

A Generic Review of  
the Tribe Liabeae (Asteraceae)

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## ABSTRACT

Robinson, Harold. A Generic Review of the Tribe Liabeae (Asteraceae). *Smithsonian Contributions to Botany*, number 54, 69 pages, 16 figures, 1983.—The neotropical tribe Liabeae is treated with approximately 157 species aligned in 15 genera and three subtribes, the Liabinae containing *Austroliabum*, *Cacosmia*, *Chionopappus*, *Ferreyranthus*, *Liabellum*, *Liabum*, *Microliabum*, *Oligactis*, and *Sinclairia*; Paranepheliinae containing *Paranephelium* and *Pseudonosseris*; and Munnoziinae containing *Chrysactinium*, *Erato*, *Munnozia*, and *Philoglossa*. The latter two subtribes are formally described herein as new. The tribe is placed in the subfamily Cichorioideae, and distinctions from the Vernoniaeae are discussed. A phylogeny of the tribe is proposed with probable central Andean origin. Various elements of the tribe are traced phyletically and geographically. The genera are seen as unusually well isolated from one another compared to genera in most of the more successful tribes of the Asteraceae. The apparent restriction of reticulating evolution to the early development of the Liabeae is suggested as a reason for the comparatively limited success of the tribe.

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*Harold Robinson*

## Introduction

The tribe Liabeae consists of approximately 155–160 species in 15 genera that are restricted to the Neotropical Region. Compared with other tribes of the family, the Liabeae are inaccessible to centers of taxonomy in the temperate and colonial areas, having no representatives in either eastern North America or in Brazil in eastern South America. The most accessible element of the tribe during the earlier periods of taxonomic study was the small series of *Liabum* species in the Greater Antilles, and this partially explains the inadequate attention given to the group in the classical treatments of the Asteraceae. The Liabeae was not recognized as a tribe until the time of Rydberg (1927). Until the various papers derived from the work of S.F. Blake (Blake, 1935; Cabrera, 1954; Sandwith, 1956), the various elements of the Liabeae were distributed in four different tribes, the Senecioneae, Heliantheae, Helenieae, and Mutisieae. All aspects of the tribe have been in need of revision. The present review follows some preliminary efforts published during the last 10 years, the two most basic being Robinson and Brettell (1974b) and Robinson (1978a). The revised concepts were briefly covered in the recent symposium treatment by Nordenstam (1977a).

Species of the Liabeae first appear in the liter-

ature as members of genera of the Astereae, such as *Solidago* and *Amellus*. A West Indian species was the first to be recognized as representing a distinct genus, *Liabum*, by Adanson (1763). A number of additional generic names were established during the next half-century, including *Munnozia* from Peru and various synonyms of *Liabum* from Central America and the northern Andes.

The most critical examination of members of the tribe before this century was by Cassini (1823, 1825, 1830), who treated the members as a section of the tribe Vernonieae. The genera recognized at that time were *Liabum* Adanson (including *Andromachia* Humboldt, Bonpland, and Kunth and *Starkea* Willdenow), *Munnozia* Ruiz & Pavon, *Cacosmia* Humboldt, Bonpland, and Kunth, and *Oligactis* Cassini. The characters cited by the various authors or by Cassini distinguished *Munnozia* by its chaffy receptacle, *Cacosmia* by its lack of a pappus, and *Oligactis* by its few disk flowers and double pappus.

The work of Lessing (1832) treated the Liabeae as a subtribe of the Vernonieae, adding one genus, *Alibum* Lessing, and relegating *Munnozia* to "Genera minus cognita." This disposition was followed in part by DeCandolle (1836), but a number of mistakes were introduced, especially in regard to two new genera. *Erato* DeCandolle was described as a new genus in the Asteroideae in the relationship of *Psiadia* (*Baccharis*), and *Philoglossa* DeCandolle was described in the Senecionideae in the relationship of *Rudbeckia* and *Encelia*,

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neither being recognized as relatives of *Liabum* or as relatives of each other. Also, two asterean elements were included in the division Liabaeae, destroying the naturalness of the group that was maintained by Cassini and Lessing.

*Paranephelius* was described by Poeppig and Endlicher in 1843 and was placed near *Liabum* by Weddell (1855–1857). The latter work also raised section *Chrysactinium* Humboldt, Bonpland, and Kunth to generic rank and resurrected *Andromachia* (including *Munnozia*). All the elements of the Liabaeae included in the work of Weddell were together in a natural group.

The work of Bentham and Hooker (1873) established a tradition lasting for over a hundred years, but, unfortunately, these authors treated the primarily neotropical groups poorly, especially the Liabaeae. All elements of the Liabaeae having a capillary pappus, except the poorly known *Allendea* Llave and Lexarza, were placed together in a single genus, *Liabum*, and transferred from the related Vernoniaeae to a highly artificial tribe Senecioneae. In the Senecioneae, *Liabum* and *Allendea* were placed in a subtribe, Liabaeae, with the helianthean genera *Schistocarpha* Lessing and *Neurolaena* R. Brown and the vernonian genus *Gongrothamnus* Steetz. All elements of the Liabaeae with a different form of pappus were placed in different tribes. *Philoglossa* DeCandolle was placed in the subtribe Melampodiinae of the Heliantheae, and the new genus *Chionopappus* Bentham, having a plumose pappus, was placed in the Mutisieae. *Cacosmia* Humboldt, Bonpland, and Kunth, which had previously been recognized as a relative of *Liabum*, was placed in the Helenieae. The treatment of the Liabaeae by Bentham in Bentham and Hooker (1873) must be considered totally incompetent, but was accepted with few changes along with other parts of the general treatment of the Asteraceae by Hoffmann in Engler and Prantl (1890–1894), and has been perpetuated with little question into the present century by such authorities as Cronquist (1955).

Even as the tradition prevailed in general works, progress was being made in isolated studies

of the Liabaeae. In *North American Flora*, Rydberg (1927) established the tribal status of the group and recognized numerous generic segregates in the Mexican and Central American species, most notably *Sinclairia* Rydberg and *Liabellum* Rydberg. Blake (1935) described the unnamed species on which Bentham in Bentham and Hooker (1873) had based his genus *Chionopappus*, and at the same time Blake pointed out the true relationship to *Liabum*. By the time that Cabrera (1954) described his *Liabellum* (= *Microliabum* Cabrera), he was able to mention the relationships of both *Cacosmia* and *Chionopappus* to *Liabum*. Sandwith (1956) described a new species of *Philoglossa*, at which time he cited an unpublished manuscript of Blake in which the liaban nature of that genus was recognized.

Recently, this author has been involved in a series of studies of the tribe (Robinson, 1976–1982; Robinson and Brettell, 1973, 1974; Robinson and Cuatrecasas, 1973), but the major results are summarized in two papers. In the first, Robinson and Brettell (1974b) placed all the elements together as a distinct tribe containing 14 genera. In the second paper, the treatment of the tribe in the *Flora of Ecuador*, Robinson (1978a) resurrected one additional genus, *Erato*, and treated the 29 species of the country with illustrations of seven of the eight genera. There remain a number of recent additions and refinements in the tribe since the first summary paper that were not included in the Ecuadorian study, however. The present paper provides a more complete review of the classification and structure of all 15 genera presently known in the Liabaeae and presents evolutionary and geographical information not previously discussed.

ACKNOWLEDGMENTS.—A number of people are to be thanked for their contributions to this study. The drawings have been prepared by Alice Tangerini of the Department of Botany, and the study has benefitted by comments from Jose Cuatrecasas, Vicki Funk, and R.M. King. The assistance of Rebecca D. Brettell in the early phases of the work is also greatly appreciated.

### Tribal Status and Evolutionary Considerations

The Liabeae have deeply lobed disk corollas, long-spurred anther bases, continuous stigmatic surfaces on the inside of the style branches, and somewhat irregular distribution of spines on the pollen. These features mark the tribe as a member of the subfamily Cichorioideae, a relationship shared with the Lactuceae, Vernonieae, Mutisieae, Cardueae, Echinopsidae, Gundelieae, Eremothamneae, and Arctotideae. Bentham's placement of the Liabeae in the Senecioneae was based on the presence of a capillary pappus and heterogamous heads, but the Senecioneae often have short-lobed disk corollas, nonspurred anther bases, often paired stigmatic lines on the style branches, and regular distribution of spines on the pollen, characteristics of the subfamily Asteroideae. In the Cichorioideae, the Liabeae compare most closely to the Vernonieae and some Lactuceae by the hairs on the abaxial surfaces of the style branches. The Liabeae differ from either of these tribes and from most other Cichorioideae by their opposite leaves and the radiate heterogamous heads.

There has been a tendency by recent authors (Nash, 1976; Jansen and Stuessy, 1980) to return the Liabeae to the position assigned to them by Cassini (1823, 1825, 1830) within the tribe Vernonieae. The position of the two groups together in the Cichorioideae is not questioned here, but it is not accepted that the two are necessarily each other's closest relatives within the subfamily. A marked phyletic gap exists between the two groups, and each tribe by its basic characteristics falls completely outside of the basic characteristics of the other tribe. One of the character differences, the heterogamous heads, was sufficiently marked to cause Bentham's removal of the Liabeae to the Senecioneae. Equally marked are the opposite leaves found in all Liabeae but found in only a few specialized Vernonieae. The leaf blades of many Liabeae are strongly trinervate, a feature never seen in the Vernonieae. The corollas of the Liabeae are usually yellow, whereas those of the Vernonieae are mostly reddish or

purplish. Only *Gongrothamnus* Steetz in the Vernonieae is said to have yellowish flowers. The Liabeae have a lax form of areolation of endothelial cells rarely found in the Vernonieae, and the few subquadrate examples of endothelial cells in the Liabeae are specialized with details of thickenings different from those of other tribes. The Liabeae lack the polygonal arrangement of spines or ridges on the pollen that is basic to the Vernonieae (Robinson and Marticorena, in prep.), and the style branches are obtuse to rounded at the tip, usually not tapering as in the Vernonieae (see below). The presence of latex seems basic to the Liabeae, a character found in the Lactuceae and a few Mutisieae but not found in the Vernonieae. In other chemistry, the Liabeae show no compounds that are particularly suggestive of the Vernonieae (Robinson et al., 1980). The cytology of the Liabeae falls outside of the pattern seen in the Vernonieae (Jones, 1977; Robinson et al., in prep.). There are no characters that are uniquely shared by the two tribes Liabeae and Vernonieae, and there are no characters by which the combined tribes could be distinguished from the Lactuceae. It is believed here that combination of the two tribes misrepresents the phyletic significance of the two groups and ignores extremely marked differences exceeding those that distinguish the Vernonieae from other tribes such as the Lactuceae. The relationship between the Liabeae and Vernonieae does remain useful as a basis for phyletic discussion.

It should be emphasized that the tribe Vernonieae includes more genera and more species and is regarded as having more subtribes than the Liabeae, and it has a much wider geographical distribution, but it does not have markedly greater diversity in its basic characteristics (Robinson et al., 1980). In the latter respect the tribes are nearly equivalent.

The tribe Liabeae is similar in size to the paleotropical tribes Arctotideae and Calenduleae, which occur mostly in the African region. The restriction of the Liabeae to the Neotropical Region encourages the idea of relationship to Vernonieae, the latter being well represented in that

area; however, any divergence between the two tribes could not have been very recent. The 15 genera of the Liabae show a considerable diversity and display some internal phyletic gaps. The genera *Philoglossa* and *Erato*, which were sufficiently distinct to have been placed in association with various members of the Heliantheae by various authors (DeCandolle, 1836; Bentham in Bentham and Hooker, 1873), are only one part of the three subtribes of the Liabae that are recognized herein. Further insights are gained by more detailed study of some individual characteristics of the tribe.

**THE ANTHERS.**—The form of the anther is one of the features that marks the Liabae as a member of the subfamily Cichorioideae. The appendage is not constricted at the base, and the bases of the thecae extend well below the point of attachment to the collar. Such anther bases present problems in both observation and terminology. In observation, the true length of the extended anther bases is often underestimated, because the upper part of the filament (collar) lies in the plane of the anther thecae. On superficial examination, insertion seems to be at the base of the collar, but the actual point of attachment is at the upper end.

The term for such anthers is also subject to confusion. The three terms sometimes used are "dorsifixed," "tailed," and "hastate." The first, "dorsifixed," is inaccurate, since the collar is attached at the base of the connective and only the thecae extend below that point. The term "tailed" is undesirable for the Liabae, since tailed anther bases such as those in the Inuleae refer to sterile basal extensions. In a few Mutisieae, rarely in the Inuleae and to a slight extent in *Chionopappus* and *Ferreyranthus* in the Liabae, there is a tail in addition to a fertile part that extends below the attachment to the collar, but it seems important to have a term that will allow distinction between the various forms. The third term, "hastate," is also undesirable, since it is also used for the very different short type of anther base found in many Heliantheae, and also it implies a pointed tip, which most Liabae and

other Cichorioideae do not have. Because of this problem, Jose Cuatrecasas has suggested (pers. comm.) adoption of the term "calcarate" or "spurred" for the type of anther base that is characteristic of the many tribes of the subfamily Cichorioideae. In some of the cases mentioned above, the anther base would be both calcarate and tailed.

The anther bases in the Liabae are all calcarate, but there is variation in the ornamentation on the base. In the Paranepheleinae and Munnoziinae, the base is essentially plain. In the Liabinae, the base of each theca is often fringed by projecting cells, and in *Chionopappus* and *Ferreyranthus*, this fringe is borne on a short but distinct sterile portion of the theca. In *F. verbascifolius*, the short tail is particularly noticeable as a fringed coil next to the strongly papillose filament.

The thecae of the anthers in the subtribe Munnoziinae of the Liabae show a black coloration that is characteristic of almost all members of the subtribe. The black color is deposited on the outside surface of the valves, although it often seems to follow the pattern of the endothecial cells. The color is particularly prominent in long narrow bands in *Erato* and *Philoglossa*. Such coloration is not found elsewhere in the Liabae but is found elsewhere in the Asteraceae, being most common in the subfamily Asteroideae in the Heliantheae. It also occurs in a few other isolated genera such as *Blepharispernum* Wight ex DeCandolle of the Inuleae. The occurrence in the Munnoziinae is the only example presently known in the Cichorioideae. The black color is not always well developed in less mature material, but it is lacking in the subtribe Munnoziinae in only *Munnozia hastifolia* and its closest relatives, *M. maronii* and *M. subviridis*.

