present and are known elsewhere in the tribe in the Pectidinae, one *Gaillardia* and in *Eclipta*. Sulfones also occur in *Flaveria* and are found elsewhere in *Acanthospermum* of the Melampodiinae, *Guizotia* of the Milleriinae, *Eclipta*, and *Gaillardia*. The sulfones of *Flaveria* are not epoxidized.

Subtribe 25. VARILLINAE

FIGURE 172

Subtribe VARILLINAE Turner & Powell ex H. Robinson, Phytologia, 41:44, 1978 [Subtribe VARILLINAE Turner & Powell, Biol. Chem. Compositae, 719, 1977 [1978], nom. nud. without type genus].

**Varilla* A. Gray.

Shrubs; plants very brittle when dry; stems sometimes with pale, carnose, glabrous surface; leaves opposite or alternate. Inflorescence terminal on branches, with heads solitary on long peduncle or clustered in corymbose panicles. Heads discoid; involucral bracts in ca. 2 series, with prominent median longitudinal reddish duct; paleae present, similar to involucral bracts. Ray flowers lacking. Disk flowers hermaphroditic; corolla with numerous glands or short hairs on lower part; throat cylindrical; lobes narrowly triangular, cells of inner surface elongate with closely sinuous lateral walls; anther thecae pale; endothecial cells short, with 1–3 thickenings on transverse walls; anther appendage without glands. Style branches with paired stigmatic lines. Ducts of involucral bracts, paleae, and corolla throats with reddish resin; ducts of corolla throats single between pairs of veins; ducts of style colorless, apparently present outside of veins at least in shaft. Achenes prismatic, with numerous costae, walls carbonized with slight striations, without regular pattern of knoblike thickenings; carpopodium obsolete, hidden within circle of costal lobes; cells of seed coat not ornamented; pappus absent or formed from short partially carbonized projections of achene body. Pollen 30–35 µm in diameter.

The subtribe contains the one genus, *Varilla*, with two species in the southwestern United States and northern Mexico. The two species differ in many characteristics. In *V. mexicana* A. Gray, the inflorescence is corymbose, the leaves often are opposite, the stems are greenish and become brown with age, the tubular throats of the corollas are more abruptly expanded at the base, the hairs of the corolla base have glandular tips, the pollen is smaller with smaller spines, and the achenes bear both trichomes and the peculiar pappus-like outgrowths at the apex. In *V. texana* A. Gray, the heads are solitary, the leaves are rigorously alternate, the stem surface becomes thickened and whitish, the corolla throats are less abrupt at the base, the hairs are not glandular, the pollen is distinctly larger and has larger spines, and the achenes are glabrous. In spite of the differences, the anatomy of the achene wall with its costae and basal lobes, the cellular detail of the corolla lobes, the duct between the pairs of veins in the corolla throat, and the anatomy of the style are the same. The uniformity of the latter characters between two species that are at least subgenerically distinct demonstrates the comparative reliability of these characters. These are a factor in the exclusion of all other genera from the present concept of the subtribe.

In the first proposal of subtribe Varillinae (Turner and Powell, 1977), five genera were mentioned, including three with paleae, one with prominent hairs on the receptacle, and one with glabrous receptacles. *Varilla* was thought to represent an ancestral "prototype" from which others might have evolved by reduction. Present observations show that two of the paleaceous genera, *Bebbia* and *Dyscritothamnus*, are unquestionably members of the Galinsoginae and are not closely related to *Varilla* or the epaleaceous genera. In contrast, between the paleaceous *Varilla*, the setiferous *Clappia*, and the totally epaleaceous *Pseudoclappia*, there are some correlations in corolla lobe structure, costate achenes, and, to some extent, resin ducts. Still, there are significant differences, as indicated under the subtribe Clappiinae, where the latter two genera are placed in this study. It remains probable that the paleaceous *Varilla* is most closely related to the epaleaceous *Clappia* and *Pseudoclappia*, but I suspect the paleae of *Varilla* are derived from epaleaceous ancestors and that all three genera are properly placed in the epaleaceous series of the Heliantheae.

The pattern of a prominent resin duct between two veins is one of the three possible basic types, but is the least common type in the tribe. This type finds its best expression in the reddish ducts in the corolla throats of the genus *Varilla*. The type is not unique to *Varilla*, however, and has been seen in less well-developed forms in some Clibadiinae, some Rudbeckiinae, and in both the corollas and styles of the genus *Clappia*.

Subtribe 26. CLAPPIINAE

FIGURES 173, 174

Subtribe CLAPPIINAE H. Robinson, Phytologia, 41:39, 1978.

**Clappia* A. Gray, **Pseudoclappia* Rydb.

Shrubs, stems becoming rather pale and carnose; leaves alternate, with narrow sessile blades. Inflorescence diffuse, with long-pedunculate heads. Heads heterogamous; involucre with bracts in 2–4 series, broad and strongly subimbricate in *Clappia*; herbaceous to subcarnose; paleae lacking, receptacle setiferous in *Clappia*. Ray flowers female; limb of corollas nearly smooth above with elongate cells. Disk flowers numerous, hermaphroditic; corolla with a narrowly cylindrical throat; lobes narrowly triangular, elongate, smooth on inner surface with elongate cells, lateral walls of cells sinuous; anther thecae pale; endothecial cells oblong, with 1 or 2 thickenings on transverse walls; anther appendages without glands. Branches of disk styles with papillae distally on outer surface, with paired stigmatic lines. Ducts with some reddish resin in *Clappia*, without reddish resin in *Pseudoclappia*, involucral bracts of *Clappia* with numerous longitudinal dark ducts; ducts of disk corolla throat solitary along veins, partially between paired veins in *Clappia*; reddish ducts in style branches of *Clappia* between paired veins. Achenes prismatic, costate, walls carbonized, indistinctly striate, with regular pattern of additional carbonized knoblike thickenings; carpopodium distinct; cells of seed coat elongate, with annulately ornamented walls; pappus of numerous capillary bristles in ca. 3 series. Pollen 35–40 μm in diameter.

The two genera of the subtribe occur in Texas and the immediately adjacent areas of Mexico and New Mexico. *Clappia* is found in the Chihuahuan Desert region, and *Pseudoclappia* is in the Tamaulipan Desert.

The genus *Clappia* has usually been placed in the Helenieae in or near the Pectidinae because of the dark resin lines in the leaves and involucres (Bentham and Hooker, 1873; Rydberg, 1923; Smith and Turner, 1975). Hoffmann (1890–1894) placed the genus in the same tribe, but in the Jaumeinae. Although recognizing the general resemblance, Rydberg (1923) placed his genus *Pseudoclappia* in the Senecioneae. A more reasonable treatment was that of Turner and Powell (1977), where both genera were placed together in a broadly circumscribed Varillinae. Some of the artificial aspects and nomenclatorial problems of the Varillinae as originally proposed by Turner and Powell are mentioned in this treatment under that subtribe, but a comparison of the Clappiinae with the genus *Varilla* is still necessary.

In the geographical distribution, xeric nature, shrubby habit, pale stems with alternate leaves, and brittle condition of the dried plants, the Clappiinae closely resemble at least one of the species of *Varilla.* Anatomical study shows additional similarities in the costate achenes, the elongate, nonpapillose cells of the disk corolla lobes, and the tendency for a reddish resin duct between paired veins in the disk corolla throat. A reddish duct is also present between paired veins in the style branches of *Clappia.* In spite of such similarities, the basic difference in the lack of paleae in the Clappiinae is reenforced by many other characters. The achenes of the Clappiinae, which have a well-developed carpopodial shield on the outer side, the pattern of knoblike thickenings in the carbonization of the achene wall that lacks evident micropunctations, the presence, where known, of ornamentation on the seed coat, the narrower anther collars with more evenly thickened walls, and the short bases of the anther thecae all differ from *Varilla.* The Clappiinae also have a prominent, multiseriate, capillary pappus, whereas a true pappus is completely lacking in *Varilla.* There is ample reason to treat the Clappiinae and *Varilla* in separate subtribes. Nevertheless, as mentioned under the Varillinae, a relationship seems probable. In such a grouping, the epaleaceous condition would seem to be more primitive, and the paleae of *Varilla* would be a structure resurrected in the form of the homologous involucral bracts.

It seems likely that the Clappiinae are also closely related to the Jaumeinae and Flaveriinae, which have costate achenes. The superficial resemblance of the resiniferous lines of *Clappia* to the secretory cavities of the Pectidinae is misleading, and the latter subtribe is more remote in relationship.

Subtribe 27. JAUMEINAE

FIGURE 175

Subtribe JAUMEINAE Benth. & Hook., Gen. Pl., 2:199, 1873.