The median endothecial cells show considerable variation in the Liabae, more than in any other group in the family of comparable size. The extensive variation appears to fall into a phyletic pattern (Figure 1). The variations are primarily in the form of the sclerified shields on the inside surfaces of the endothecial cells and in the pattern



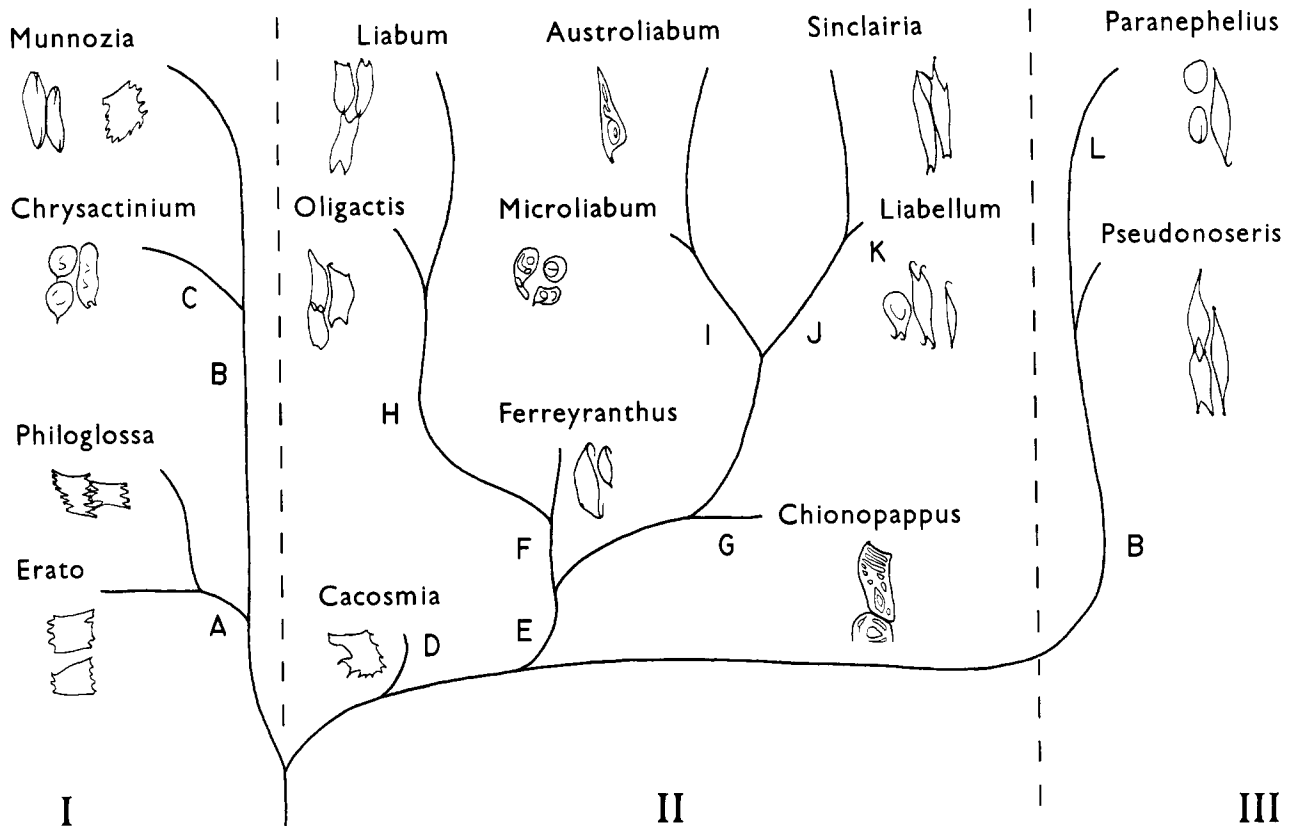


FIGURE 1.—Suggested evolutionary scheme for the Liabeae with illustrations of representative endothelial cells: I, Munnoziinae with anther thecae black, bases of anther thecae unfringed, and cells of achene wall with quadrate raphids; II, Liabinae with anther thecae pale and bases of anther thecae fringed or tailed; III, Paranepeliinae with anther thecae pale, cells of achene wall with elongate raphids, style branches long, spines of pollen regularly disposed, basal baculae vestigial or absent, habit rosulate or subrosulate. (A = stiff hairs with bulbous bases, 2-4 angles on achene; B = spines of pollen regularly disposed; C = cells of anther collar with dense annular thickenings; D = pappus absent; E = anther thecae tailed; F = latex absent; G = pappus bristles plumose, paleae present; H = cells of achene wall with quadrate raphids, style branches of disk flowers usually long; I = Argentina and southern Bolivia; J = Mexico and Central America; K = with tuberous root; L = heads sessile, bases of anther thecae not fringed.)

of thickenings or extensions of these shields onto the periclinal walls between the endothelial cells.

In the Munnoziinae, the pattern of the shields and their thickenings is different in each of the genera. In *Chrysactinium*, thickenings are often solitary at the lower ends of short cells. In *Munnozia*, the thickenings vary from solitary at the upper and lower ends and strongly arching inwards, to multiple and scattered, or sometimes essentially lacking. In *Munnozia* subgenus *Kastnera*, the endothelial cells provide the best example of a well-

developed radial pattern of thickenings in the tribe, with a number of thickenings on both vertical and transverse walls. In *Erato* and *Philoglossa*, where elongate black deposits on the thecae are particularly notable, the thickenings of the endothelial cells are lacking from the transverse walls, and the cells form distinct series. In *Philoglossa*, the individual series of short cells are accentuated by the dense thickenings along the vertical walls, but in *Erato*, such thickenings are very weak, and the endothelial cells are difficult

to see against the background of the black deposits. The Munnoziinae shows a comparatively high proportion of its members with the sclerified shields filling the width of the endothelial cells with thickenings on the vertical walls. These include *Erato*, *Philoglossa*, and many atypical members of *Munnozia* such as the subgenus *Kastnera*.

In the remaining two subtribes of the Liabeae, the endothelial cells, with few exceptions, have sclerified shields distinctly narrower than the endothelial cells. In these, which are similar to the endothecium type in typical *Munnozia* and *Chrysactinium*, the distinct strap-shaped or oval sclerified shields on the inner surface, themselves, superficially look like discontinuous cells. The shields are often plain, but in some genera such as *Chionopappus* and *Austroliabum*, the shields are ornamented with lines or pockets of greater or lesser thickness. The thickenings on the walls between the cells are usually few and are often on very long extensions of the shield. Usually only one thickening occurs at the end of a cell, but two or three closely spaced extensions, in a lacinate pattern, are not rare. In *Ferreyranthus*, *Sinclairia*, *Liabellum*, and *Paranephelius*, the endothelial cells are notable for having long extensions with nodular thickenings on only one end, these usually arching strongly inward. There is a tendency for the nodular points in *Paranephelius* to be more common on the lower ends of the cells. In *Liabum* and *Oligactis*, the shields are similar to those of related genera but more often fill most of the cell and usually have single or double thickenings at both ends that more closely abut with those of adjacent cells.

In *Cacosmia*, which has a habit and leaf surface like *Ferreyranthus*, there are shields in the endothecium that more completely fill the cells, and there are scattered thickenings that are often on vertical walls. In many thecae of *Cacosmia*, there are continuous annulations in the endothelial cells that are restricted to one end of the cell. The form in *Cacosmia* is unlike those in other members of the subtribe Liabinae, but it approaches the forms seen in various members of the Munnoziinae.

It would be useful to assign a phyletic direction to the many patterns of variation in the endothelial cells of the Liabeae, but this is not easily done. Functional considerations are of little help, since the normal function of endothelial thickenings is mostly replaced in the Asteraceae by the plunger action of the style. In fact, the broad median band of endothelial cells in many Liabeae is probably more important as a weakened area in the valve and not capable of providing torsion that would help open the valve. The basic endothelial cell, as seen in most families of angiosperms, is short with well-developed annulations. Such cells are closely approached in the Asteraceae in the Eupatorieae, a tribe showing other comparatively unspecialized features within the family (Robinson, 1981). The endothelial cells are also of a radial form, but weaker and completely incapable of function, in most Veronieae. The latter tribe also shows comparatively unspecialized features, though not as consistently as the Eupatorieae. A simple extension of the idea of the primitiveness of the radial pattern would imply that the broader shields with thickenings on the lateral walls in three genera of the Munnoziinae were ancestral in the subtribe, and *Cacosmia* would be interpreted as the most primitive element in the subtribe Liabinae.

Actual evidence seems to indicate a different evolutionary sequence. The broad endothelial shields in the Munnoziinae are of two different types and can be interpreted as two separate specializations. Those of *Erato* and *Philoglossa* are not truly radial but are transversely polarized, and in *Munnozia* subgenus *Kastnera*, the endothelial type that most closely approaches the truly radial form is in an unquestionably derived element within the genus.

The alternate form of endothecium, with weakly connected shields, presents a different picture with very similar types in *Chrysactinium* and typical *Munnozia* of the Munnoziinae, in all of the Paranepheleinae, and in most of the Liabinae. Being farthest from the primitive radial form in structure, the weakly connected shields should be regarded as specialized in the family. Still, it is a

specialized form that has been attained by such diverse members of the Asteraceae as many calicioid Senecioneae, such subtribes as the Chaenactidinae and Gaillardinae in the Heliantheae, and even *Adenoön* Dalzell of the Vernoniae. It is easiest to assume that the genetic basis for such polarized types of endothelial cells was firmly established in the Asteraceae at an evolutionary level above that of the Eupatorieae but below the level of most other tribes such as the Heliantheae and Liabeae. Some of the variations as seen in *Erato* and *Philoglossa* can be interpreted as little more than rotations of the axis of polarization in shortened endothelial cells. Close examination of the endothelial cells in *Munnozia* subgenus *Kastnera* shows that they are mostly interpretable as having an oblique axis of polarization. Even the more completely radial types in some other tribes, such as in *Dahlia* L. and *Rudbeckia* L. of the Heliantheae, would seem to be reversions from polarized types, although the mechanism is not entirely clear.

On the basis of present evidence, the endothelial form in *Cacosmia* should be regarded as specialized from more polarized types. Nevertheless, the difference in the endothelial type, combined with evidence from other characters, would still suggest a position for the genus comparatively remote from others in the subtribe Liabinae.

The apparent ease of reversals in endothelial cell type in the Asteraceae seems to confirm the absence of any significant selective pressures regarding the structure in the family.

The anther appendage is without notable specializations in the Liabeae except in *Oligactis* subgenus *Oligactis*. In this subgenus, the ends of the cells project from the surface to form distinct short papillae. The rest of the Liabeae, including *Oligactis* subgenus *Andromachiopsis*, have the normal smooth anther appendages.

**THE STYLE.**—The structure that has proven to be most important in all the classical studies of the Asteraceae is the style, and the style remains the one most valuable complex of characters for the evaluation of relationships of the Liabeae. The undivided stigmatic surfaces on the inside of

the style branches and the hairs on the backs of the branches and on the upper shaft immediately mark the tribe as a part of what is here recognized as the subfamily Cichorioideae sensu Carlquist (1976) including the Vernonioideae Turner ex Jansen and Stuessy (1980). The close similarity in detail of the styles of the Liabeae and the Vernoniae is the principle reason for the combination of the two tribes by various authors (Cassini, 1823, 1825, 1830; Turner and Powell, 1977; Jansen and Stuessy, 1980), and it is worthy of a detailed review.

The style of the Asteraceae is a highly functional structure, and it must be treated as such in phyletic speculations. In the family, the basic function of receiving pollen is complicated by the specialization of the style as a plunger for pushing pollen out of the encircling ring of anthers. In spite of various short-term evolutionary variations, the basic patterns of stylar evolution in the Asteraceae use the style to expel pollen but at the same time to prevent automatic self-pollination. This is done in three basically different ways.

The first and least effective method of preventing self-pollination in styles of the Asteraceae involves the development of an enlarged sterile stylar appendage that pushes the pollen from the styles ahead of the emerging stigmatic surfaces. This form is most highly developed in the tribe Eupatorieae of the subfamily Asteroideae. The development of such an appendage may be related to the origin of the sterile band that separates the stigmatic surface into two lines on each style branch, a separation that is basic in the whole subfamily Asteroideae, excluding some specialized groups.

The second and most effective method of preventing self-fertilization is the separation of the flowers into two types, those with anthers and sterile styles serving as plungers and those with fertile styles but no anthers. This design is most common in the subfamily Asteroideae above the level of the Eupatorieae. Included are various Heliantheae, Inuleae, Calenduleae, Astereae, Anthemideae, and Senecioneae with partial to complete separation of flower types in the same heads

or inflorescences or on separate plants. Such separation is rare in the Cichorioideae but is found in an incomplete form in the Arctotideae and in incomplete to complete forms in the Mutisieae.

The third form of protection of the stigmatic surface in the Asteraceae is basic to most Cichorioideae. The stigmatic papillae are completely enclosed between the young branches as the style elongates and pushes through the ring of anthers. The surfaces do not become exposed until the style is exerted and the branches begin to separate. Such enclosed stigmatic surfaces are comparatively rare in the subfamily Asteroideae, where they occur as apparent reversions in specialized groups such as the subtribe Helianthinae of the Heliantheae and the cacalioid members of the Senecioneae.

The functional aspects of the style in the Cichorioideae insure, or at least allow for, the basic similarity of the style structure in the subfamily. The stigmatic surface is continuous and enclosed in all members of the subfamily, and the entire outer surface is available for pollen-collecting hairs or scabrosity extending downward onto the shaft. Hairs are restricted to the apex in only a few specialized members of the Cichorioideae such as the Nassauviinae of the Mutisieae. For the rest of the subfamily, variation tends to be restricted to two aspects, the sharpness of the lower boundary of the scabrous or hairy surface and the proportion of the width of the style-plunger mechanism, which is formed by the hairs or scabrae. Thicker styles as in the Arctotideae, Cardueae, and many Mutisieae need only short scabrae to collect the pollen, whereas thinner styles such as those of the Vernonieae, Liabeae, and Lactuceae need longer hairs to achieve the same function. It is notable that the tribes in which the upper style is thickened to serve as a plunger also tend to have a sharper lower boundary of the scabrous collecting surface at the point where the style becomes narrower. From this simple functional point of view, the co-occurrence of narrower styles with longer pubescence in the Vernonieae, Lactuceae, and Liabeae cannot be regarded as such a certain sign of relationship.

The actual evolutionary history of the style form in the Cichorioideae is not certain from present evidence. There is no evidence that ancestors of the subfamily ever had a stylar appendage or a divided stigmatic surface, and there is no value in speculation on that topic, but it would be useful to determine whether the ancestral style was closer to that of the Arctotideae with a broad tip and short scabrae or to that of the Vernonieae with a narrow tip and longer hairs. Both style types occur with various head types, homogamous or heterogamous, and both are associated with various types of pollen. Variations of the style in the phyletically diverse Mutisieae raise the question of stability of the style form at the tribal level. Also, *Pseudostiffia* H. Robinson shows strong evidence of a position in or near the Vernonieae, though it has a broad tip on the style. The narrower form of style with longer hairs also occurs anomalously in the Eremothamneae, which has heterogamous heads and a capillary pappus but which proves most closely related to the Arctotideae as indicated by Leins (1970) and Norlindh (1977). The style of *Eremothamnus* remains distinct from the other narrow types in the subfamily by the bicellular hairs, which are divided by a longitudinal wall. It seems certain that both the broad and narrow style types in the Cichorioideae have arisen more than once. For these reasons I regard the designation of a primitive style type in the subfamily impossible at this time, but the situation is sufficiently complex that possible separate origins of narrow style forms in the Vernonieae and Liabeae are worthy of further investigation.

It should be noted that, aside from the narrow form, the details of the styles in the Liabeae and Vernonieae are basically different. A long tapering and pointed style branch is basic to the Vernonieae, with only a few specialized genera such as *Centratherum* having less-tapered or short-pointed style branches. In the Liabeae, the style branches in most genera are comparatively short, often less than half as long as the hispidulous part of the style shaft, and the tips are narrowly obtuse to rounded. Longer style branches occur in the

Liabeae but seem restricted to two groups that are considered here as specialized in the tribe, the generic pairs *Liabum-Oligactis* and *Paranephelius-Pseudonosseris*. Of these, only the latter genus-pair has a notable tapering of the branches, and none have tips as sharp as in the Vernoniaeae. Both in *Liabum* and in the ray flowers of *Paranephelius*, there is a tendency for the long style branches to be spiralled, a tendency not known in the Vernoniaeae.

The length of the style branches is not subject to the same type of functional constraints as other aspects of the style discussed above. Still, longer branches may be functional by having longer exposed stigmatic surfaces and by recurving and coiling so as to allow self-pollination. In any case, in the Liabeae, the hispidulous portion of the style seems to be a comparatively fixed quantity, with longer branches generally correlated with a shorter hispidulous region on the shaft. The shorter form of branch has been considered more primitive in the tribe in this study because of its occurrence in most of the genera and in the most diverse groups such as the Munnoziinae, *Sinclairia*, and *Austroliabum*. The longer form of branches occur in one case in the obviously specialized higher elevation genus *Paranephelius* and in the other case in the *Liabum-Oligactis* generic pair, where longer branched forms are specialized within the group. An interesting intermediate is seen in *Chionopappus*, which has short branches with the papillae of the stigmatic surface continuing below the branches well down into the stylar canal. The actual level of separation of the branches and development of stigmatic papillae seems very plastic in the Liabeae, but that itself is a characteristic that seems different from most Vernoniaeae.

THE PAPPUS.—Both the Liabeae and Vernoniaeae seem to share a basic type of pappus having a short, often squamellate outer series and a long capillary inner series. Exceptions exist in both tribes, such as *Paranephelius* in the Liabeae and *Chresta* and *Eremanthus* in the Vernoniaeae, where there is no marked differentiation of an outer series. In these cases, the outer series is not simply

defective but only irregularly shortened and intergrading with the inner pappus. The pappus of these latter genera seems to be specialized within the respective tribes. As a result of the similar pappus, the isolated achenes of the Liabeae and Vernoniaeae are not easily distinguished; however, caution should be used in attempting to relate the tribes on this basis. There is ample reason to believe that a capillary form of pappus is primitive in the Asteraceae (Robinson, 1981), and among the tribes having a capillary pappus, a short outer series is not rare. A short outer series is seen in many Eupatorieae and Astereae and even in some Lactuceae (*Krigia*) and Heliantheae (*Pectis*, *Sartwellia*, *Eutetras*).

The teeth of the pappus setae in some Vernoniaeae and Liabeae share a detail of some interest. The character is seen only with special preparation using a clearing agent with an index of refraction like that of Hoyer's solution. Pappus setae mounted in water show no anomaly in the tips of the teeth when examined under the microscope, but in Hoyer's solution, under the high-power lens, an area of the tip of the tooth seems to disappear because of its index of refraction, leaving a denser central core that resembles a short mucro. The character appears in *Oligactis* and in all but one West Indian specimen seen of *Liabum*, and it also appears on the tips of the long rays of the plumose pappus in *Chionopappus*. The same type of mucro-tip is even more pronounced in a number of species of *Vernonia* (Robinson, 1980b), but a similar aberration, differing only by a denser and still visible outer wall, is seen in the pappus of *Eremothamnus* of the Eremothamneae.

RAPHIDS OF THE ACHENE WALL.—The achenes of the Liabeae all have raphids in their walls, as is true of all tribes of the subfamily Cichorioideae and all but the Eupatorieae and Heliantheae in the subfamily Asteroideae. The raphids in the Liabeae occur in two distinct forms, elongate and subquadrate, which do not intergrade. Each genus consistently has raphids of one type or the other. For those with a microscope and cleared preparations, the raphids are the most convenient

method for an initial separation of the genera into two groups. Most of the genera have elongate raphids, but the subquadrate form is characteristic of two distinctive groups, the Munnoziinae with four genera and the *Liabum-Oligactis* generic pair in the Liabinae.

Because of the simple nature of the raphids, it would be convenient to interpret their two forms as representing two basic lines of development in the tribe. In addition, the subquadrate form, occurring as it does in elongating cells, is not quite matched in any of the other tribes observed, and it would be natural to assume that it was derived within the tribe from a single origin. Unfortunately, the pattern is not so simple. The two groups with subquadrate raphids strongly contrast in most of their other characters and seem to represent two extremes within the tribe. Genera more intermediate in other characters have elongate raphids. Thus, it is necessary to assume parallelism or reversions, or even intergeneric hybridizations, to explain the distribution of raphid types in the tribe. Since the Munnoziinae seem to arise from the earliest divergence in the tribe, it is possible that the subquadrate raphids were present in the common ancestral type of all existing Liabeae and that the subquadrate raphids in *Liabum* and *Oligactis* are a reversion or a tenuous relict of this earlier type.

**GEOGRAPHICAL CONSIDERATIONS.**—The tribe Liabeae is restricted to the Neotropical Region and is further confined within that region to the more mountainous parts. In spite of an erroneous original claim regarding *Munnozia maronii* (Andre) H. Robinson (Robinson, 1977a), there are no members of the tribe presently known from Brazil. Furthermore, there are only a few representatives of *Liabum* in the Greater Antilles. The tribe is primarily found in the western cordilleras of the Americas from central Mexico in the north to northern Argentina in the south. Only two phyletic lines, *Liabum* and the *Sinclairia-Liabellum* generic pair, account for almost all the range extensions northward from South America. The center of distribution of the tribe is in the older portion of the Andes, with 11 of the 15 genera in Peru

and eight genera in Ecuador. Such a distribution helps explain the fact that the temperate-based classical taxonomists failed to understand the true nature of the tribe.

The center of diversity of the tribe may have been a factor in the limited distribution compared to most other tribes. Groups of Asteraceae originating in middle elevations of the Andes seem to be among the least mobile geographically, if evidence from the Eupatorieae is correct (Robinson and King, 1977). In the latter tribe, the Andean groups tend to remain restricted to the cordilleran chain, usually terminating northward in western North America and in the south in Argentina. It is groups spreading from eastern North America and from Brazil in eastern South America that tend to reach the Eastern Hemisphere. In this regard, it is notable that geological evidence suggests the Andes first formed as offshore islands that were isolated until the emergence of the surrounding lowlands at the end of the Tertiary (Pliocene) (Haffer, 1981).

The pattern of distribution of the Liabeae within the Neotropical Region is somewhat complex. The pattern can be made clearer by reviewing the subtribal elements one at a time.

Accepting that the tribe originated in the area of Peru or southern Ecuador, the subtribe *Paranepheleinae* has extended its range in only one direction, upward. The genus *Paranepheleus* seems very specialized for the high elevations where it occurs in Peru and Bolivia. The distribution of *Pseudonosseris* in various parts of Peru is consistent with the assumption based on structural features, of relationship to *Paranepheleus*. The considerable diversity between the three species of *Pseudonosseris*, the occurrence at somewhat lower elevations, and the more generalized form of inflorescence indicate a less specialized, possibly older, or even relictual element in the subtribe. On this basis, the characters of *Pseudonosseris* are regarded as a better guide to the ancestral form of the tribe.

The subtribe Munnoziinae is somewhat less restricted in its distribution, with two of the genera, *Munnozia* and *Erato*, ranging from Costa Rica and Columbia in the north to Bolivia in the

south. The center of diversity of the subtribe is shared between Ecuador and Peru, with both *Munnozia* and *Chrysactinium* occurring nearly equally in both countries. *Erato* actually has a center of diversity in Ecuador. Only *Philoglossa* is primarily Peruvian, and it has been suggested (Robinson and Cuatrecasas, 1973) that the latter genus originated in the floristically distinctive coastal range of Peru. Four of the five species of *Philoglossa* are restricted to the latter area, while one species extends its range from southern Colombia to the interior of Peru with an outlier in Bolivia. It seems unlikely that the Munnoziinae and Paranepheliinae can be traced to different regions of origin on the basis of existing evidence, but it is evident that the Munnoziinae have been very successful in Ecuador and other areas north of the distribution attained by the Paranepheliinae. It is notable that many species of *Munnozia* have individually attained distributions extending from Costa Rica or Colombia in the north to Bolivia in the south, exceeding the entire range of the Paranepheliinae.

The Liabinae is the most widely ranging of the subtribes and also is the most internally complex. *Liabum* is the most widely distributed genus in the tribe and the only representative in the West Indies. The genus, nevertheless, seems comparatively uniform in structure, and the distribution probably is rather recent in origin. The West Indian members include some species diversity, but all are closely related and evident derivatives of a single introduction. The Mexican and Central American distribution is based on a single species, *L. bourgeaui*, which is closely related to two species in the Andes.

The primary area of speciation of *Liabum* and the closely related *Oligactis* is in the northern Andes, north of the center of diversity of the tribe. Nevertheless, *Liabum* has some of its most divergent forms, such as *L. sandemanii* and *L. steinbachii*, in Peru and Bolivia. *Oligactis* has its most specialized elements to the north in Colombia, Venezuela, and Costa Rica, while the less specialized subgenus *Andromachiopsis* is centered in Ecuador. Overall, diversity and geography would indicate

that the *Liabum-Oligactis* group was among the first elements of the tribe in the northernmost Andes, perhaps moving into the area as the habitats in the younger northern Andes were first becoming available.

The two woody genera of the tribe, *Cacosmia* and *Ferreyranthus*, present no geographical complications. Both are restricted to Peru and Ecuador with principal diversity in the adjacent parts of these countries. These genera share the basic style and raphid form with *Chionopappus* from the coastal region of Peru, also within the general area where the tribe is concentrated; however, the remaining two generic pairs in the subtribe represent major geographical extensions. *Microliabum* and *Austroliabum* occur in Argentina and adjacent Bolivia, while *Sinclairia* and *Liabellum* are found in Mexico and Central America. The genera are all sufficiently alike to indicate a related complex extending from Mexico through the Andes to Argentina, but they are also sufficiently distinct to indicate that the dispersal is not of recent origin.

In the case of *Austroliabum* and *Microliabum*, the northernmost occurrence is in the Santa Cruz region of Bolivia, the same general area in which *Munnozia*, *Liabum*, and *Paranephelius* seem to reach their southernmost limits. This gives the impression of a continuous distribution for the tribe; however, a significant change occurs in the Santa Cruz region: the front of the Andes changes direction from a northwest-southeast direction to a north-south direction. The part northwest of Santa Cruz, continuing into Peru, faces northeast and shelters a more tropical flora. The part south of Santa Cruz, continuing into Argentina, faces east and has a more temperate flora. It can be seen that in geography, as in structure, the *Austroliabum-Microliabum* group is discontinuous with the Liabaeae of the neighboring area to the north.

The *Sinclairia-Liabellum* generic pair presents a different geographical problem, being the only group in the Mexican-Central American area that gives evidence of any age. The Central American region has been separated from South America until the creation of the Panamanian isthmus

in the late Pliocene, ~3 million years ago. Even after that time, less moist, savanna-type floras were more predominant in the area (Matthews, 1980). It is notable that one of the generic pair, *Liabellum*, is perhaps the most xeric-adapted genus in the tribe, being a small herb with a perennial tuber. The specializations within the generic pair and the overall diversity of the group would indicate that *Sinclairia* and *Liabellum* belong to an element established in the Mexico–Central America area before the climatic shift to a more moist flora and probably before the formation of the isthmus. The other genera in Central America, *Munozia* (2 species), *Erato* (1 species), *Oligactis* (1 species), and *Liabum* (1 species), are evidently recent immigrants since the climatic changes and, with the exception of *Liabum*, have not reached beyond Costa Rica.

Considering the *Sinclairia* and *Austroliabum* groups together, both share many structural features, and both share specializations toward less moist environments. As such, it is possible to suspect that, in spite of their wide separation, they represent a related group that made the earliest successful migration beyond the area of origin of the tribe, both to the north and south.

The geographical distribution of the Liabae shows an interesting correlation with chromosome numbers. According to available records, the genera centered closest to the presumed center of origin of the tribe mostly have numbers interpreted as diploid, whereas the genera centered farther from the Peruvian center, at least to the north, seem basically polyploid.

**PHYLETIC CONCLUSIONS.**—The evolutionary divergence within the Liabae is accentuated by the apparent lack of intergeneric hybridization. In this way the tribe differs from many of the larger more successful tribes where intergeneric or even intersubtribal hybridization seems to occur. The hybridization in the latter tribes seems to be the source of much of their diversity, and it seems to be at least partially responsible for the greater success of those tribes. Evidence of intergeneric hybridization has been seen in the Vernoniaeae (Robinson, unpublished), Eupatorieae

(King and Robinson, in prep.), Heliantheae (Robinson, 1981), and Senecioneae (Robinson and Brettell, 1974a), and it will probably be found in others. It should be noted that many of the processes that increase evolutionary success complicate the taxonomy of the groups. As such, the lack of intergeneric hybridization in modern Liabae might help explain the comparative lack of success of the tribe.

The apparent lack of intergeneric hybridization results in comparatively simple distinctions of genera and subgenera in the tribe and allows for unusually precise keys. Unlike the situation in most other tribes of the Asteraceae, it is possible to take some advantage of the hierarchical nature of the nonreticulating evolutionary patterns. Some species appearing to be intermediate between genera have proven to be the result of convergence as indicated in the discussion of *Liabum*.

The subtribe Munnoziinae is considered the most phyletically distinct group of the Liabae. The subtribe consists of four genera that seem to be the opposite of the *Paranephelius* group in a number of important characters: the anthers are usually black, the style branches are almost always less than half as long as the hispidulous part of the style shaft, and the raphids in the achene wall are always quadrate. There is also a tendency in the group for long-pedunculate heads, and the group contains all members of the tribe that consistently bear single-headed scapose or long-pedunculate inflorescences. The group is readily divided into two parts, each containing two genera. *Munozia* and *Chrysactinium* have a tomentose pubescence that is characteristic of most of the tribe, both have a capillary pappus that sometimes is reduced to as few as five or 10 setae, and both have eight to 10 ribs on the achene as found in most Liabae. The other two genera, *Erato* and *Philoglossa*, lack tomentum on the leaves, having instead long stiff hairs with enlarged bases. One of the four species of *Erato* and all five species of *Philoglossa* have a reduced noncapillary pappus, and the angles of the achene are reduced to four in *Erato* and two in *Philoglossa*.