**Jaumea* Pers. (including *Coinogyne* Less.).

Perennial herbs with creeping branched rootstocks, glabrous; leaves opposite, narrow, sessile, fleshy, fused at base into short, distinct sheath. Heads solitary, terminal, sometimes appearing axillary, on distinct peduncles. Heads with or without rays; involucre of fleshy bracts in ca. 3 series; paleae lacking. Rays when present female; limb of corolla smooth on upper surface, tip with 2 or 3 short narrow lobes. Disk flowers hermaphroditic; corolla throats narrowly cylindrical; lobes short, smooth; anther thecae pale; endothecial cells short oblong or subquadrate, with 2 or 3 thickenings on transverse walls; anther appendages ovate, without glands. Style branches with rounded tips, with stigmatic lines joining at top. Ducts with prominent reddish resin; ducts solitary along veins of disk corolla throat, ducts of style branches inside veins. Achenes prismatic, multi-costate, glabrous, walls carbonized, without striations; carpopodium short and broad, sometimes with spicules in upper part; cells of seed coat not ornamented; pappus of short narrow squamellae or absent, without obvious median veins. Pollen ca. 45 μm in diameter.

The subtribe is limited here to two species, *Jaumea carnosa* (Less.) A. Gray of western North America, having ray flowers and lacking a pappus, and *J. linearifolia* (Juss.) DC. of southern South America, which lacks ray flowers and has a short pappus. Other species that have been placed in *Jaumea* are treated here in the genera *Espejoa* and *Hypericophyllum* in the subtribe Chaenactidinae. The latter genera differ by the longer disk corolla lobes with pubescent surfaces, the single thickenings on the transverse walls of the endothecial cells, the lack of reddish resin in the corollas, the unribbed, usually pubescent achenes, and the tendency for strong central veins in the pappus elements.

Various genera have been placed in the Jaumeinae in the past, including *Olivaea* Sch.-Bip. of the Astereae (DeJong and Beaman, 1963) and *Cacosmia* H.B.K. of the Liabeae (Robinson and Brettell, 1974b). Helianthean genera include *Clappia* (treated here in the Clappiinae), *Arnicastrum* and *Venegasia* (treated here in the Chaenactidinae), and *Geissopappus*, which is included in *Calea* of the Neurolaeninae (Robinson, 1975).

Turner and Powell (1977) include the Juameinae in their new tribe Coreopsideae, but the typical members of the latter group are characterized by paleaceous receptacles and obcompressed achenes. The closest relationship of the Jaumeinae is probably to such subtribes as the Clappiinae and Flaveriinae, which also have multi-costate achenes.

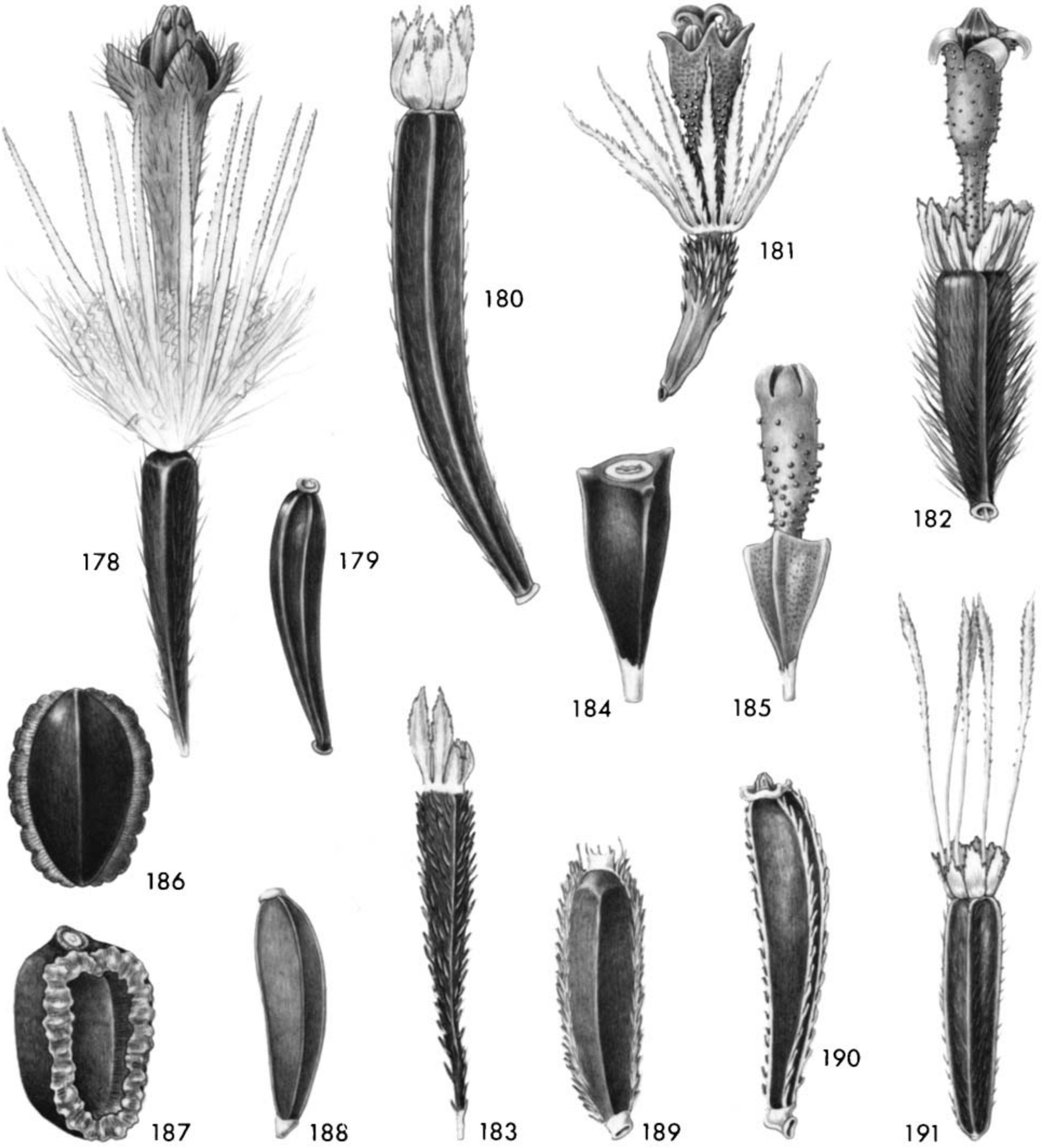
Subtribe 28. MADIINAE

FIGURES 176–181

Subtribe MADIINAE Benth. & Hook., Gen. Pl., 2:198, 1873.
Tribe MADIEAE Jepson, Fl. West. Middle Calif., 486, 1901.
Subtribe RAILLARDELLINAE Rydb., N. Amer. Fl., 34(4):318, 1927.

**Achyrachaena* Schauer (including *Lepidostephanus* Bartl.), **Adenothamnus* Keck, **Argyroxiphium* DC., **Blepharipappus* Hook.f., **Blepharizonia* Greene, **Calycadenia* DC. (including *Osmadenia* Nutt.), **Dubautia* Gaud., **Hemizonia* DC. (including *Centromadia* Greene, *Hartmannia* DC.), **Holocarpha* (DC.) Greenm., **Holozonia* Greene, **Lagophylla* Nutt., **Layia* Hook. & Arn. ex DC., nom. cons., non Hook. & Arn., 1833 (including *Calliachyris* Torr. & Gray, *Callichroa* Fisch. & Mey., *Calliglossa* Hook. & Arn., *Eriopappus* Arn. in Lindl., *Oxyura* DC., *Tollatia* Endl.), **Madia* Molina (including *Amida* Nutt., *Anisocarpus* Nutt., *Harpaecarpus* Nutt., *Madaria* DC., *Madariopsis* Nutt., *Madorella* Nutt.), **Raillardella* A. Gray in Benth. & Hook., **Wilkesia* A. Gray.