The second most phyletically distinct group of the Liabeae is treated in this study as the subtribe Paranepheleinae, with two genera, *Paranephelius* and *Pseudonosseris*. The extreme form of the subtribe, *Paranephelius*, is a sessile rosulate herb with sessile heads. The genus occurs at higher elevations than any other in the tribe, in areas subjected to snow fall. The distinct nature of the subtribe is less evident in the related genus *Pseudonosseris* occurring at lower elevations, having a branching inflorescence and a short-caulescent habit that is paralleled in other members of the tribe such as *Liabellum* and *Microliabum*. *Pseudonosseris* differs from *Paranephelius* by the noncoiled style branches of the ray flowers and by the lack of high ridges on the receptacle between the areolae. The rather large achenes with broadly sclerotized ribs tend to relate the two genera, even though there is no reason to suppose that those of *Pseudonosseris* have the longer viability that is suspected for *Paranephelius*. The style branches are elongate in both genera, and the raphids in the walls of the achenes are also long, but neither character is unique to the group, only the combination of the two characters. The best confirmation of relationship of the two genera seems to be in the details of the pollen-wall structure, neither genus having large baculae such as are seen in most other members of the tribe and in most members of the subfamily (Robinson and Marticorena, in prep.).

The combinations of characteristics in the previous two groups have led to their recognition as distinct subtribes in the present treatment. The remaining genera of the tribe are treated herein in a single subtribe, but, nevertheless, considerable diversity is involved. Many, but not all, members are notable for short tails or fringes on the bases of the anther thecae, a trait not found in the Munnoziinae or Paranepheleinae.

The subtribe Liabinae can be broken down for purposes of discussion into four generic pairs plus one other individually distinctive genus. The first pair, *Liabum-Oligactis*, is distinct from the others by the elongate branches of the disk styles and by the quadrate raphids of the achene wall. The

elongate style branches are the only feature the group has in common with the Paranepheleinae, and they are probably of separate origin. Similarly, the subquadrate raphids of the achene wall do not seem to relate directly to those of the Munnoziinae. The generic pair apparently consistently lacks latex.

If the differentiated minute mucros on the teeth of the pappus are any indication, *Liabum* and *Oligactis* are probably closest to *Chionopappus*, which has such points on the rays of the plumose pappus segments; however, *Chionopappus* otherwise is a very unlikely relative, having a reduced number of pappus segments in one series, elongate raphids in the achene wall, shorter branches on the disk styles, and the only examples of true paleae on the receptacle in the tribe. The reddish disk flowers of *Chionopappus* are also rather distinctive, being unlike any other member of the subtribe Liabinae but similar to one species of *Philoglossa* in the more distantly related Munnoziinae.

The combination of shorter style branches in the disk flowers and longer raphids in the achene wall, as seen in *Chionopappus*, also are seen in the remaining three generic pairs in the subtribe. The generic pair *Sinclairia-Liabellum* is notable for its distribution in the Mexican and Central American region, for its elongate, somewhat lobed nectaries, and for the only discoid heads in the tribe. The two genera, however, show marked differences, the former being larger, often scandent plants, and the latter being a small herb with a basal tuber. The latter also has the most dissected leaves in the tribe. In contrast, the genera *Austroliabum* and *Microliabum* are the southernmost element of the tribe having achenes with prominent ribs on which the pubescence appears distinctive and having a fragile inner pappus series. *Microliabum* is distinct by its extremely reduced size and a unique form of broad inner pappus segments.

The final pair of genera in the Liabinae, *Cacosmia* and *Ferreyranthus*, provides the most significant insight into the evolution of the subtribe. The genera are similar in habit, leaf texture, and nodal sheaths, but *Cacosmia*, as indicated under

the genus, differs in many details of head structure, achenes, and leaf venation. Most significantly, the endothelial cells of *Cacosmia* have shields showing the cell limits, with scattered thickenings and variable annulations, whereas those of *Ferreyranthus* have more specialized strap-shaped shields with few thickenings at the upper and lower ends. In *Cacosmia* the anthers are not noticeably tailed, and latex has been recorded from the stems of some specimens. In *Ferreyranthus* the anthers have the most highly developed tails in the tribe, and the tests for latex are all negative. The general characterization of *Ferreyranthus* is consistent with the broad generic relationship including *Liabum*, *Oligactis*, and *Chionopappus*, whereas *Cacosmia* does not fit this group. Actually, *Cacosmia* shows characteristics such as the endothelial cells that suggest that it diverged from the base of the subtribe Liabinae, even before the point of divergence of the Paranepheliinae.

The evolution of the tribe Liabae remains generally simple, but details of the Liabinae as represented by *Cacosmia*, *Ferreyranthus*, *Chionopappus*, *Oligactis*, and *Liabum* indicate some complexity. No simple phyletic scheme can be provided for these genera in which many of the characters are not in conflict. Too many assumptions of parallelism or reversion seem necessary. A solution seems to be the assumption that the past primitive Liabinae, unlike modern members of the tribe, formed an active plexus of intergeneric hybridization. Such a conclusion is not difficult to accept, considering the commonness of the phenomenon in other, more successful tribes. In this way the rather specialized raphids of the achene wall in the Munnoziinae and the *Liabum-Oligactis* generic pair can be considered of common origin, also the tailed anther bases and lack of latex in the typical element of the subtribe Liabinae, and the specialized endothelial cells of some Liabinae and Munnoziinae. Even the woody habits and bullate leaf surfaces of *Cacosmia* and *Ferreyranthus* might have a remote common origin.

The probable general relationships within the Liabae are summarized by the diagram in Fig-

ure 1, where the divergent and hierarchical nature of most tribal elements is evident. The pattern seems unusual in the extent to which most of the ultimate units consist of clear generic pairs. An arrangement has been adopted here that represents the best correlation of most characters, but it is notable that no single characteristic completely follows the pattern.

### Description of the Tribe Liabae

Tribe VERNONIEAE sect. LIABAE Cassini, Dict. Sci. Nat., 57:338, 1828.

Tribe VERNONIEAE subtribe LIABINAE Lessing, Linnaea, 6:696, 1831.

Tribe SENECEONEAE subtribe LIABINAE Bentham in Bentham and J.D. Hooker, Genera Plantarum, 2:207, 1873.

Tribe LIABAE Rydberg, N. Amer. Fl., 34(4):289, 1927.—H. Robinson and Brettell, Phytologia, 25(6):405, 1973.

Mostly perennial herbs and subshrubs, sometimes scandent; annuals in *Microliabum* and some *Munnozia* subgenus *Kastnera*; shrubs or small trees in *Cacosmia* and *Ferreyranthus*. Roots usually not specialized, but *Liabellum* with underground tuber, *Paranephelium* often with prominent fusiform lateral roots. Latex usually present, consistently lacking only in *Liabum*, *Oligactis*, and *Ferreyranthus*. Tomentum usually present on at least undersurfaces of leaves, often on both leaf surfaces, stems, and involucre. *Erato* and *Philoglossa* with stiff hairs having enlarged bases on leaves, stems, and involucre, and without tomentum except sometimes on tips of involucral bracts.

Leaves opposite or congested in rosette, usually petiolate or with petioliform base, rarely sessile; leaf bases often with stipule-like wing or nodal disk, sometimes fused into sheath; leaf blades linear to broadly triangular with pinnate or trinervate venation. Inflorescence simple or subcymose, sometimes forming a pyramidal panicle, scapose or subscapose from a short leafy stem in *Chrysactinium*, some *Pseudonosseris*, *Liabellum*, *Microliabum*, and some *Liabum*; inflorescence most often open with few long peduncles in Munnoziinae.

Heads never compound or forming complexes. Involucre usually subimbricate with bracts in many graduated series, subequal with somewhat

foliose outer bracts in some Munnoziinae. Receptacle alveolate, often with projecting crests or points, with true paleae in *Chionopappus*. Ray flowers usually present, 3–230, lacking in *Liabulum* and some *Sinclairia*. Disk flowers 3–150, bisexual. Corollas usually yellow, ray and disk flowers reddish in *Pseudonosseris szyszyłowiczii*, disk flowers purple in *Chionopappus benthamii*, *Philoglossa purpureodisca*, and some *P. peruwiana*, and ray and disk flowers whitish or tardily lavender in many *Munnozia jussieu* and *M. campii*.

Ray flowers in 1 to many series, always fertile with no anthers; limb always present, usually rather narrow; adaxial cells elongate and non-papillose; cuticle often smooth, with longitudinal ridges in *Austroliabum* and longitudinal striation in *Munnozia* (Baagøe, 1978); achenes not differentiated from those of disk flowers. Disk corollas usually narrowly funnellform, throat somewhat to distinctly expanded at base in most Munnozinae and some *Oligactis*; corolla surfaces smooth, the cells elongate with sinuous lateral walls; lobes elongate, usually linear, usually with stomates along margin, lacking stomates in *Cacosmia* and *Oligactis*, and with stomates rare or lacking in *Liabum*; pubescence often of *Hieraceum*-type with long broad bases and small glandular tips; lobe tips sometimes with multiseriate spicules or crests. Filaments usually smooth in lower part, papillose in *Ferreyranthus verbascifolius*; anther collar mostly with short-oblong cells, with walls usually unornamented, walls ornamented with annular thickenings in *Chrysactinium*; thecae usually pale, blackened in all Munnoziinae except *Munnozia hastifolia* and 2 related species, bases of thecae calcarate, extending well below point of insertion on collar, bases broad and unfringed in Munnoziinae, more or less fringed in many Liabinae, fringed and coiled in *Ferreyranthus verbascifolius*; endothelial cells often elongate with noncontiguous sclerified shields and polarized thickenings on transverse walls, short with more lateral thickenings in many Munnoziinae and *Cacosmia*; anther appendage thin, longer than wide, not constricted at base, not keeled, usually smooth, papillose in *Oligactis* subgenus *Oligactis*. Nectary cylindrical, truncate

in *Chionopappus*, *Cacosmia*, and *Ferreyranthus*, sometimes elongate with upward projecting lobes as in *Sinclairia*. Style base glabrous, usually with evident enlargement; upper style shaft and backs of branches covered with hairs; branches with stigmatic papillae over entire inside surface, with little or no appendage; style branches of rays elongate and sometimes spiralled as in *Paranephelius*; branches of disk flowers short (less than 1/3 to 1/4 as long as hispidulous upper style shaft) and blunt in Munnoziinae and such genera as *Chionopappus*, elongate in such genera as *Liabum* and *Ferreyranthus*, noticeably tapered only in *Pseudonosseris*.

Achenes usually prismatic or subterete with 5–10 ribs, 4-ribbed in *Erato*, compressed with 2 ribs in *Philoglossa*, long-fusiform in *Paranephelius*; surface with stiff twin-hairs and/or glands, with some arachnoid hairs in *Paranephelius*; cells of achene wall with raphids, raphids usually elongate, subquadrate in *Liabum*, *Oligactis*, and the Munnoziinae; carpopodium disciform, annuliform, stopper-shaped, or cylindrical, symmetrical or nearly so, usually with small cells in 5–10 series, sometimes with moderate sized cells in 2–5 series, cell walls densely beaded to moderately thickened. Achene viability apparently usually short, probably longer in *Paranephelius*.

Pappus usually with numerous long capillary bristles in inner series and with a short outer series, inner series of reduced number, and squamellae of outer series broad in some *Munnozia* subgenus *Kastnera* and in *Austroliabum*, latter also with inner series easily deciduous, inner series of lamelliform segments similar in breadth to outer squamellae in *Microliabum*, pappus of 5 plumose bristles in single series in *Chionopappus*, reduced to short deciduous awns in *Erato sodiroi* and *Philoglossa mimuloides*, a pair of short awns connected by a series of squamellae in *P. purpureodisca*, totally lacking in *Cacosmia* and 2 *Philoglossa* species; pappus bristles white in *Chrysactinium* but sordid or darker in *Munnozia*; scabridulae or lateral hairs with minute structurally differentiated mucro in *Liabum*, *Oligactis*, and *Chionopappus*.

Pollen 25–50  $\mu\text{m}$  in diameter, spinose, spines

regularly to somewhat irregularly arranged, never lophate, large baculae usually present and grouped or with a central cavity under each spine, cavus variously developed in *Paranepheliinae*, *Philoglossa*, and *Munnozia*.

A few characters provide special problems of interpretation. Latex production often seems erratic. Greenhouse specimens of *Erato polymnioides* usually show some latex, but the amount varies depending on available water and time of day. Some weaker tests might not have been recognized as latex in the field. A plant tested at night showed no latex.

The upper surface of the leaf blades often bears a coarse pilosity that has frequently been used as a taxonomic character. Unfortunately, the character varies within species in many genera such as *Munnozia* and *Chrysactinium* and varies between closely related species in *Liabum*.

The receptacle has true paleae in only *Chionopappus*. In other genera the projections and crests in the same positions are unarticulated outgrowths. The latter are particularly prominent in *Munnozia*, being one of the characters originally cited by Ruiz and Pavon (1794), but the receptacles of *Munnozia* subgenus *Kastnera* completely lack crests. The length of the crests or chaff is of taxonomic value in *Chrysactinium* but is difficult

to use, since the heads are often solitary and cannot be dissected without destroying a herbarium specimen.

Many specialized features of the tribe have occurred more than once. The pappus has been lost in both *Philoglossa* in the *Munnoziinae* and *Cacosmia* in the *Liabinae*. Scandent habits are found in two separate genera of the *Liabinae*, *Oligactis* of the northern Andes and *Sinclairia* of Mexico and Central America. Reduced habits with basal leaves and a scapose inflorescence have evolved many separate times, in *Liabellum* in the *Sinclairia* relationship, in *Microliabum* in the *Austroliabum* relationship, to some extent in *Liabum*, all in the *Liabinae*, in *Chrysactinium* in the *Munnoziinae*, and in *Pseudonosseris* in the *Paranepheliinae*. These and other characters reviewed above are regarded as evidence of a complex evolution with marked phyletic gaps. This contrasts to the superficial appearance of a continuum that led Bentham (1873) to place most members of the tribe in a single genus, *Liabum*.

### Keys to the Genera of the Liabae

Two keys to the genera of the tribe are provided. The first key is based on more obvious characters and is highly artificial. The second key is based on more technical characters and is in some parts phyletic.

#### Artificial Key to the Genera of the Liabae

1. Heads sessile in a basal rosette of leaves; style branches of ray flowers spiralled; plants at higher elevations in the central Andes ..... ***Paranephelius***
1. Heads short- to long-pedunculate, not sessile in basal rosette of leaves, style branches usually evenly curved, rarely spiralled ..... 2
  2. Leaves not tomentose, hairs of leaves and stems stiff, with enlarged bases ..... 3
    3. Small, mostly decumbent herbs; leaf blades trinervate at base; achenes compressed, with 2 ribs; pappus reduced or lacking ..... ***Philoglossa***
    3. Robust erect herbs or subshrubs; leaf blades with 5–9 veins radiating from base; achenes mostly 4-angled; pappus of many awns or bristles ..... ***Erato***
  2. Leaves usually tomentose, at least on undersurface; hairs not stiff with enlarged bases ..... 4
    4. Pappus lacking ..... ***Cacosmia***
    4. Pappus present ..... 5
      5. Pappus bristles plumose; receptacle with long narrow strap-shaped paleae; flowers of disk red or purple and rays yellow ..... ***Chionopappus***

- 5. Pappus setae not plumose; receptacle without paleae, with or without crests or spines; disk flowers not reddish and rays yellow ..... 6
- 6. Inner and outer series of pappus both broadened and flattened; minute plants to 10 cm high ..... **Microliabum**
- 6. At least the inner pappus setiform; larger plants over 10 cm high ..... 7
  - 7. Anther thecae usually blackish; style branches of disk flower less than 1/3 as long as hispidulous upper part of shaft ..... 8
    - 8. Pappus white; cells of anther collar with walls obscured by annular thickenings; scapose plants with leaves rosulate or on short stems; latex absent? ..... **Chrysactinium**
    - 8. Pappus sordid or colored; cells of anther collar not obscured by annular thickenings; plants usually with elongate leafy stems; latex present ..... **Munnozia**
  - 7. Anther thecae pale; style branches of disk flowers often 1/2 as long as hispidulous upper part of shaft or longer ..... 9
    - 9. Inflorescence with all bracts or with all but the basal bracts and branches subopposite or alternate; receptacle scarcely alveolate, without hairs, chaff, or projections ..... 10
      - 10. Plants with short or rosulate leafy stems; leaf venation essentially pinnate; pollen caveate ..... **Pseudonosseris**
      - 10. Plants with prominent erect leafy stems, primary leaves strongly trinervate; pollen not caveate ..... **Austroliabum**
    - 9. Inflorescence with all or at least primary bracts and branching opposite; receptacle with minute hairs or chaff or projections ..... 11
      - 11. Leaves with pinnate venation; achenes bearing both glands and setulae ..... 12
        - 12. Scandent shrubs; leaf bases not stipulate or with only an adjacent lobe on node; raphids in achene walls quadrate; tips of cells of pappus teeth differentiated in thin-walled mucro ..... **Oligactis**
        - 12. Shrubs and small trees; leaf bases with stipules fused into small sheath; raphids in achene walls elongate; tips of cells of pappus teeth not differentiated ..... **Ferreyranthus**
  - 11. Leaves trinervate; achenes with setulae, with or without glands .. 13
    - 13. Small, few-headed plants with underground tuber; leaves usually deeply palmately or subpinnately lobed; ray flowers lacking ..... **Liabellum**
    - 13. Small to large herbs or vines, without underground tuber; ray flowers present or absent ..... 14
      - 14. Leaf bases sagittate ..... **Munnozia hastifolia** group
      - 14. Leaf bases cuneate or rounded ..... 15
        - 15. Petiole bases and nodes without wings or lobes, leaves sometimes in whorls of 3 or more; stems usually not white-tomentose, mostly terete; latex present; inflorescence in thyrsoid or corymbose panicle; ray flowers sometimes lacking; achenes with

- elongate raphids in walls; tips of teeth of pappus setae not differentiated; pollen grains 35–50  $\mu\text{m}$  in diameter ..... ***Sinclairia***
15. Petiole bases or nodes with wings or lobes, leaves always opposite; stems usually white-tomentose or flocculose pubescent; latex absent; inflorescence a cymose or subumbellate panicle; ray flowers always present; achenes with subquadrate raphids in walls; tips of teeth of pappus setae with thin-walled mucro; pollen grains 25–35  $\mu\text{m}$  in diameter ..... ***Liabum***

### Technical Key to the Genera of the Liabae

1. Cells of achene wall with subquadrate raphids; anthers with or without black thecae ..... 2
2. Anther thecae pale, with bases bearing teeth or projecting cells; pappus with tips of projecting cells bearing a minute thin-walled mucro; lobes of disk corollas without evident stomata; shaft of disk style with hispidulous part less than twice as long as style branches; plants without latex ..... 3
3. Small to large herbs, rarely scandent; leaves slightly to strongly trinervate; inflorescence cymose or subcymose; achenes with only setulae and no glands; style with hairs often scarcely extending onto upper part of shaft ..... ***Liabum***
3. Scandent shrubs; leaves pinnately veined; inflorescence a corymbose or thyrsoid panicle; achene with glands and setulae; style with hairs distinctly extending onto upper part of upper shaft ..... ***Oligactis***
2. Anther thecae usually blackish, with bases not bearing teeth or projecting cells; pappus with tips of projecting cells not specialized; lobes of disk corollas with stomata; shaft of disk style with hispidulous upper part usually twice as long as branches or longer; plants often with latex ..... 4
4. Leaves not tomentose, hairs of leaves and stems stiff, with enlarged bases ..... 5
5. Small mostly decumbent herbs; leaf blades trinervate at base; achenes compressed with 2 ribs; pappus reduced or lacking ..... ***Philoglossa***
5. Robust erect herbs or subshrubs; leaf blades with 5–9 veins radiating from base; achenes mostly 4-angled; pappus of many awns or setae ..... ***Erato***
4. Leaves usually tomentose below; hairs not stiff with enlarged bases ..... 6
6. Pappus white; cells of anther collar with walls obscured by annular thickenings; scapose plants with leaves rosulate or on short stems; inflorescence of single heads on very long unbranched peduncles; disk corolla lobes with nearly sessile glands scattered over outer surface, without longer glands or hairs; latex absent? ..... ***Chrysactinium***
6. Pappus sordid or colored; cells of anther collar not obscured by annular thickenings; plants small to robust herbs with distinct leafy stems, usually with branching inflorescence; disk corolla lobes usually with elongate hairs or glands near tips; latex present ..... ***Munnozia***
1. Cells of achene wall with elongate raphids; anthers with thecae never black ..... 7
7. Branches of disk style filiform, longer than the hirtellous upper part of the shaft; tube of disk corolla longer than the limb; plant small with leaves congested on short stems or in rosette; leaf venation pinnate or weakly trinervate ..... 8

- 8. Heads sessile in basal rosette of leaves; style branches of ray flowers spirally contorted; pappus outer series of irregularly shorter setae, not sharply differentiated; plants with or without latex ..... **Paranephelius**
- 8. Heads raised in unbranched or alternately branched inflorescence above a short but distinct leafy stem; style branches of ray flowers not spirally contorted; pappus with outer series of distinct short squamellae; plants with latex ..... **Pseudonosseris**
- 7. Branches of disk style narrowly oblong to linear, shorter than the hirtellous upper part of the shaft; tube of disk corolla shorter than limb; plant small to large, never a sessile rosette; leaf venation pinnate to strongly trinervate ..... 9
- 9. Pappus of 8–10 plumose setae; heads with yellow rays and purple disk flowers; receptacle with long slender paleae ..... **Chionopappus**
- 9. Pappus without plumose setae, sometimes absent; heads with all flowers yellow; receptacle without paleae, sometimes with short crests or projections ..... 10
- 10. Woody shrubs or small trees of the northern Andes; leaves usually with bullate upper surfaces, with petiole bases of leaf pair fused into a sheath; involucre bracts closely and regularly multiseriate ..... 11
- 11. Pappus lacking; achenes glabrous, 4–5-angled; leaves trinervate with strongly ascending secondary veins; heads cylindrical with ~10 flowers ..... **Cacosmia**
- 11. Pappus present, with capillary setae; achenes setuliferous or glanduliferous, 10-ribbed; leaves pinnately veined; heads campanulate with 20–35 flowers ..... **Ferreyranthus**
- 10. Herbs or vines; leaves without obvious bullate upper surfaces, with bases of petioles rarely forming a sheath; involucre bracts usually in few or irregular series ..... 12
- 12. Plants of Argentina and Bolivia; inner pappus easily deciduous; pubescence of achene usually different on ribs; ray flowers always present; branching of inflorescence mostly or entirely alternate ..... 13
- 13. Minute herbs of higher elevations; inner pappus of broad laminate segments ..... **Microliabum**
- 13. Coarse herbs of medium elevations; inner pappus of capillary elements ..... **Austroliabum**
- 12. Plants of Mexico and Central America; inner pappus moderately persistent; pubescence of achene not different along ribs; ray flowers often lacking; branching of inflorescence often opposite ..... 14
- 14. Leaves sessile or winged to base, usually palmately lobed; small herbs with basal tuber; style with broad often nodular base ..... **Liabellum**
- 14. Leaves petiolate, without wings or stipules, not lobed; plants often large or scandent, without basal tuber; style with narrow base ..... **Sinclairia**

**The Subtribes and Genera of the Liabeae**

The present treatment recognizes three subtribes and 15 genera in the Liabeae, which are arranged as follows: subtribe Liabinae containing *Austroliabum*, *Cacosmia*, *Chionopappus*, *Ferreyranthus*, *Liabellum*, *Liabum*, *Microliabum*, *Oligactis*, and *Sinclairia*; subtribe Paranepheleinae containing *Para-*

*nephelius* and *Pseudonosseris*; and subtribe Munnoziinae containing *Chrysactinium*, *Erato*, *Munnozia*, and *Philoglossa*.

**Subtribe LIABINAE**

Annuals, perennial herbs, vines, shrubs, or small trees; leaves mostly ovate to linear, rarely

with angulate margins, pinnately or trinervately veined. Heads in cymose, corymbose, or subumbellate panicles; disk corollas with bases of throats usually not abruptly expanded; anthers pale, thecae often with lobes or teeth at base; shields of endothelial cells usually not contiguous, usually with thickenings polarized on transverse walls; style branches short to elongate; raphids of achene wall quadrate to elongate. Pollen grains with spines somewhat irregularly disposed, spines with small to large columellae that are hollow or in groups.

The subtribe contains the majority of the genera and species of the Liabeae and has the widest geographical distribution, reaching from Mexico and the West Indies in the north to Argentina in the south. The nine genera are as follows.

### *Austroliabum*

#### FIGURE 2

*Austroliabum* H. Robinson and R.D. Brettell, *Phytologia*, 28(1):48, 1974. [Type-species: *Liabum candidum* Grisebach.]

Perennial herbs or subshrubs, with milky sap. Leaves opposite, becoming alternate in inflorescence, distinctly petiolate, petioles winged or stipitate at the base; blade triangular to lanceolate, trinervate at the base, margin serrate to dentate, white-tomentose below and sometimes on both surfaces. Inflorescence mostly cymose, alternately branched at least above, pedicels often elongate. Heads broadly campanulate; involucre bracts 50–75 in ~3–4 series, unequal to subequal, narrowly oblong to lanceolate, inner bracts narrowly attenuate, often densely covered with long-stipitate glands on outer surface, sometimes white-tomentose; receptacle essentially glabrous. Flowers yellow. Ray flowers 20–30 in 1–2 series, corolla with tube slender, hirsute, limbs linear with few, sparse, nonglandular, biseriate hairs; style branches elongate, not spiralled. Disk flowers 30–175, corolla narrowly funnelform, not abruptly expanded at base of throat, tube narrow, tube and most of throat sparsely hirsute; lobes with

stomates along margins, mostly glabrous, with some hairs distally; filament smooth or papillose, walls of cells of anther collars not strongly annulated; anther thecae pale, long and narrowly tapering at base with a few projecting cells, scarcely tailed, median endothelial cells oblong, thickened shields noncontiguous, oval or linear, irregularly ornate, attenuate and uncinately with 1–3 points at lower end, appendages long-ovate, 1½–2 times as long as wide, smooth, cells shortly oblong with truncate to somewhat oblique end-walls; nectary short, not or scarcely lobed, often obscure; style base with large, distinct, abrupt node; style branches slender, less than 1/2 as long as the hispidulous portion of the shaft. Achenes prismatic, obovate, distinctly narrowed below, strongly costate with ~10 ribs, densely setiferous on the ribs and often also in the furrows; cells of the achene walls with elongate raphids; carpodium narrow rim of ~3–5 rows of rather small subquadrate cells, cell walls slightly thickened, porose; pappus with 20–30 rather easily deciduous inner setae in 1 series, teeth of setae simple, shortly and stiffly spreading; pappus outer series of slightly to distinctly squamiform small to large elements. Pollen grains 35–45 μm in diameter, spines unevenly disposed, with distinct internal columellae.

*Austroliabum* and the related *Microliabum* together form the southernmost element of the tribe. The former genus occurs along the eastern slopes of the Andes in the area from central Bolivia into northern Argentina. The northern limit is near Santa Cruz, where the escarpment of the Andes turns westward and tends to shelter a more tropical flora. As such, the northernmost limit of *Austroliabum* scarcely reaches the southernmost limits of the large Andean genera *Liabum* and *Munozia*.