Annual or perennial herbs, or rarely shrubs as in *Dubautia*, rosuliform or caulorosula in *Argyroxiphium*. Leaves opposite at least in early stages, often becoming subopposite or alternate, sometimes bearing specialized, multicellular, capitate glands. Inflorescence terminal, usually cymose or with cymose branches, sometimes elongate or virgate with some acropetal development, rarely with solitary heads. Heads usually heterogamous, rays lacking in *Dubautia*, *Raillardella*, *Wilkesia*, and *Layia discoidea* Keck; involucral bracts in a single series except in *Hemizona angustifolia* DC., each bract usually enfolding a ray flower; when rays lacking, a single series of bracts surround disk; paleae usually in single series subtending outer disk flowers, arranged in a circle and more or less connate (except in *Achyrachaena*); interior of disk usually epaleaceous (with inner paleae in *Blepharipappus*, typical *Hemizonia*, *Holocarpha*, and 2 species of *Layia*); involucral and receptacular bracts with strands of fibers usually separate from and alternating with veins. Ray flowers when present female; corolla limb papillose on upper surface, strongly trilobed at tip. Disk flowers hermaphroditic (functionally male in at least some disk flowers of *Hemizonia* sect. *Centromadia* and sect. *Deinandra*, *Holocarpha*, and 4 species of *Madia*); corolla lobes short and papillose on inner surface, with few helianthean hairs; anther thecae usually darkened; endothecial cells short, usually with 1 or 2 thickenings on transverse walls; anther appendages without glands, with cell walls often elaborately thickened. Style branches with paired stigmatic lines; styles of disk flowers usually with a short triangular or acuminate appendage, lower abaxial surfaces of branches usually smooth (numerous hairs continuing onto shaft in *Blepharipappus*); styles in functionally male flowers often reduced, often without stigmatic papillae. Pectic intercellular deposits in leaves and sometimes in bracts (except in vernal annuals *Achyrachaena* and *Layia*). Duct system usually reduced, present in stems and leaf-bases in *Achyrachaena*, *Adenothamnus*, *Wilkesia*, a few species of *Layia*, *Madia*, and *Raillardella*, present in corollas and styles of *Achyrachaena*, *Lagophylla*, some species of *Dubautia*; ducts sometimes solitary along veins of corolla throat, ducts with reddish resin prominently paired along veins of corolla throat and inside veins of style branches in *Achyrachaena*, traces of 4 ducts seem evident outside of veins in



FIGURES 178–191.—Madiinae-Hymenopappinae-Lycapsinae-Perítylinae: 178, 179, *Layia glandulosa* (Hook.) Hook. & Arn. (178, disk achene, × 12; 179, ray achene, × 12); 180, *Wilkesia gymnoxiphium* A. Gray, achene, × 12; 181, *Dubautia laxa* Hook. & Arn., achene with corolla, × 12; 182, *Hymenopappus filifolius* Hook., achene with corolla, × 8; 183, *Loxothysanus pedunculatus* Rydb., achene, × 17; 184, 185, *Villanova titicacensis* Mey. & Walp. (184, achene, × 17; 185, achene with corolla, × 17); 186, 187, *Galeana pratensis* (H.B.K.) Rydb., achenes, outer and inner view, × 13; 188, *Lycapsus tenuifolius* Philippi, ray achene, × 17; 189, *Perityle emoryi* Torrey, achene, × 17; 190, *Amauria rotundifolia* Benth., achene, × 17; 191, *Eutetras palmeri* A. Gray, achene, × 12.

style shaft of *Holocarpha*. Achenes prismatic, curved or sometimes slightly compressed, walls carbonized, usually with striations but obscured by dense cell layers in *Hemizonia* and *Holocarpha*, carbonization unbroken but slightly grooved in *Calycadenia*; where seen, cells of seed coat without ornate thickenings, with strongly sinuous walls in *Holocarpha*, with pustulate inner surface in *Achyrachaena* and *Layia*; pappus of various bristles, awns, or squamellae, or lacking, usually radially arranged. Pollen 30–35 μm in diameter.

Members of the Madiinae are generally known as tarweeds, evidently because of the common occurrence of abundant pectic material in the leaves. The subtribe has a distinctive distribution, with most genera concentrated along the Pacific coast of the United States and Baja California. A few genera occur in the Hawaiian Islands, and one or two species of *Madia* occur as a disjunct element in Chile.

The subtribe has been reviewed recently in an anatomical study by Carlquist (1959), and that study contains citations of various other papers of that author dealing with members of the group. With few exceptions, the group can be recognized by the single series of subequal involucral bracts enfolding the ray florets and the single series of usually partially connate paleae surrounding the disk. Carlquist (1959) cited a few developmental trends within the subtribe, the development of distinct fiber strands in the involucral bracts and paleae, the loss of secretory canals or resin ducts, and the presence of capitate trichomes with biseriate stalks which are modified into more complex structures in some genera. The achene walls of the Madiinae seem to be basically striate, and the cells of the seed coat basically inornate, but interesting variations occur in both structures.

Traditionally, the subtribe has been placed among the paleaceous Heliantheae, and the darkened anther thecae might seem to support such a position. No close relatives are evident among the paleaceous Heliantheae, however, and in many respects the Madiinae resemble members of the epaleaceous series. Under the microscope, as preserved in Hoyer's solution, the pigment of the anther thecae of the Madiinae appears reddish. Except for reddish pigments in a few genera such as *Smallanthus* and *Ichthyothere* of the Melampodiinae, the pigments of the most genera of the paleaceous subtribes appear blackish or greenish under the microscope. In this study, the Madiinae are regarded as remote from other dark-anthered members of the tribe, and are aligned among the basically epaleaceous subtribes of the Heliantheae.

Stuessy (1977) suggested that the reduced annual herb *Faxonia*, of Baja California, might belong to the Madiinae. The genus has been examined and has been placed in the subtribe Galinsoginae in this study.

Subtribe 29. HYMENOPAPPINAE

FIGURES 182–187

Subtribe HYMENOPAPPINAE Rydb., N. Am. Fl., 34(1):43, 1914.

**Galeana* La Llave & Lex. (including *Chlamysperma* Less.)*Hymenopappus* L'Hér. (including *Rothia* Lam., nom. rej., non Schreb., nec *Rothia* Pers., nom. cons.), **Loxothysanus* B. L. Robins., **Trichocoryne* Blake?, **Villanova* Lag., nom. cons., non Ortega (including *Vasquezia* Phil.).

Annual, biennial, or perennial herbs or shrubs. Leaves opposite or alternate, sometimes in basal rosettes. Inflorescence subscapose, or terminal on leafy branches, cymose. Heads heterogamous or discoid; involucre of subequal herbaceous bracts in 2 or 3 series, mostly ovate; paleae lacking (except in *Hymenopappus newberryi* (A. Gray) Johnston). Ray flowers when present female; corolla limbs papillose on upper surface. Disk flowers hermaphroditic; corolla glanduliferous on outer surface, throat campanulate; lobes 5, papillose on inner surface; anther thecae pale; endothecial cells short, with usually 2 or 3 thickenings on transverse walls; anther appendages ovate, with or without glands. Style branches with paired stigmatic lines, papillose only near tip abaxially, short-pointed or truncate at tip. Without evident colored resin; ducts of style, if present, outside of veins. Achenes rather trigonous or quadrangular, with shortly to longly stipitate base, surfaces winged or tuberculate in *Galeana*, walls carbonized, without striations, carbonization with additional pattern of knoblike thickenings; cells of seed coat elongate, with ornate thickenings restricted to lateral walls or lacking; pappus lacking or of radially arranged squamellae, squamellae with central cells forming distinct costa. Pollen 25–35 μm in diameter.

The subtribe is concentrated in the region of Mexico and the southwestern United States with one genus, *Villanova*, having some species endemic in western South America.

The subtribe forms part of a series of five (Hymenopappinae, Peritylinae, Baeriinae, Chaenactidinae, and Gaillardiinae), which I consider unquestionably closely related. These form the core of what was recognized by Bentham and Hooker (1873) and Hoffmann (1890–1894) as the tribe Helenieae. The Hymenopappinae differ from the others of the series by the distinctly carbonized achene walls lacking striations. The achenes of the Hymenopappinae also tend to be distinctive in the trigonous or quadrangular shape and the stipitate bases. In both *Hymenopappus* and *Loxothysanus*, where a pappus is present, the squamellae have a similar differentiated costal region.

The subtribe contains two elements of very different habits. *Hymenopappus* contains biennial or perennial often subscapose plants with alternate leaves forming a basal rosette. The remaining annual genera *Galeana* and *Villanova*, and the shrubby *Loxothysanus*, branch above the base and have opposite leaves in at least the lower part of the plant.

The genus *Trichocoryne* was described by S. F. Blake in 1924 with a single species, *T. connata* Blake. Relationship to *Galeana* was suggested, but the more numerous bracts and flowers of the heads were noted. The genus appears to have been overlooked by more recent summaries of the epaleaceous Heliantheae. Examination of the type specimen from Durango, Mexico, leaves the position of the genus in question, but the non-striate, generally trigonous achenes would favor placement near the Hymenopappinae. The four small plants on the sheet seem more like annuals than perennials as described by Blake. The leaves are linear and opposite, and are fused into a short sheath at the base. The pedunculate heads are solitary on the tips of the stems and branches. There are 10 broadly rounded involucral bracts having subhyaline margins. The receptacle was described as convex or low-conical, but it is very highly conical. Paleae are lacking. The 5–7 rays were described as sterile with "inane" achenes, but they have styles and are only lagging in development. The corollas are 5-lobed and are covered with short, clavate, uniseriate hairs. The base of the achene is not stipitate, and the cells of the seed coat are slightly distorted with no ornamentation on the walls. The plant is, by all indications, a member of the epaleaceous series, but the anther thecae are distinctly blackened. The thickenings of the endothecial cells are numerous and radially or subradially disposed.