The genus *Austroliabum* differs from both *Liabum* and *Munozia* by the elongate raphids in the cells of the achene wall. The elongate raphid form is shared with other genera of the Liabeae such as *Chionopappus*, *Cacosmia*, *Ferreyranthus*, *Pseudonosoris*, and *Paranephelium* of the Andes and the distant *Sinclairia* of Central America. *Austroliabum* also has



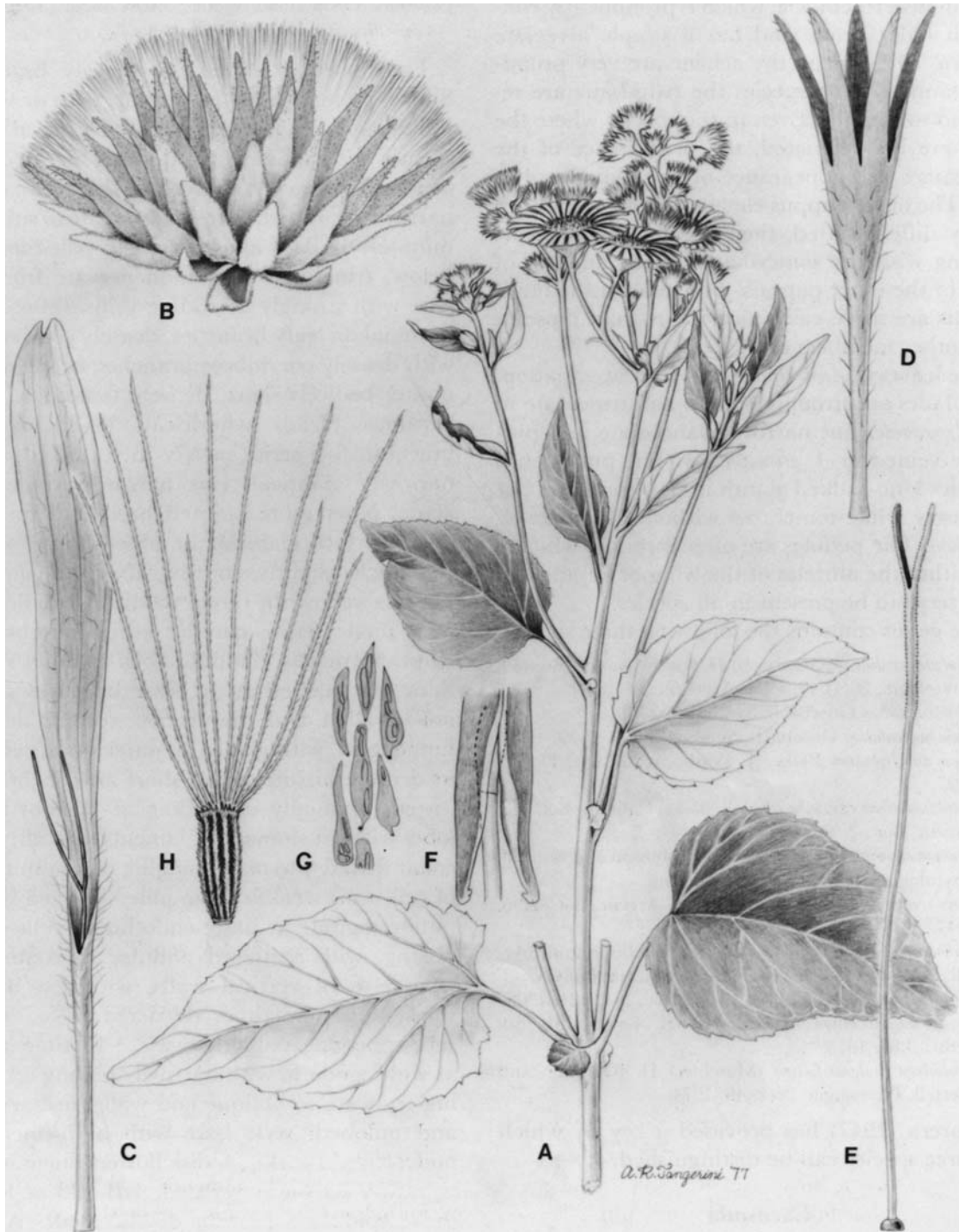


FIGURE 2.—*Austroliabum candidum* (Grisebach) Robinson & Brettell: A, habit,  $\times \frac{1}{2}$ ; B, head, post anthesis,  $\times 4$ ; C, ray corolla,  $\times 8$ ; D, disk corolla,  $\times 8$ ; E, disk style,  $\times 8$ ; F, bases of anther thecae,  $\times 35$ ; G, median endothelial cells;  $\times 400$ ; H, achene,  $\times 8$ .

a distinctive receptacle, which is prominently convex in older heads and has a simple alveolate pattern. The ribs on the achene are very prominent, and in some species the twin-hairs are restricted to the ribs. Even in the species where the hairs are not restricted, the prominence of the ribs causes the appearance of unequal distribution. The outer pappus elements of all species are highly differentiated, their greater breadth correlating with the somewhat reduced number of setae in the inner pappus. The setae of the inner pappus are more easily deciduous than those in most other members of the tribe.

The leaves of *Austroliabum* show great variation. The blades are strongly deltoid and trinervate in *A. polymnioides* but narrowly lanceolate and pinnately veined in *A. eremophilum*. The pubescence includes long-stalked glands in *A. polymnioides* but is densely white-tomentose without glands in *A. candidum*. The petioles are often strongly winged, and either the auricles of the wing or stipule-like lobes seem to be present in all species.

The genus contains the following three species.

- Austroliabum candidum* (Grisebach) H. Robinson and Brettell. *Phytologia*, 28(1):49, 1974. Argentina.  
*Liabum candidum* Grisebach. *Symbolae*, 203, 1879.  
*Liabum auriculatum* Grisebach, *Symbolae*, 203, 1879.  
*Liabum subcirrhosum* Blake, *J. Wash. Acad. Sci.*, 17:293, 1927.  
*Liabum candidum* var. *subcirrhosum* (Blake) Cabrera, *Bol. Soc. Argent. Bot.*, 2:95, 1947.  
*Austroliabum eremophilum* (Cabrera) H. Robinson and Brettell. *Phytologia*, 28(1):49, 1974. Argentina.  
*Liabum eremophilum* Cabrera, *Bol. Soc. Argent. Bot.*, 2:96, 1947.  
*Austroliabum polymnioides* (R.E. Fries) H. Robinson and Brettell. *Phytologia*, 28(1):49, 1974. Argentina. Bolivia.  
*Liabum polymnioides* R.E. Fries, *Arkiv Bot.*, 5(13):24, 1906.  
*Liabum mulgediifolium* Muschler, *Engl. Bot. Jahrb.*, 50, Beibl., 3:85, 1913.  
*Austroliabum mulgediifolium* (Muschler) H. Robinson and Brettell. *Phytologia*, 28(1):49, 1974.

Cabrera (1947) has provided a key by which the three species can be distinguished.

### **Cacosmia**

#### FIGURE 3

*Cacosmia* Humboldt, Bonpland, and Kunth, *Nov. Gen. et Sp.*, ed. fol. 4:227, 1818. [Type-species: *Cacosmia rugosa* Humboldt, Bonpland, and Kunth; originally monotypic.]

*Clairvillea* DeCandolle, *Prodr.*, 5:636, 1836. [Type-species: *Clairvillea quinquenervia* DeCandolle.]

Erect shrubs, sometimes densely branching. Stems terete, densely pubescent, with or without milky sap. Leaves opposite, bases fused into a sheath, with petioles or subsessile; blades oblong-ovate to narrowly lanceolate, base broadly to narrowly rounded, margins serrulate to subentire, minutely bullate above, densely pale-tomentose below, trinervate or quinquenervate from near base with strongly ascending veins. Inflorescence terminal on leafy branches, densely corymbose or with densely corymbose branches, branching opposite; pedicels short, densely tomentose to puberulous. Heads cylindrical; 20–25 involucre bracts in 5–6 series mostly in 5 ranks, ovate to narrowly elliptical, tips narrowly rounded to acute, inner more pointed bracts not in ranks, outer surface glabrous or obscurely pubescent; receptacle slightly convex, alveolate, glabrous. Flowers yellowish, rarely whitish. Ray flowers 5 in a single series; corolla narrow; limbs short, elliptical, mostly glanduliferous on outer surface, minutely trilobed at tip, style branches slender, not spiralled. Disk flowers 5–6; corollas narrowly funnelliform, with glands on outer surface, slightly to densely hirsute, tubes short and slightly narrowed, gradually expanding at base of throat; lobes without stomates; filaments smooth; anther collar with few to many bulging cells, annulations of cell walls weak; thecae pale, untailed but minutely digitate at base; endothecial cells shortly oblong, with scattered nodular thickenings on transverse or vertical walls, with few annular thickenings sometimes restricted to one end of cell; appendages oblong-ovate, ~1½ times as long as wide, smooth, with narrowly oblong cells having truncate to oblique end walls; nectary short and unlobed; style base with a distinct large node; style branches of disk flowers linear, shortly to rather narrowly pointed, 1/3–2/3 as long as the hispidulous portion of the shaft. Achenes prismatic, outer sometimes subtriquetrous, inner with 4–5 angles, faintly costate, 8–10-veined, glabrous, walls of achene with elongate raphids; carpodium indistinct, born on abruptly nar-

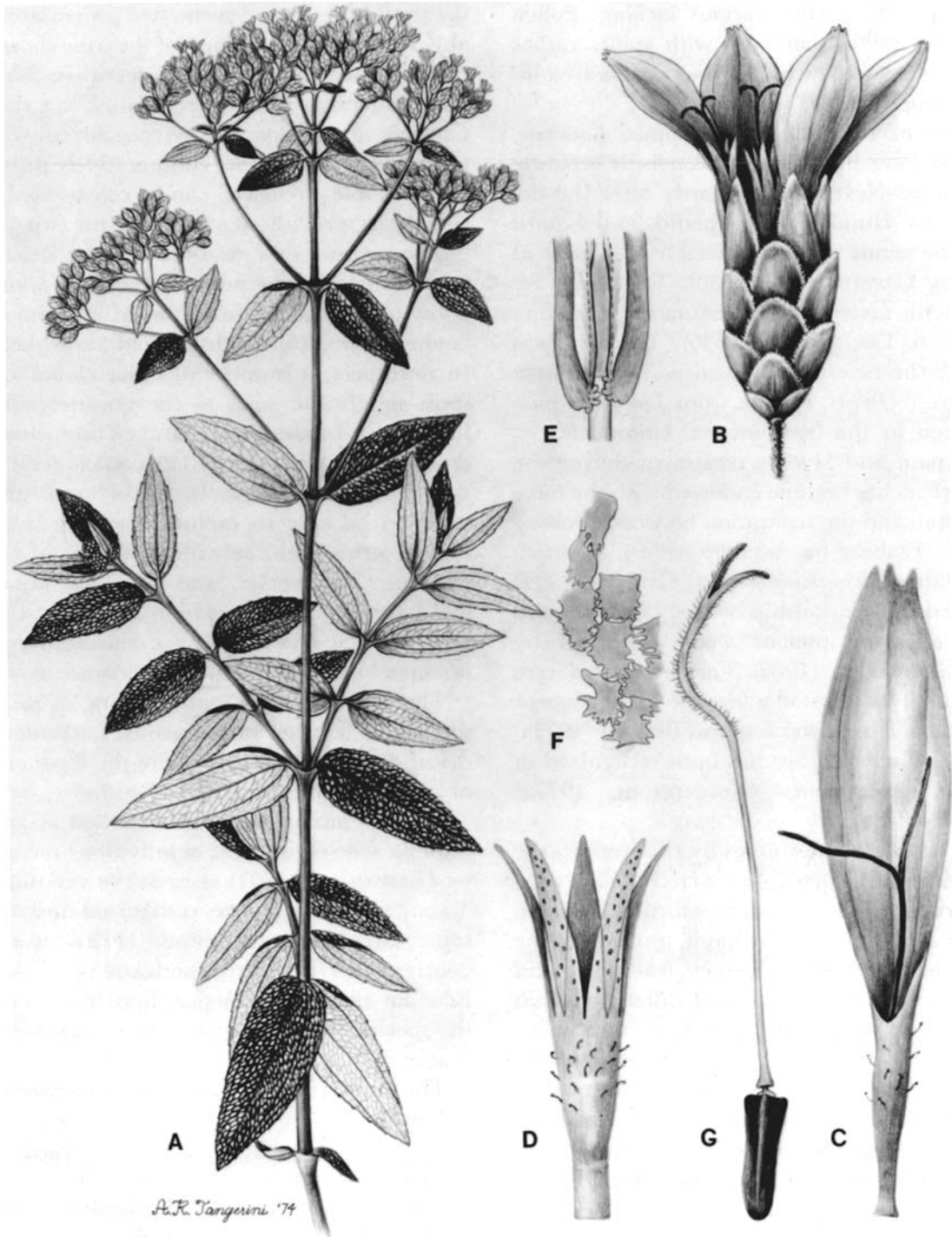


FIGURE 3.—*Cacosmia rugosa* Humboldt, Bonpland, and Kunth: A, habit,  $\times \frac{1}{2}$ ; B, head with 1 ray removed,  $\times 10$ ; C, ray corolla,  $\times 10$ ; D, disk corolla,  $\times 10$ ; E, bases of anther thecae,  $\times 35$ ; F, median endothelial cells,  $\times 400$ ; G, disk achene with style,  $\times 10$ .

rowed base of achene; pappus lacking. Pollen grains  $\sim 30 \mu\text{m}$  in diameter, with spines rather unevenly dispersed, with distinct internal columellae grouped under spines.

Because of the lack of a pappus, *Cacosmia*, during its long history, has been kept separate from *Liabum*. Nevertheless, shortly after the description by Humboldt, Bonpland, and Kunth (1818), the genus was recognized as a relative of *Liabum* by Cassini (1825, 1830). The genus remained with *Liabum* in the treatments of Lessing (1832) and DeCandolle (1836). *Cacosmia* was placed in the new tribe Helenieae by Bentham and Hooker (1873), remote from *Liabum*, which was placed in the Senecioneae. Unfortunately, the Bentham and Hooker treatment during the last 100 years has become endowed with the force of tradition, and the separation between *Cacosmia* and other Liabeae has become widely accepted. Still, isolated authorities such as Cabrera (1954) recognized the relationship between *Cacosmia* and *Liabum*, and the pollens were compared by Skvarla and Turner (1966). The two genera were more formally associated under the tribal concept of the Liabeae by Robinson and Brettell (1973a, 1974b). The relationship has been recognized in all recent treatments (Nordenstam, 1977a; Robinson, 1978a).

During most of the studies by this author, the genus *Cacosmia* has been considered a close relative of *Ferreyranthus* of the same subtribe. The two genera share a more woody habit, a sheath at the node formed of the fused paired leaf bases, and bullate upper leaf surfaces. Some differences such as the lack of pappus in *Cacosmia* seem obvious but would not necessarily bar close relationship. The consistently pinnate venation of *Ferreyranthus* contrasts totally with the nearly longitudinal 3–5 veins in *Cacosmia*, but some variation between pinnate and trinervate venation is seen within related groups elsewhere in the tribe, e.g., *Liabum-Oligactis*. The differences in involucre form and achene shape do present more serious considerations, and they call the closeness of relationship into question. It is the form of the thickenings in the endothelial cells, however, that indicates that

the similarities between the two genera are probably spurious. An overview of the tribe shows that the endothelial cells are a conservative character of considerable phyletic reliability, yet those of *Cacosmia* are comparatively specialized, whereas those of *Ferreyranthus* are comparatively primitive. No workable phylogeny can be constructed using this character without separating the two genera.

The present view would derive *Cacosmia* from near the base of the subtribe Liabinae above the point of divergence from the Munnoziinae but before the point of origin of the Paranepheliinae. In retrospect, a number of other characteristics seem significant, such as the minutely digitate but untailed bases on the anther thecae and the documented presence of latex in at least some specimens of *Cacosmia*. It makes more phyletic sense to be able to exclude *Cacosmia* from the typical series in the subtribe Liabinae of *Liabum*, *Oligactis*, *Ferreyranthus*, and *Chionopappus*, which will have some tail formation on the base of the anther thecae and which have consistently shown no latex in those for which reports are available.

The involucre of *Cacosmia* is one of the most distinctive features of the genus. Both the cylindrical shape and the ranking of the median series of bracts are unique in the tribe.

*Cacosmia* has usually been regarded as containing one species, and the subdivisions recognized by Hieronymus (1901) were at the varietal level. Two new species were recognized recently in rapid succession by Robinson (1976a) and Nordenstam (1977b). All the species occur in southern Ecuador near the Peruvian border, and two of the species are nearly to completely restricted to that area.