Subtribe 30. LYCAPSINAE

FIGURE 188

Subtribe LYCAPSINAE H. Robinson, Phytologia, 46:120, 1980.

**Lycapsus* Phil.

Small perennial herbs. Leaves closely spirally inserted; petioles long and slender from short broadened bases, blades fleshy, irregulary divided into a few narrow lobes. Inflorescence axillary, with single heads on long slender peduncles. Heads heterogamous; involucre with slightly herbaceous narrow bracts irregularly disposed in ca. 2 series; paleae present. Ray flowers present, female; limb of corolla broad, papillose on upper surface, tip broadly trilobed. Disk flowers hermaphroditic; corollas 4-lobed; inner surface of lobes papillose, outer surface with glands and a few short, 2–3-celled, uniseriate hairs; anther thecae pale; endothecial cells with 2 or 3 thickenings on transverse walls; anther appendage without glands. Style base distinctly nodulose, branches with paired stigmatic lines, tips short acute, triangular, papillose on abaxial surface of appendage. Ducts not evident, without colored resin. Achenes prismatic, fusiform with ca. 4 costae, walls carbonized in an even and continuous coating, without striations, without additional pattern of knoblike thickenings, marked with only cell outlines and micropunctations; cells of seed coat not seen. Pappus absent. Pollen ca. 27 μm in diameter.

The subtribe Lycapsinae consists of a single species, *Lycapsus tenuifolius* Phil., that is geographically isolated, being endemic to the remote, rather inaccessible islands of San Ambrosio and San Felix off the coast of Chile.

The genus *Lycapsus* is initially distinguishable by the closely spirally inserted leaves with deeply pinnately dissected, fleshy laminae. On the basis of inadequate information, the genus was reduced to synonymy under *Alomia* H.B.K. in the tribe Eupatorieae by Reiche (1901), and the species was treated as a member of that genus by B. L. Robinson (1913). The genus was resurrected and removed from the Eupatorieae by Johnston (1935) who noted the radiate condition of the heads. According to Johnston, "The plant has fertile pistillate marginal florets with a 3-toothed ligule about once and a half the length of the tube. The tubular inner florets appear to be hermaphroditic and sterile. The style branches are linear, flattened and abruptly contracted into a short triangular apex. The receptacle bears conspicuous slender scales which seem to separate the marginal florets from the inner ones. Except for the bracteate receptacle the plant is very suggestive of some of the helenioids or even certain asterioids." The material seen in this study differs from the Johnston description only by the presence of distinct paleae among as well as around the disk flowers and by the more evident fertility of the disk flowers. The plant is clearly a member of the Heliantheae as defined here.

The genus is sufficiently distinctive to be placed in a separate subtribe. In fact, the closest relationship within the tribe is only tentatively resolved. As noted by Johnston (1935), the genus is suggestive of the helenioids, although it has paleae. Present observations find distinctly petiolate leaves, 4-lobed corollas, and nonstriate achenes with an even layer of carbonization, all as in the subtribe Peritylinae. The costae and carpopodial structure of the achenes are matched by members of the latter subtribe, especially *Eutetras*. It is suggested here that the Lycapsinae are close to the latter opposite-leaved, epaleaceous subtribe, and that the paleaceous receptacle and less regular involucre represent a reversion from an epaleaceous condition, a situation equivalent to that seen in *Varilla*.

Geographically, the Lycapsinae are isolated from the primary ranges of potentially related subtribes such as the Peritylinae in western North America. Nevertheless, the disjunct occurrences of *Madia* of the Madiinae and of *Perityle emoryi* Torr. of the Peritylinae in northern Chile are two examples of separate, more recent introductions of such subtribes into areas near to San Ambrosio and San Felix.

Subtribe 31. PERITYLINAE

FIGURES 189–191

Subtribe PERITYLINAE Rydb., N. Amer. Fl., 34(1):11, 1914.
Subtribe AMAURIINAE Rydb., N. Amer. Fl., 34(1):29, 1914.

**Amauria* Benth., **Correllia* Powell, **Eutetras* A. Gray, **Pericome* A. Gray, **Perityle* Benth. (including *Closia* Remy, *Laphamia* A. Gray, *Leptopharynx* Rydb., *Monothrix* Torrey, *Nesothamnus* Rydb., *Pappothrix* (A. Gray) Rydb.).

Annual or perennial herbs or subshrubs, rarely low shrubs. Leaves usually opposite, at least near base of plant; petioles distinct. Inflorescence rather laxly cymose or with densely subcorymbose branches, heads distinctly pedunculate. Heads heterogamous or sometimes discoid; involucre with numerous narrow herbaceous bracts, mostly uniseriate; paleae lacking. Ray flowers when present female; limb of corolla papillose on upper surface, tip usually distinctly trilobed. Disk flowers hermaphroditic; corollas usually 4-lobed; inner surface of lobes weakly to strongly papillose, outer surface often with peglike hairs; anther thecae pale; endothecial cells with 1–3 thickenings on transverse walls; anther appendage without glands. Style branches with paired stigmatic lines, tips acute, abaxial surface with many hairs on at least the distal half. Ducts without colored resin; ducts of style outside of veins. Achenes slightly to strongly compressed, usually with 2 or 4 costae, walls carbonized, usually in even, continuous coating without striations, often without additional pattern of knoblike thickenings and having only cell margins and micropunctations evident; cells of seed coat not ornamented, sometimes with sinuous or zigzig walls; pappus of bristles or scales, usually arranged bilaterally, pappus absent in *Amauria* and some species of *Perityle.* Pollen 23–27 μm in diameter.

The subtribe occurs in the southwestern United States and northern Mexico, with one species, *Perityle emoryi* Torrey, having a disjunct range in North America, Peru, and Chile.

The taxonomic history has been reviewed recently in a survey of the subtribe by Powell and Turner (1974). Those authors state, "The unifying characters of the Peritylinae are radially flattened achenes with conspicuous to inconspicuous callous margins; a pappus of short laciniate squamellae and/or rather stout short-ciliate bristles; one or two equal to subequal series of involucral bracts which partially enclose the peripheral achenes; narrow slightly flattened, subulate-filiform style branches; and four-lobed disk corollas." The Powell and Turner survey, nevertheless, retained three genera in the subtribe, *Eatonella*, *Oxypappus*, and *Hulsea*, which have 5-lobed disk corollas. Also, *Hulsea* has a 2–3-seriate involucre. The present treatment excludes these three genera, which differ from the natural element of the subtribe by their striate achenes, their sessile leaves, and their chromosome numbers not based on $X = 18$. *Eatonella* and *Oxypappus* with $X = 10$ seem to be members of the subtribe Baeriinae, and *Hulsea* with $X = 19$ is a member of the Chaenactidinae.

Amauria, *Correllia*, and *Perityle* have a distinctive form of achene wall carbonization with an even layer of deposition interrupted only by well-spaced micropunctations. This seems to be a specialization within the subtribe, although similar achene walls occur in some species of *Lasthenia* in the related subtribe Baeriinae. The remaining two genera of the Peritylinae, *Pericome* and *Eutetras*, have a more conventional form of achene wall with a granular structure and an additional regular pattern of knoblike thickenings. In *Pericome*, the conventional wall structure seems to underlie a layer of the *Perityle*-type, but in *Eutetras*, the *Perityle*-type layer is completely lacking.

The endothecial cells of all but one genus of the subtribe are characterized by 2 or 3 thickenings on the transverse walls. In *Pericome* the endothecial cells usually have single thickenings on the transverse walls.

Subtribe 32. BAERIINAE

FIGURES 192–196

Subtribe BAERIINAE Benth. & Hook., Gen. Pl., 2:200, 1873.
Subtribe ERIOPHYLLINAE Rydb., N. Amer. Fl., 34(2):81, 1915.

**Amblyopappus* Hook. & Arn. (including *Aromia* Nutt., *Infantea* Remy in Gay), **Antheropeas* Rydb., **Baeriopsis* Howell, **Eatonella* A. Gray, **Eriophyllum* Lag., **Lasthenia* Cass (including *Baeria* Fisch. & Mey., *Burrielia* DC., *Crockeria* Greene ex A. Gray, *Dichaeta* Nutt., *Hologymne* Bartl., *Ptilomeris* Nutt., *Rancagua* Poepp. & Endl., *Xantho* Remy), **Lembertia* Greene, **Monolopia* DC., **Oxypappus* Benth., **Pseudobahia* (A. Gray) Rydb.