The three presently recognized species are as follows.

- Cacosmia harlingii* Nordenstam, Bot. Notiser, 130:283, 1977. Ecuador.
- Cacosmia hieronymi* H. Robinson, Phytologia, 34(1):46, 1976. Ecuador.
- Cacosmia rugosa* var. *arachnoidea* Hieronymus, Engl. Bot. Jahrb., 28:619, 1901.
- Cacosmia rugosa* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp., ed. fol., 4:228, 1818. Ecuador, Peru.
- Clairvillea quinquenervia* DeCandolle, Prodr., 5:636, 1836.

*Cacosmia quinquenervia* (DeCandolle) Steudel, Nomen. Bot., ed. 2, 1:377, 1840.

*Cacosmia rugosa* var. *nivea* Hieronymus, Engl. Bot. Jahrb., 28:619, 1901.

*Cacosmia rugosa* var. *kingii* H. Robinson, Phytologia, 34(1):48, 1976.

Keys to the three species and to the three varieties of *Cacosmia rugosa* have been provided by Nordenstam (1977b) and Robinson (1978a).

### ***Chionopappus***

#### FIGURE 4

*Chionopappus* Bentham in Bentham and Hooker f., Gen. Plant., 3:485, 1873. [Lectotype: *Chionopappus benthamii* Blake; genus originally described without a named species.]

Erect shrubs, moderately branched. Stems terete with thinly evanescent arachnoid tomentum, latex not noted. Leaves opposite, bases of petiole pair fused to form short sheath, petioles very short; blade ovate, base broadly rounded to subtruncate, margins serrate to serrulate, nearly smooth above, pale-tomentose below, strongly trinervate from near base. Inflorescence with heads in groups of 3 at tips of branches, cymose; pedicels 4–50 mm long, 1 or usually 2 small foliose bracts at base of head. Heads broadly campanulate; 50–55 involucre bracts in ~5 unequal graduated series, ovate to narrowly lanceolate, tips acute to shortly acuminate, outer bracts with distinct herbaceous tips, outer surface with evanescent arachnoid pubescence; receptacle convex, with long, narrow, strap-shaped paleae. Rays yellow, ~40 in 1–2 series; base of corolla extremely narrow; limbs linear, minutely bilobed at apex, glabrous; style branches elongate, not spiralled. Disk flowers red, corollas narrowly funnellform; tubes extremely narrow, gradually expanding at base of throat, outer surface glabrous, lobes with stomates near margins; filament smooth, cells of anther collar without strong annular thickenings on walls; thecae pale, shortly tailed and minutely digitate at base; median endothelial cells oblong, with strap-shaped to oval, somewhat spirally ornamented sclerified shields, often with attenuate uncinat

tips at lower end; appendages smooth, oblong to oval, cells mostly elongate with truncate to oblique end walls; nectary short and unlobed; style base with distinct node; style branches of disk flowers less than 1/2 as long as the hispidulous upper portion of the shaft; stigmatic papillae extending far down into the styler canal. Achenes prismatic, with 8–10 ribs, with minute usually appressed setulae, walls of achene with elongate raphids; carpodium indistinct, born on abruptly narrowed base of achene; pappus of 8–10 long, plumose, persistent setae, tips of lateral hairs appearing minutely mucronate in Hoyer's solution, outer series of pappus lacking. Pollen grains 35–37  $\mu\text{m}$  in diameter, with spines rather unevenly dispersed, with distinct internal columellae grouped under spines.

*Chionopappus* was originally described by Bentham in Bentham and Hooker (1873) and was placed in the Mutisieae in spite of its opposite leaves that were nearly unique in that tribe. The plumose pappus was evidently a factor in the disposition, since plumose setae of a different detailed structure are found in the Mutisieae. The genus was stated to include a single species from Peru, but the species was not named. Blake, in 1935, was the first to name the species on which Bentham had based his genus over 50 years before, and at the same time Blake indicated the proper position of *Chionopappus* as a relative of *Liabum*. Subsequent mentions of the genus have followed the disposition of Blake (Cabrera, 1954; Robinson and Brettell, 1974b).

*Chionopappus* is unique in the Liabeae in the form of its pappus, both in the plumose condition and in the reduced number of setae in a single series. The lateral hairs of the pappus segments have the type of complex, internally differentiated tips that are seen on the pappus teeth in *Liabum* and *Oligactis*. Other peculiarities of *Chionopappus* include the reddish-purple flowers of the disk, a character once thought to be unique in the tribe, but recently the character has been found in a species of *Philoglossa*. The style has shorter branches as in most genera of the tribe, but material cleared and mounted on microscope

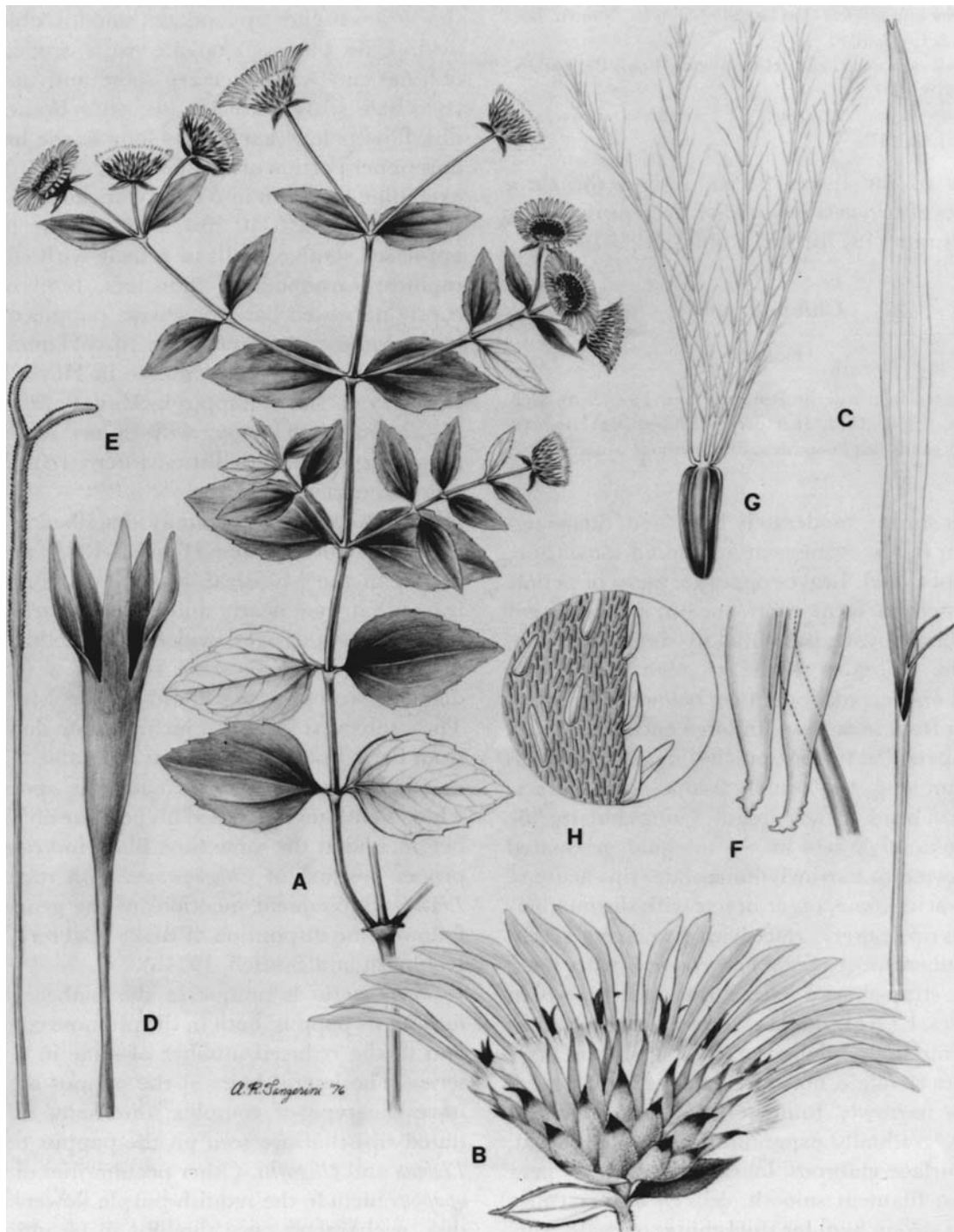


FIGURE 4.—*Chionopappus benthamii* Blake: A, habit,  $\times \frac{1}{2}$ ; B, head  $\times 2\frac{1}{2}$ ; C, ray corolla,  $\times 10$ ; D, disk corolla,  $\times 10$ ; E, disk style,  $\times 10$ ; F, bases of anther thecae,  $\times 35$ ; G, achene,  $\times 10$ ; H, achene wall showing setulae and raphids,  $\times 200$ .

slides shows that the stigmatic papillae do not stop at the base of the branches but continue well down into the stylar canal. The style branches differ from the longer forms in *Liabum* and *Oligactis* by only the fusion that persists above the lower level of the stigmatic papillae. The achene has a reduced number of ribs or angles, and its base is abruptly constricted to a nearly obsolete carpopodium, both characters reminiscent of *Cacosmia*. The short but distinct tails on the anthers are more reminiscent of *Liabum*, *Oligactis*, and *Ferreyranthus*.

The thickenings of the endothelial cells with extensions on only the lower ends are most like those of the *Sinclairia* group in Mexico and Central America and the *Austroliabum* group in Argentina and southern Bolivia.

The genus contains only the one known species, which is restricted to the coastal region of Peru.

*Chionopappus benthamii* Blake, Journ. Wash. Acad. Sci., 25:492, 1935. Peru.

The species is treated in detail by Blake (1935).

### ***Ferreyranthus***

#### FIGURE 5

*Ferreyranthus* H. Robinson and Brettell, Phytologia, 28(1):50, 1974. [Type-species: *Andromachia verbascifolia* Humboldt, Bonpland, and Kunth.]

Shrubs or small trees, moderately branched. Stems terete to slightly hexagonal, without apparent milky sap. Leaves opposite, bases of petiole pairs fused into distinct sheath; petioles distinct, narrowly winged; blade ovate to elliptical, base usually rounded, margin serrate to subentire, usually rugose with minutely bullate upper surface, pale tomentose below, pinnately veined. Inflorescence densely corymbose paniculate, branching mostly opposite; pedicels short, whitish-tomentose. Heads broadly campanulate; 45–55 strongly graduated involucre bracts in ~5 series, ovate to lanceolate, tips acute to short acuminate, outer surface with evanescent arachnoid pubescence; receptacle with distinct short chaff. Flowers yellow. Rays 8–12 in single series; base of

corolla extremely narrow; limbs short, mostly glabrous; style branches not spiralled. Disk flowers 12–25; corollas narrowly funnelform, tubes slightly narrowed, gradually expanding at base of throat, outer surface with glands, with few hairs sometimes on tips of lobes; lobes with stomates near margins; filaments smooth to densely papillose, cells of anther collar with few or no annulations on walls; thecae pale, short-tailed and strongly fringed at base; median endothelial cells oval to oblong, usually with short protruding single nodular thickenings at upper and lower ends of sclerified shields; appendages oblong-ovate, 1½–2 times as long as wide, smooth with elongate cells having mostly oblique end walls; nectary short and unlobed; style base with a distinct node; style branches of disk flowers elongate, ~10–12 times as long as wide. Achenes prismatic, ~10-ribbed, variously setiferous and glanduliferous, cells of achene wall with elongate raphids; carpopodium stopper-shaped, cells rather small, in 6–10 series, with thickened walls; pappus with inner series of 10–15 persistent setae, tips slightly to distinctly broadened, pointed, teeth simple, with outer series of 10–15 short narrowly squamiform setae. Pollen grains 25–40 µm in diameter, with spines rather unevenly dispersed, with distinct internal columellae grouped under spines.

*Ferreyranthus* has a pappus with a capillary inner series and a short outer series, the type of pappus that is found in *Liabum* and most other genera of the tribe. For this reason, the position of the species of *Ferreyranthus* in *Liabum* was not questioned until the tribal revision of Robinson and Brettell (1974b). The genus is most easily distinguished from *Liabum* by the shrubby or arborescent habit, but also it differs by the shorter style branches of the disk flower, the mixed glands and setulae of the achenes, the presence of elongate raphids in the cells of the achene walls, and the presence of stomates on the disk corolla lobes. *Ferreyranthus* remains in the relationship of *Liabum* by the apparent lack of latex in the stems and by the presence of well-developed tails on the anther bases, but the teeth of the pappus setae do not



FIGURE 5.—*Ferreyranthus verbascifolius* (Humboldt, Bonpland, and Kunth) Robinson & Brettell: A, habit,  $\times \frac{1}{2}$ ; B, head,  $\times 3\frac{1}{2}$ ; C, disk corolla,  $\times 18$ ; D, upper filament and bases of anther thecae,  $\times 35$ ; E, disk style,  $\times 18$ ; F, achene,  $\times 15$ .



have the minute mucro-tips that are seen in *Liabum*, *Oligactis*, and *Chionopappus*. The shrubby habit, bullate leaf surfaces, and nodal sheaths of the petiole bases might reflect a close relationship between *Ferreyranthus* and *Cacosmia*, but a number of characters, including the form of the sclerified shields in the endothelial cells, have led to a rejection of that idea in this treatment. The latter points are discussed under *Cacosmia*.

The genus *Ferreyranthus* is notable for some of the largest members of the tribe, with specimens of *F. verbascifolius* and *F. excelsus* being described as small trees. The anthers of *Ferreyranthus* have the most highly developed tails in the tribe, with a fringe of long projecting cells near the tip. The common *F. verbascifolius* is the only member of the tribe with a hirtellus anther filament, such projecting cells apparently being absent from even the closely related *F. rugosus*. Four of the species of *Ferreyranthus* have bullate leaves, but the upper leaf surface in *F. excelsus* and its relatives is smooth or nearly so.

*Ferreyranthus* was once common on slopes along roads in southern Ecuador, but according to R.M. King in his most recent visit, this and other woody plants have mostly disappeared in recent years, apparently the victims of a mobile, mechanized pulping operation. It will be interesting to see if there is any capacity for recovery.

The genus *Ferreyranthus* is mostly restricted to Peru, where all seven species occur. The most common species, *F. verbascifolius*, also occurs in southern Ecuador.