Annual or perennial herbs; leaves opposite or sometimes alternate, crowded on short stems in *Baeriopsis*; petioles lacking or indistinct. Inflorescence terminal, with heads solitary on erect peduncles, laxly cymose, or in subcorymbose clusters. Heads usually heterogamous, sometimes discoid; campanulate to cylindrical; involucral bracts herbaceous, in ca. 2 series, ovate to orbicular, narrow in *Oxypappus*; paleae lacking. Ray flowers when present female; corolla limb papillose on upper surface, weakly to strongly trilobed at tip. Disk flowers hermaphroditic; corollas usually 5-lobed; inner surface of lobes papillose, outer surface often with few to many short, flattened, biseriate, nonglandular hairs, glabrous in *Oxypappus*; anther thecae pale; endothecial cells short, usually with 2–5 thickenings on transverse walls (with radial thickenings in *Lasthenia*; cells elongate with thickenings on lateral walls in *Oxypappus*); anther appendages with or without glands. Style branches with paired stigmatic lines, tips subtruncate or shortly apiculate. Ducts without colored resin; ducts of style shaft apparently outside of veins, veins of style branches near outer surface and ducts possibly absent, ducts apparently present inside of veins in branches and upper shaft of *Oxypappus* style. Achenes prismatic to compressed, walls carbonized, with striations, usually with additional knoblike thickenings, with a smooth layer of carbonization in some species of *Lasthenia*; cells of seed coat not ornamented; pappus of awns or squamellae or lacking, awns and squamellae without sharply demarcated costal region. Pollen mostly 25–30 μm in diameter.

Members of the subtribe are concentrated in the western United States and northern Mexico. One species, *Amblyopappus pusillus* Hook. & Arn., has a disjunct distribution extending to Peru and Chile in South America.

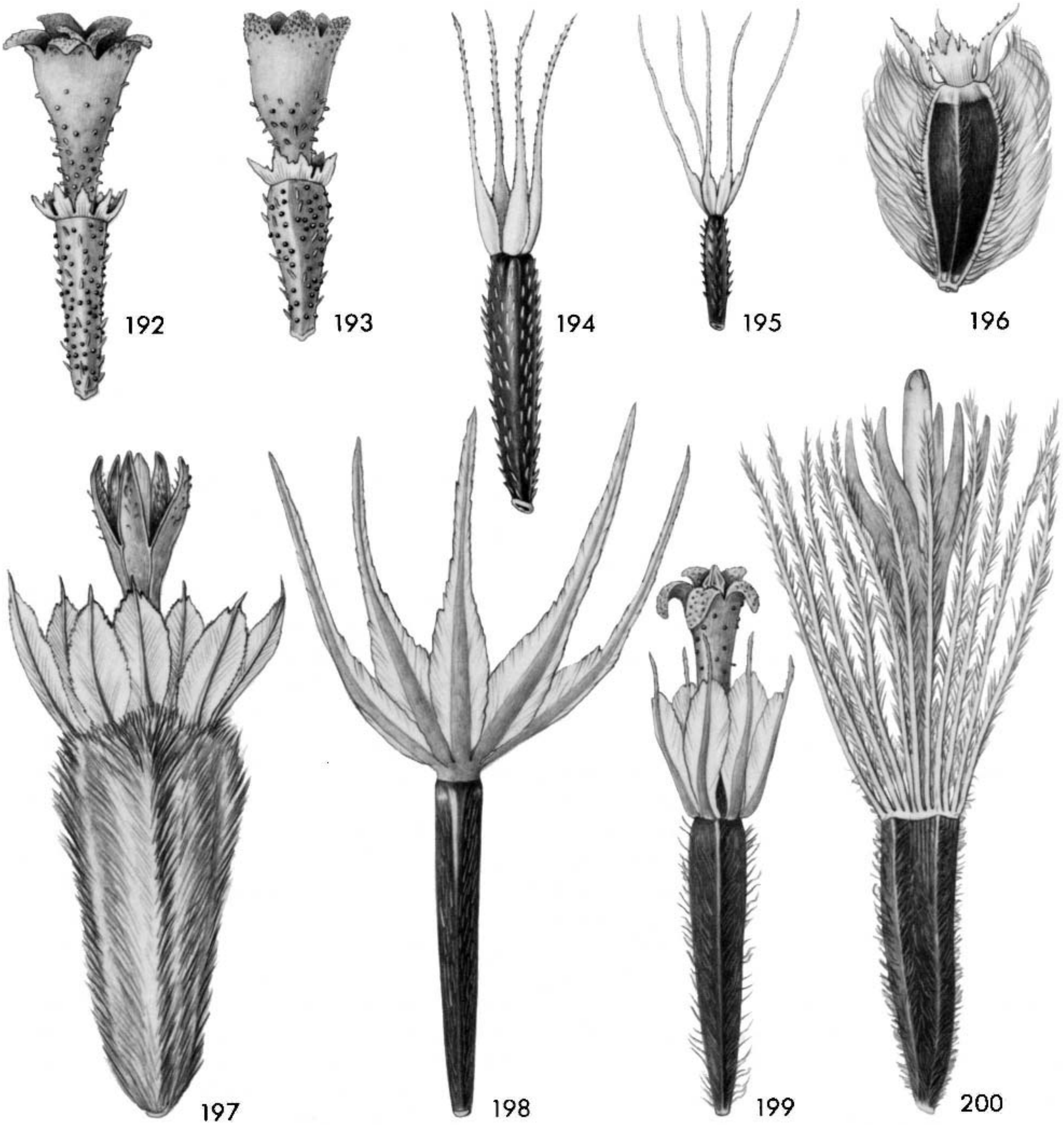
Within the related series of epaleaceous subtribes, the Baeriinae differ by the lack of distinct petioles on the leaves, by the carbonized achenes with distinct striations, and by the usually short endothecial cells with 2–5 thickenings on the transverse walls. The short clavate hairs on the disk corolla lobes of a number of the genera always seem to be biseriate rather than monoseriate as in some of the other subtribes in the series. Most genera of the Baeriinae are further distinguished from the related Peritylinae by the broader involucral bracts.

Oxypappus is evidently related to this subtribe by the form of the leaves and the achenes. However, the genus has a number of anomalous features: an involucre with narrow bracts of the *Perityle*-type, elongate endothecial cells with thickenings on the vertical walls, and resin ducts of the style inside the veins in the upper part of the shaft.

Various members of the subtribe that have been examined show weakly to strongly developed conical receptacles. Also, a number of members, including *Eatonella*, *Monolopia*, and parts of *Lasthenia*, have compressed achenes. The achene of *Monolopia* is of particular interest. The shape of the carpopodium indicates that the achene ordinarily lies against the conical receptacle in a tangential position, but the veins of the style are continuous with the edges of the achene, rather than with the flattened surfaces, showing that the achene is anatomically compressed rather than obcompressed.

The genus *Lasthenia* is here considered a natural genus which can be distinguished anatomically from others of the subtribe by the more radial pattern of thickenings on the endothecial cells. The genus is also of interest chemically. It is one of the two elements in the Heliantheae that has long been known to contain anthochlor pigments (Bohm et al., 1974), and Bohm (1977) mentions that *Lasthenia*, on the basis of five species in two sections, differs from other "Helenieae" by having polyacetylenes based on the ene-tetrayne-ene series rather than the pentaynene series. The monothiophenes in *Lasthenia* of the ene-tetrayne-ene series are particularly notable. It seems to be coincidence that both types of chemicals, the anthochlors and the ene-tetrayne-ene thiophenes, are most prominent elsewhere in the tribe in the subtribe Coreopsidinae. Contrary to the suggestion of Harcombe (1977), there is no other reason to associate *Lasthenia* with the Coreopsidinae.

Previously unnoticed in *Lasthenia* is the internal structure of the achene wall, which varies between two types. *Lasthenia chrysostoma* (Fisch. & Mey.) Greene, *L. coronaria* (Nutt.) Ornduff, *L. leptalea* (A. Gray) Ornduff, *L. minor* (DC.) Ornduff, and *L. platycarpha* (A. Gray) Greene have walls with evenly deposited phytomelanin interrupted only by micropunctations and striations. *Lasthenia chrysantha* (Greene ex A. Gray) Greene, *L. glaberrima* DC., *L. glabrata* Lindl., and *L. microglossa* (DC.) Greene have the phytomelanin more irregular and granular, with an additional pattern of knoblike thickenings. The wall type in the first series



FIGURES 192–200.—Baeriinae-Chaenactidinae: 192, 193, *Baeriopsis quadalupensis* J. T. Howell, disk flowers with achenes, × 12; 194, *Lasthenia chrysostoma* (Fisch. & Mey.) Greene, disk achene, × 17; 195, *Oxypappus seemannii* (Sch.-Bip.) Blake, disk achene, × 17; 196, *Eatonella congdonii* A. Gray, achene, × 12; 197, *Espejoa mexicana* DC., achene, × 8; 198, *Palafoxia sphacelata* (Nutt. ex Torr.) Cory, disk achene, × 8; 199, *Bahia absinthifolia* Benth., disk achene with corolla, × 12; 200, *Hypericophyllum multicaule* Hutchins., achene, × 6.

is the same as that seen without striations in the typical members of the subtribe Peritylinae. Examination of a series of *L. microglossa* indicates the character is stable within a species. Attempts to correlate with the groups of Ornduff (1966) show the first type of wall in sections *Baeria*, *Platycarpha*, *Ptilomeris*, and one species of *Burrielia*. The second wall type is in sections *Hologymne*, *Lasthenia*, and another species of *Burrielia*. Only in section *Burrielia* has hybridization been reported by Ornduff between species shown here to have different wall types, and those hybrids were sterile.

The variation in the achene wall in *Lasthenia* can be compared also with the results of the detailed study of the flavonoid pigments in the genus (Bohm et al., 1974). The first type of achene wall, the *Perityle*-type, is found in groups with the most highly developed anthochlor chemistry as well as those with the nonanthochlor flavonoid patuletin. The second wall type is found in species which have less complex anthochlors or species with no specialized flavonoids. In the flavonoid study, the species with anthochlors are regarded as primitive within the genus, and the species without anthochlors are considered derived. As such, the *Perityle*-type of achene wall would also be primitive within the genus. It is notable that neither the Ornduff sections, the flavonoid types, nor the achene wall types correlate completely. It is notable, also, that anthochlors and *Perityle*-type achene walls are not found in the other genera of the Baeriinae, and they almost certainly are not primitive in the subtribe. Just as the anthochlors do not seem to reflect close relation to the Coreopsidinae, the evenly deposited phytomelanin of the achene wall does not seem to reflect a direct relationship of *Lasthenia* to *Perityle*.

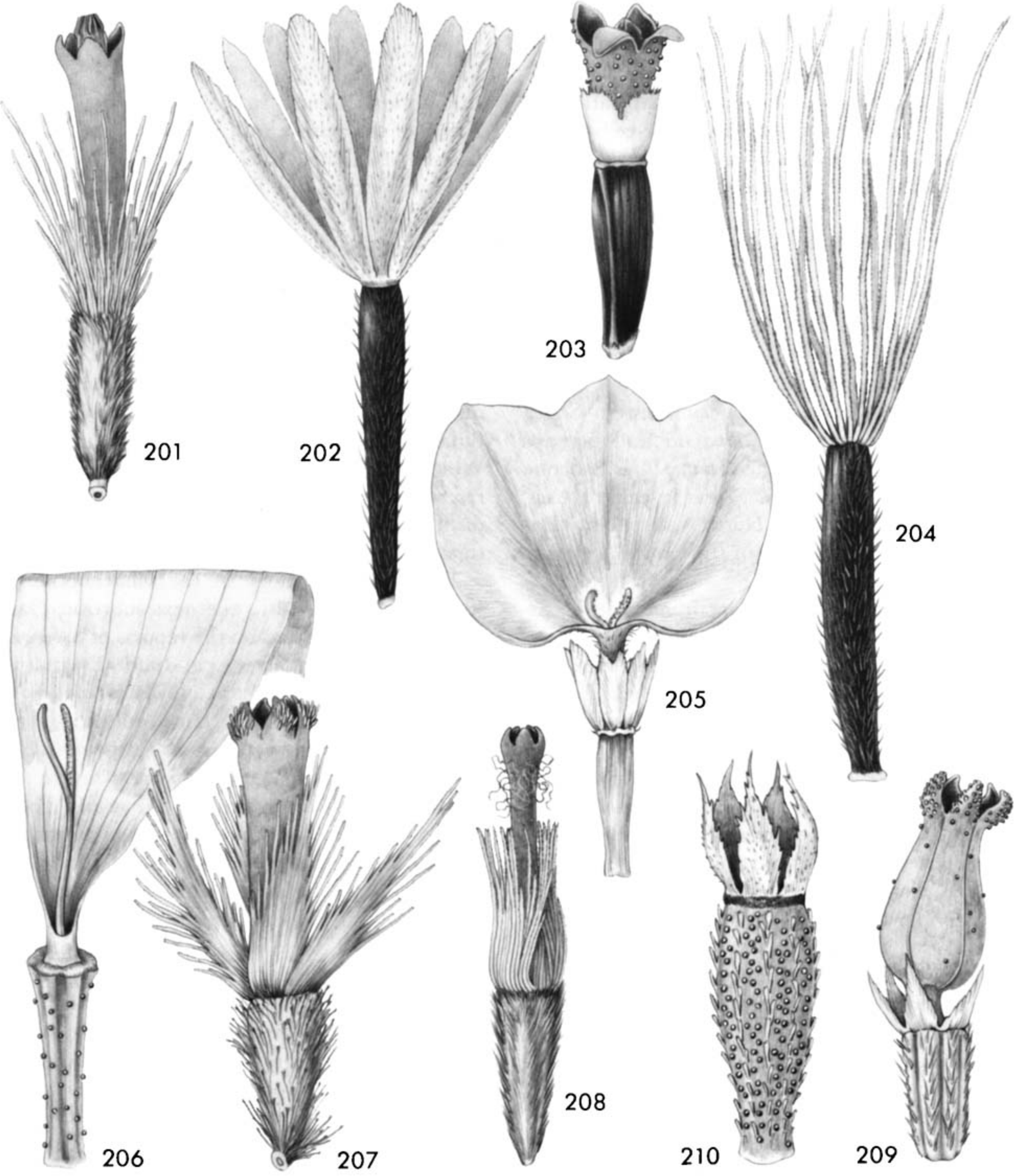
Subtribe 33. CHAENACTIDINAE

FIGURES 197–204

Subtribe CHAENACTIDINAE Rydb., N. Amer. Fl., 34(1):63, 1914.
Subtribe BAHIINAE Rydb., N. Amer. Fl., 34(1):31, 1914.
Subtribe PALAFOXIINAE Rydb., N. Amer. Fl., 34(1):58, 1914.

**Achyropappus* H.B.K., **Arnica* L., **Arnicastrum* Greenm., **Bahia* Lag. (including *Amauriopsis* Rydb., *Picradeniopsis* Rydb., *Stylesia* Nutt., *Virletia* Sch.-Bip. ex Benth. & Hook. in syn.), **Bartlettia* A. Gray, **Chaenactis* DC. (including *Acarphaea* Harv. & Gray ex Gray, *Acicarphaea* Walp., *Macrocarphus* Nutt.), **Chamaechaenactis* Rydb., **Espejoa* DC., **Florestina* Cass., **Hulsea* Torrey & Gray, **Hymenothrix* A. Gray (including *Trichymenia* Rydb.), **Hypericophyllum* Steetz, **Jamesianthus* Sherff & Blake, **Mallotopus* Franch. & Sav., **Orochaenactis* Coville, **Palafoxia* Lag. (including *Loxaxeta* Raf., *Othake* Raf., *Paleolaria* Cass., *Polypteris* Nutt.), **Peucephyllum* A. Gray, **Platyschkuhria* Rydb., **Psathyrotopsis* Rydb. (including *Pseudobartlettia* Rydb.), **Schkuhria* Roth., nom. cons., non *Sckuhria* Moench (including *Cephalobembix* Rydb., *Chamaestephanum* Willd., *Hopkirkia* DC., non Spreng., *Mieria* La Llave in La Llave & Lex., *Tetracarphum* Moench), **Syntrichopappus* A. Gray, **Thymopsis* Benth. in Benth. & Hook., nom. cons., non Jaubert & Spach (= *Neothymopsis* Britt. & Millsp.), **Venegasia* DC., **Whitneya* A. Gray.

Annual, biennial, or perennial herbs (a shrub in *Peucephyllum*). Leaves opposite, alternate, or basal, with or without distinct petioles. Inflorescence of many heads or of single heads on erect peduncles, sometimes subscapose to laxly cymose or clustered at tips of short leafy branches. Heads usually heterogamous, sometimes discoid; involucre of 2 or 3 series of herbaceous bracts, bracts broadly to narrowly ovate or lanceolate, usually subequal; paleae lacking. Ray flowers when present female; corolla limbs usually papillose on upper surface, nearly smooth in *Bahia*. Disk flowers hermaphroditic (functionally male in *Neothymopsis polyantha* Urb.?); corollas usually with 5 lobes; inner surfaces of lobes smooth or papillose; anther thecae pale; endothecial cells short or long, with 1 or 2 thickenings on transverse or end walls, thickenings only on vertical walls in *Chamaechaenactis*; anther appendage with or without glands. Style base usually glabrous as in other subtribes, but with hairs in *Arnica*, *Chaenactis*, and *Chamaechaenactis*; style branches with paired stigmatic lines. Without colored resin; shaft of style with ducts outside of veins. Achenes usually terete or



FIGURES 201–210.—Chaenactidinae-Gaillardiinae-Marshalliinae: 201, *Peucephyllum schottii* A. Gray, achene, × 8; 202, *Chaenactis douglasii* Hook. & Arn., achene, × 8; 203, *Thymopsis thymoides* Griseb., achene, × 17; 204, *Arnica cordifolia* Hook., disk achene, × 8; 205, *Psilostrophe tagetina* (Nutt.) Greene, ray floret with persistent corolla, × 12; 206, *Baileya multiradiata* Harv. & Gray, ray floret with persistent corolla, × 12; 207, *Trichoptilium incisum* (A. Gray) A. Gray, achene, × 12; 208, *Psathyrotes annua* (Nutt.) A. Gray, achene, × 12; 209, *Helenium autumnale* L., disk achene, × 17; 210, *Marshallia graminifolia* (Walt.) Small, achene, × 17.

prismatic, obcompressed in *Bartlettia*, walls carbonized, with or without additional pattern of knoblike thickenings, with striations; cells of seed coat usually not ornamented, with weakly annulated walls in *Psathyrotopsis;* pappus of bristles, awns, or squamellae, in 1-many series, with or without differentiated central costa, sometimes with long vascular trace. Pollen 27–40 µm in diameter.

The subtribe is predominantly North American with most genera in the western United States, Mexico, or Central America. A few species of *Bahia* and *Schkuhria* occur in western South America. The poorly understood and perhaps improperly assigned genus *Thymopsis* is endemic to the West Indies. *Mallotopus* is in eastern Asia, and *Arnica* extends from North America into Europe. A number of species of *Hypericophyllum* occur in Africa.

The genera of the Chaenactidinae can be divided roughly into two groups on the basis of the endothecial cells of the anthers. The series of genera that includes *Bahia*, *Achyropappus*, *Espejoa*, *Florestina*, *Hymenothrix*, *Hypericophyllum*, *Palafoxia*, *Platyschkuhria*, and *Schkuhria* has mostly short endothecial cells in regular rows with well-defined transverse walls. The group shows some general trends toward smooth surfaces on the ray corollas and more strongly nerved pappus elements. The pappus elements often contain vascular traces, the capillary pappus in *Hypericophyllum* is sometimes vascularlized to 2/3 its length, and *Palafoxia* has awns with veins more than half the length. The achenes of the group usually show a regular pattern of knoblike thickenings in the carbonization at full maturity.

The typical group of the Chaenactidinae, which includes *Arnica*, *Arnicastrum*, *Chaenactis*, *Chamaechaenactis*, *Hulsea*, *Jamesianthus*, *Mallotopus*, *Orochaenactis*, *Peucephyllum*, *Psathyrotopsis*, and *Whitneya*, has elongate, often elliptical endothecial cells that are not in distinct rows and are pointed at the ends. The pappus in the group is mostly more delicate, with little or no central costa and no vascular trace. *Arnica*, *Chaenactis*, and *Chamaechaenactis* have hairs on the base of the style, a character found elsewhere in the family only in the tribe Eupatorieae. Genera in the group have carbonization of the achene wall lacking any additional pattern of knoblike thickenings.

Two subtribes, the Bahiinae and Chaenactidinae, could be recognized on the basis of the foregoing alignment, but a few genera included in the present concept do not fall easily into either of the two groups. One of these singularly distinctive genera is *Venegasia*, which is unique in the stalked glands on the anther filaments. Another genus, *Bartlettia*, has the only truly obcompressed disk achenes in the tribe outside of the Coreopsidinae-Fitchiinae group. *Thymopsis*, a reduced West Indian genus, is placed in the subtribe with reservations, but it has striate prismatic achenes, distinctly petiolate leaves, and usually single thickenings on the endothecial cells.

The typical element of the Chaenactidinae seems closely related to the next subtribe, Gaillardiinae, as indicated by the reports of helenanolide sesquiterpene lactones in *Arnica* (Evstratova et al., 1971; Poplawski et al., 1971). The carbonized versus uncarbonized achene wall is the character by which the two subtribes are distinguished here. This character receives its most severe test in the genera *Psathyrotes* and *Psathyrotopsis*. These two genera share a strikingly distinctive pappus form, and they have been treated as parts of a single genus in the monograph by Strother and Pilz (1975), but they recognized cytological, geographical, and some structural differences between the two elements. The two genera were listed separately by Nordenstam (1977). The present study shows that the genus *Psathyrotopsis* of the Chihuahuan region has corollas glanduliferous throughout, corolla lobes with biseriate bilobed hairs on the outer surface and evenly distributed papillae on the inner surface, anther appendages that are ovate and glanduliferous, style branches that are haired abaxially to the base, achene walls that are carbonized, and cells of the seed coat that are ornamented with annulate thickenings. *Psathyrotes* of the Sonoran and Great Basin regions has corollas that are glabrous below, corolla lobes with uniseriate hairs outside and long papillae forming a marginal fringe inside, anther appendages that are spathulate and without glands, style branches that are haired only at the tips, achene walls that are not carbonized, and cells of the seed coat that are not ornamented. The two genera may yet prove closely related, but no character except the pappus has been found to suggest this. For the present, the two are placed in separate subtribes. *Psathyrotopsis* is a member of the Chaenactidinae, whereas typical *Psathyrotes* is placed in the Gaillardiinae close to *Trichoptilium.*

The African *Welswitschiella* Hoffm. has not been seen in this study, but the conventional placement is near *Hypericophyllum.*

Subtribe 34. GAILLARDIINAE

FIGURES 205–209

Subtribe GAILLARDIINAE Less., Linnaea, 6:516, 1831.
Subtribe HELENIINAE Less., Synopsis Gen. Comp., 237, 1832.
Tribe HELENIEAE Benth. & Hook., Gen. Pl., 2:199, 1873.
Subtribe RIDDELLIINAE Hoffm., Nat. Pflanzenfam. IV, 5: 253, 1891.
Family HELENIACEAE Bessey, Ann. Missouri Bot. Gard., 2: 163, 1915.
Subtribe TETRANEURINAE Rydb., N. Amer. Fl., 34(2):100, 1915.
Subtribe PSILOSTROPHINAE Turner & Powell, Biol. Chem. Compositae, 723, 1977 [1978], based on RIDDELLIINAE Hoffm.

**Actinospermum* Elliott, **Amblyolepis* DC., **Baileya* Haw. & Gray ex Torrey, **Balduina* Nutt., nom. cons. (*Mnesiteon* Raf.), **Gaillardia* Foug. (including *Agassizia* Gray & Engelm., *Calonnea* Buchoz, *Cercostylos* Less., *Guentheria* Spreng.), **Helenium* L. (including *Actinea* Juss., *Brassavola* Adans. nom. rej., non R. Br., nom. cons., *Cephalophora* Cav., *Dugaldia* Cass., *Espeletiopsis* Sch.-Bip. ex Benth. & Hook. in syn., *Graemia* Hook., *Hecubaea* DC., *Heleniastrum* Fabricius, *Leptophora* Raf., *Leptopoda* Nutt., *Mesodetra* Raf., *Oxylepis* Benth., *Tetrodus* Cass.), **Hymenoxys* Cass. (including *Actinella* Juss. ex Nutt. nom. rej., non Pers. nec Lewis nom. cons., *Phileozera* Buckl., *Picradenia* Hook., *Rydbergia* Greene), **Macdougalia* A. Heller, **Platyleima* (A. Gray) Cockerell, **Plummera* A. Gray, **Psathyrotes* (Nutt.) A. Gray, **Psilostrophe* DC. (including *Riddellia* Nutt.), **Tetraneuris* Greene (including *Actinella* Pers. nom. rej., non Lewis), **Trichoptilium* A. Gray.

Annual, biennial, or perennial herbs or small shrubs; caulescent or rarely acaulescent; leaves alternate or basal, petiole usually not well delimited, sometimes lacking. Inflorescence often scapose or subscapose with one or a few heads, more rarely with heads in densely corymbose clusters. Heads usually heterogamous, sometimes discoid; involucre with herbaceous bracts in ca. 2 or 3 series, usually subequal; receptacle plane or convex to subglobose, usually alveolate without paleae, sometimes with a few bracts between rays and disk, more or less fimbrillate with short-conical to elongate spinelike fimbrillae in *Gaillardia*, or with spinose crests in *Balduina.* Ray flowers when present usually female, sterile in many species of *Gaillardia* and some *Helenium*; corolla limbs often with elongate rugose cells adaxially, usually strongly trilobed at tip, rays papery and remaining attached to achene in *Baileya* and *Psilostrophe.* Disk flowers usually hermaphroditic, functionally male in *Plummera*; corollas with inner surfaces of lobes somewhat papillose, often with glands on outer surface; anther thecae pale; median endothecial cells more elongate, often elliptical, with 1 or 2 thickenings on end walls; anther appendage without glands. Branches of fertile styles with paired stigmatic lines. Colored resin not evident. Achenes prismatic, with wall not carbonized, cells of wall with distinct raphides; cells of seed coat not ornamented, ovules containing distinct raphides; pappus with various shaped awns or squamellae, with 5 paleae dissected above into numerous bristles in *Trichoptilium*, with numerous coarse to fine bristles in 1–4 series in *Psathyrotes.* Pollen 30–40 µm in diameter.

The subtribe is widely distributed in the Western Hemisphere with a concentration in the drier parts of western North America. Some species of *Helenium*, *Gaillardia*, and *Hymenoxys* occur in South America in the region from Peru southward. A few species are widely cultivated and adventive.

This typical element of the Bentham tribe

Helenieae is now widely accepted as an integral part of the Heliantheae (Stuessy, 1977; Turner and Powell, 1977). Stuessy (1977) expanded the traditional concept of the subtribe to include such genera as *Balduina*, which had been placed in the Galinsoginae, and *Psilostrophe* and *Baileya*, which had been placed in a separate subtribe Riddelliinae by Hoffman (1890–1894). The Stuessy concept of the Gaillardiinae correlates closely with the distribution of the character of noncarbonized achene walls, a character not used by Stuessy in deriving his concept.

In treating the same genera, Turner and Powell (1977) differ from Stuessy (1977) in a number of details, including their retention of a separate subtribe Psilostrophinae (Riddelliinae). The latter group is traditionally distinguished by the persistent, papery ray corollas that fall with the achenes, but the two genera also differ by the achene walls having closely spaced, fibrous costae.

The discoid genera *Psathyrotes* and *Trichoptilium* were not included in the Gaillardiinae by Stuessy (1977). Both genera have broad cells covering the surface of the achene with dark granular inclusions in the lumina, unlike other genera of the subtribe. The pappus of *Trichoptilium* is a set of five squamellae, each dissected distally into a series of numerous bristles. *Psathyrotes* has a pappus with bristles of similar structure which are borne separate to the base and are borne in more than one series. The two forms are undoubtedly related, although the pattern of bristle attachment is totally different. The *Psathyrotes* pappus is remarkably similar to that seen in the genus *Psathyrotopsis* in the Chaenactidinae. Other characters indicate the genera, one with carbonized achene walls and the other without, are not so closely related as once believed. Nevertheless, it is possible that the tendency for reduced carbonization seen in the typical Chaenactidinae has given rise to two separate lines that totally lack carbonization in the achene walls.

The specialized sesquiterpene lactones, the helenanolides, are notable for their near restriction to the subtribe Gaillardiinae. They have been reported in the genera *Baileya*, *Balduina*, *Gaillardia*, *Helenium*, *Hymenoxys*, and *Tetraneuris* (Herz, 1973), a distribution closely supporting the concept of the subtribe by Stuessy (1977). Helenanolides also have been reported from *Arnica* of the closely related subtribe Chaenactidinae and from two genera, *Geigeria* Griessel. and *Inula* L., of the closely related tribe Inuleae (Herz, 1973).

The distinctive polyacetylenes, the epoxysulfones, seem to be restricted to the genera *Gaillardia* and *Helenium* (Bohlmann et al., 1973). Other less specialized sulfones also are present, but such nonepoxidized forms occur elsewhere in the Heliantheae, as indicated under the Flaveriinae.

There is no support from this study for the suggestion by Stuessy (1977) that the Gaillardiinae are closely related to the Helianthinae. The Stuessy suggestion was based on such characters as the large solitary heads, the alternate or basal leaves, and the tendency toward elongate receptacles found in the Gaillardiinae and various elements that he included in the Helianthinae. *Rudbeckia* and *Gaillardia* are particularly similar in superficial appearance, but all other evidence dictates against close relationship.

The name Gaillardiinae has priority at the subtribal level over the name Heleniinae. Until recently, however, I have believed the name Heleniinae would take priority when used within a segregate tribe Helenieae. This was apparently true under older versions of the *International Code of Botanical Nomenclature* as reflected by Solbrig (1963), but by present versions of the Code (Stafleu et al., 1978), such priority for subtribal names based on the type genus of the tribe occurs only in the subtribe containing the type genus of the family, i.e., the subtribe Asterinae in the tribe Astereae. It should be noted that names of subtribes such as the Helianthinae could be displaced if older names are found.

Subtribe 35. MARSHALLIINAE

FIGURE 210

Subtribe MARSHALLIINAE H. Robinson, Phytologia, 41:42, 1978.

**Marshallia* Schreb. nom. cons., non J. F. Gmel (including *Persoonia* Michx. nom. rej., non J. E. Smith, nom. cons. nec Willd., *Phyteumopsis* Juss. ex Poir., *Trattenikia* Pers. non *Trattinickia* Willd.).

Perennial herbs; leaves alternate or basal. Inflorescence scapose or subscapose, with 1-few heads. Heads discoid; involucral bracts herbaceous, subequal, in 2–3 series; receptacle convex or conical, with rigid linear paleae. All flowers disciform, hermaphroditic; corollas lavender or becoming violet; outer surface with numerous uniseriate hairs, often with interspersed glands; basal tube long and slender, throat very short; lobes linear, papillose on inner surface, with expanded cushion or firm papillae on outer surface at tip; anther thecae slightly to strongly violet; endothecial cells short, with 2 or 3 thickenings on transverse walls; anther appendages ovate, strongly carinate, without glands. Style branches with paired stigmatic lines, style tip subtruncate or with a short blunt appendage, outer and lateral surfaces distally with numerous, long, blunt papillae. Ducts and resin not evident. Achenes turbinate, with 5 main costae and 5 weaker intercostal veins, with setae and glands, walls not carbonized, with laxly quadrate or oblong cells, raphides minute; carpopodia symmetrical, annuliform, with cells wider than high; seed coat with cells of one of the layers quadrate, not ornamented; pappus of 5 lanceolate or triangular-ovate, acute squamellae, with outer surface scabrid. Pollen ca. 40 μm in diameter.

The single genus of the subtribe, *Marshallia*, is endemic to the eastern United States.

The Marshalliinae are remote from other subtribes of the Heliantheae. Uncarbonized walls of the achene are found in only one other subtribe, the Gaillardiinae, but otherwise there is no evidence of close relationship. The Gaillardiinae and the subtribes to which it is related are all basically epaleaceous, whereas the Marshalliinae have prominent rigid paleae of a distinctive form. In the Heliantheae, the presence of paleae seems to be correlated with some asymmetry of the carpopodium, but in *Marshallia* the carpopodium is expanded and symmetrical with larger cells than in other members of the tribe.

There have been recent suggestions that *Marshallia* belongs in the tribe Eupatorieae (Stuessy, 1977; Turner and Powell, 1977), but the keeled anther appendage with a constricted base, and the polarized thickenings of the endothecial cells are totally foreign to that tribe. The uncarbonized achenes, which are unusual in the Heliantheae, are even more unusual in the Eupatorieae, and the latter tribe never has well-developed raphides.

The relationship of *Marshallia* seems to be reflected better in the recent discovery of prenyl flavonoids in *M. grandiflora* Bead. & Baynt. (Bohlmann et al., 1979). These unusual flavonoids are known elsewhere in the family only in *Flourensia* and *Xanthium* of the Heliantheae and in *Helichrysum* of the Inuleae. These are the two tribes with which *Marshallia* shares structural features. In the keeled anther appendages, colored anther thecae, and the pappus of five lanceolate squamellae, *Marshallia* seems closest to the Heliantheae, and it is retained in the tribe in the present study. Nevertheless, the lack of carbonized walls in the achene is characteristic of the Inuleae, and short to medium-length tails can be seen on the bases of anthers in some species of *Marshallia.* Careful redefinition of the limits between the two tribes may eventually show that the Marshalliinae can be best accommodated in the Inuleae.

Because of the isolated position of *Marshallia* compared to other members of the Heliantheae, the genus with one chromosome report of $n = 9$ (Jones, 1970) cannot be assumed to share the polyploid ancestry suggested for other members of the tribe (Robinson et al., in press).

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