- Ferreyranthus excelsus* (Poeppig and Endlicher) H. Robinson and Brettell, *Phytologia*, 28(1):51, 1974. Peru.  
*Andromachia excelsa* Poeppig and Endlicher, *Nov. Gen. & Sp.*, 3:44, 1843.  
*Liabum excelsum* (Poeppig and Endlicher) Blake, *Journ. Wash. Acad. Sci.*, 17:293, 1927.  
*Ferreyranthus fruticosus* (Muschler) H. Robinson, *Phytologia*, 51(3):169, 1982. Peru.  
*Liabum fruticosum* Muschler, *Engl. Bot. Jahrb.* 50, Beibl., 3:81, 1913.  
*Oligactis fruticosa* (Muschler) H. Robinson and Brettell, *Phytologia*, 28(1):58, 1974.  
*Ferreyranthus ramonii* H. Robinson, *Phytologia*, 51(3):170, 1982. Peru.

- Ferreyranthus rugosus* (Ferreyra) H. Robinson and Brettell, *Phytologia*, 28(1):51, 1974. Peru.  
*Liabum rugosum* Ferreyra, *Publ. Mus. "Javier Prado" Bot.*, ser. B., 20:3, 1965.  
*Ferreyranthus vaginans* (Muschler) H. Robinson and Brettell, *Phytologia*, 28(1):51, 1974. Peru.  
*Liabum vaginans* Muschler, *Engl. Bot. Jahrb.* 50, Beibl., 3:79, 1913.  
*Ferreyranthus verbascifolius* (Humboldt, Bonpland, and Kunth) H. Robinson and Brettell, *Phytologia*, 28(1):51, 1974. Ecuador, Peru.  
*Andromachia verbascifolia* Humboldt, Bonpland, and Kunth, *Nov. Gen. et Sp.*, ed folio, 4:79, 1818.  
*Liabum verbascifolium* (Humboldt, Bonpland, and Kunth) Lessing, *Linnaea*, 6:700, 1831.  
*Liabum salviifolium* Hieronymus, *Engl. Bot. Jahrb.*, 28:622, 1901.  
*Liabum pseudosalviifolium* Hieronymus, *Engl. Bot. Jahrb.*, 36:502, 1905.  
*Ferreyranthus pseudosalviifolius* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):51, 1974.  
*Ferreyranthus vernonioides* (Muschler) H. Robinson and Brettell, *Phytologia*, 28(1):51, 1974. Peru.  
*Liabum tovarii* Cabrera, *Bol. Soc. Argent. Bot.*, 10:29, 1962.  
*Ferreyranthus tovarii* (Cabrera) H. Robinson and Brettell, *Phytologia*, 28(1):51, 1974.

There is no key to all the species, but the distinctions of some are mentioned by Robinson (1978a), and those with smooth upper leaf surfaces are discussed by Robinson (1982).

## ***Liabellum***

FIGURE 6

- Liabellum* Rydberg, *North Amer. Flora*, 34(4):294, 1927.  
 [Type-species: *Liabum palmeri* A. Gray.]

Low, unbranched or rarely branched, perennial herbs from a tuberous root. Stems short, with short internodes, terete, with dense white arachnoid tomentum, with milky sap? Leaves opposite, sessile, narrowly to broadly perfoliate, base sometimes constricted and petioliform, margins usually lobed to deeply lobed, sometimes bipinnatifid, rarely simply serrulate, rather smooth and pilose above, densely white-tomentose below, strongly trinervate from near basal 1/3 or 1/4. Inflorescence thyrsoid to scapose, branching opposite below or alternate throughout; pedicels elongate, 3–10 cm long, white-tomentose, with or

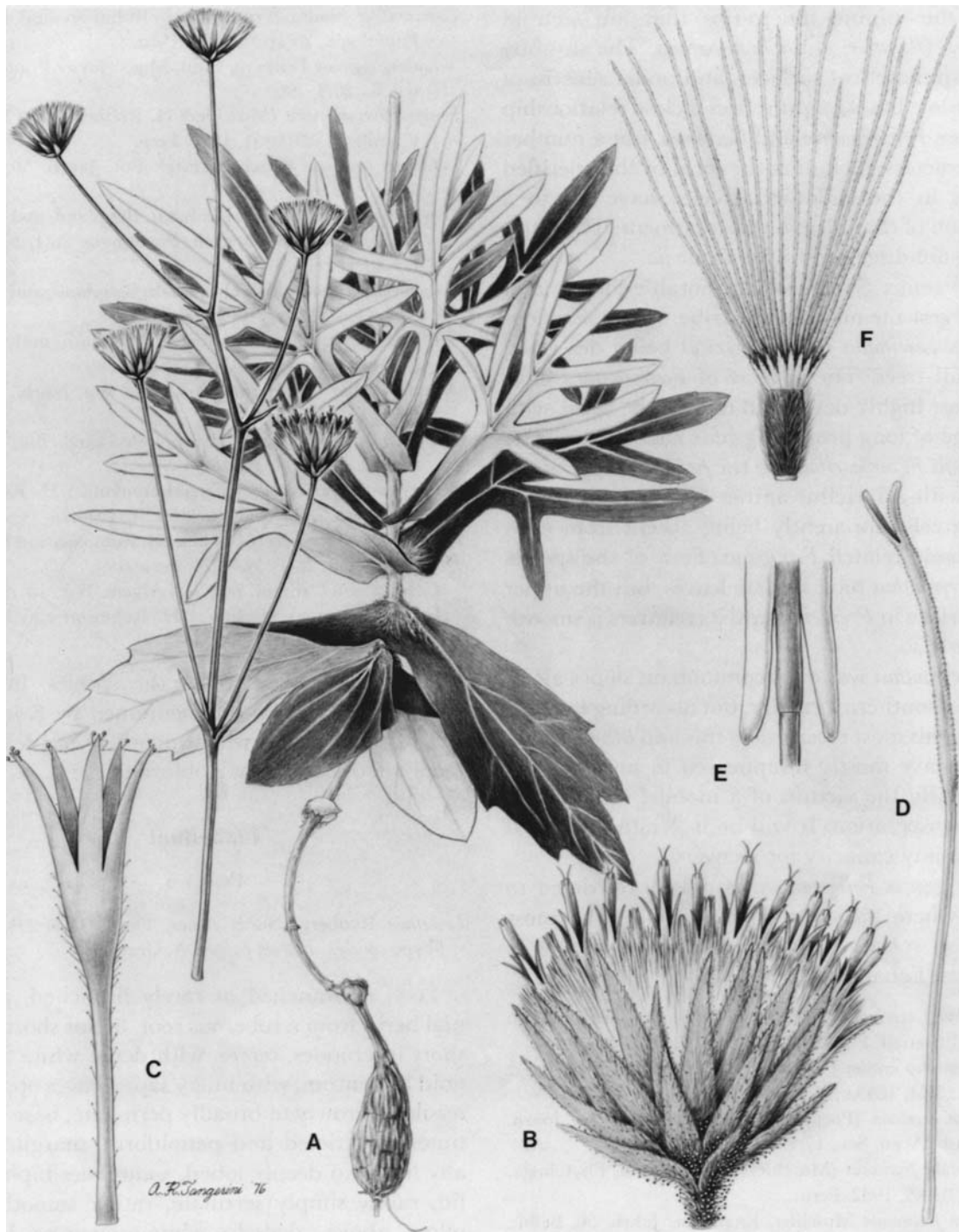


FIGURE 6.—*Liabellum palmeri* (A. Gray) Rydberg: A, habit,  $\times \frac{1}{2}$ ; B, head  $\times 2\frac{1}{2}$ ; C, corolla,  $\times 6$ ; D, style,  $\times 6$ ; E, bases of anther thecae,  $\times 35$ ; F, achene,  $\times 10$ .

without purple long-stipitate glands. Heads broadly campanulate; 20–40 involucre bracts in ~4 series, unequal, narrowly ovate to lanceolate, tips narrowly obtuse to acuminate, outer surface with whitish arachnoid tomentum, with or without purple long-stipitate glands; receptacle plane to slightly convex, slightly alveolate, with or without short hairs. Rays lacking. Disk flowers yellow, 25–35; corollas narrowly funnelform; tubes narrow, moderately expanding at base of throat, outer surface puberulous to hirsute; lobes with stomates near the margins, often with stipitate glands at tip; filament smooth, cells of anther collar without obvious annular thickenings on walls; thecae pale, scarcely crenulate at base; median endothelial cells oblong, with oval to strap-shaped sclerified shields bearing spiral ornamentation and 1 to many nodes usually at lower ends; appendages oblong-ovate, 1½ times as long as wide, smooth, elongate cells with truncate to oblique walls; nectary nearly twice as high as wide, with irregularly crenulate margin; style base broadened above nectary, but node indistinct until shaft withers; style branches 1/4–2/3 as long as the hispidulous upper portion of the shaft. Achenes up to 3 mm long, prismatic, with ~10 ribs, densely long-setuliferous, cells of achene wall with elongate raphids; carpodium a narrow rim with rather small subquadrate cells in 4–8 series, walls slightly thickened, densely beaded; pappus of 40–50 persistent setae, up to 7–13 mm long, tips not broadened, teeth simple, with outer series of 20–40 short usually narrowly squamiform setae. Pollen grains mostly 40–45 µm in diameter, with spines rather unevenly dispersed, with a few large distinct internal columellae grouped under spines.

*Liabellum* is closely related to *Sinclairia*, with which it forms a northern element of the tribe centered in Mexico. The species of *Liabellum* are mostly restricted to western Mexico in the area of Jalisco and Sinaloa. In the original description of the genus, Rydberg (1927) mentioned the herbaceous habit and tuberous roots, which are the most notable distinctions from *Sinclairia*. Rydberg also emphasized the acute involucre bracts in

*Liabellum*, but such bracts are also found in species placed here in a broadened concept of *Sinclairia*. The leaf dissection cited by Rydberg is true of all members of *Liabellum* except the recently described *L. gentryi*, but all species of *Liabellum* have leaves that are sessile or lobed from the base. In *Sinclairia*, all the species have unwinged petioles and lack lobes at the nodes.

All species of *Liabellum* and some species of *Sinclairia* lack rays, being the only discoid members of the tribe Liabeae. The condition is unquestionably derived in the tribe.

*Liabellum* has an unenlarged style base or a base that appears broader only after the style shaft has withered, a condition close to that of *Sinclairia*; however, the nectary is not as elongate as in *Sinclairia*.

The genus contains the following four species from southwestern Mexico.

- Liabellum angustissimum* (A. Gray) Rydberg, North Amer. Flora, 34(4):295, 1927. Mexico.  
*Liabum angustissimum* A. Gray, Proc. Amer. Acad., 22:432, 1887.  
*Liabellum cervinum* (B.L. Robinson) Rydberg, North Amer. Flora, 34(4):294, 1927. Mexico.  
*Liabum cervinum* B.L. Robinson, Proc. Amer. Acad., 29:317, 1894.  
*Liabellum gentryi* H. Robinson, Phytologia, 41(1):46, 1978. Mexico.  
*Liabellum palmeri* (A. Gray) Rydberg, North Amer. Flora, 34(4):295, 1927. Mexico.  
*Liabum palmeri* A. Gray, Proc. Amer. Acad., 22:432, 1887.

A key to the three species with dissected leaves is provided by Rydberg (1927).

## *Liabum*

### FIGURE 7

- Liabum* Adanson, Fam., 2:131, 1763. [Lectotype: *Liabum broceni* Cassini (= *L. umbellatum* (L.) Schultz-Bipontinus).]  
*Starkea* Willdenow, Sp. Pl., 3:2216, 1803. [Type-species: *Amellus umbellatus* L.; originally monotypic.]  
*Andromachia* Humboldt and Bonpland, Pl. Aequin., 2:104, 1809. [Type-species: *Andromachia igniaria* Humboldt, Bonpland, and Kunth.]  
*Allendea* Llave and Lexarza, Nov. Veg. Descr., 1:10, 1824. [Type-species: *Allendea lanceolata* Llave and Lexarza (= *Liabum bourgeauii* Hieronymus).]

*Viviania* Willdenow ex Lessing, *Linnaea*, 4:318, 1829. [Type-species: *Viviania bicolor* Willdenow ex Lessing (= *Liabum melastomoides* (Humboldt, Bonpland, and Kunth) Lessing).]

Terrestrial perennial herbs or subshrubs, sparingly branched, rarely subscented. Stems scarcely to strongly hexagonal, thinly to densely tomentose, rarely glabrous, apparently without milky sap. Leaves opposite, bases of petioles connected across the node by a wing which is often expanded into a nodal disk; petioles narrowly to broadly winged; blade broadly ovate to narrowly elliptical or lanceolate, base acute to slightly cordate, never angulate, margins remotely to closely serrulate or denticulate, upper surface nearly flat or with slightly prominulous veins, densely tomentose below, trinervate from near base (pinnate in *L. diehlii*). Inflorescence cymose, often subumbellate, terminal or partly axillary; pedicels less than 5 cm long, covered with white arachnoid tomentum. Heads broadly campanulate; 50–150 involucral bracts in ~5 unequal series, mostly lanceolate to linear, acute to acuminate, outer surface usually with evanescent arachnoid pubescence; receptacle with bristly chaff or high ridges. Flowers yellow. Rays 20–120, usually in 2 series; corolla with tube narrow, nearly glabrous, or puberulous above, limb short, mostly glabrous, minutely bilobed at tip; style branches not spiralled. Disk flowers 10–85; corollas narrowly funnellform, glabrous or with upper tube and lower throat puberulous, throat not abruptly expanded at base, lobes with stomates rare or lacking, tips smooth or densely spiculiferous, sometimes with slender arachnoid hairs; filament smooth; cells of anther collar with walls not strongly annulated; thecae pale, digitate at base, median endothelial cells oblong to elliptical with 1–2 thickenings on transverse walls; anther appendages oblong-ovate, cells rather elongate with truncate or oblique end walls; nectary short, not or scarcely lobed; style base with small to large node; style branches of disk flowers elongate, filiform, often coiled, hispidulous part usually not or scarcely extending onto shaft (extending onto shaft in *L. solidagineum*), tips narrowly obtuse.

Achenes prismatic, 10-ribbed, setuliferous with straight white hairs (also with glands in *L. sandemanii*), cells of achene wall containing small quadrate raphids; carpodium distinct, stopper-shaped or annuliform, the small subquadrate cells in 4–8 series, walls of cells with large, dense, beaded thickenings; pappus with 17–40 capillary inner setae, with teeth of setae appearing mucronate-tipped in Hoyer's solution, with an outer series of short narrow squamellae or setae. Pollen grains 25–35  $\mu\text{m}$  in diameter, with spines rather unevenly dispersed, with distinct internal columellae in groups under spines, columellae sometimes very narrow and numerous.

The pollen of the *Liabum-Oligactis* generic pair is 25–35  $\mu\text{m}$  in diameter, which is smaller than that in many other genera of the tribe. The lack of stomates on the lobes of the disk corolla is also an unusual condition in the tribe, stomates being present in all other genera except *Cacosmia*.

The Andean members of *Liabum* were placed in a separate genus, *Andromachia*, by Humboldt and Bonpland (1809), and the Mexican species was the basis of *Allendea* Llave & Lexarza described in 1824. Both names seem to owe their existence to purely geographical considerations, since the species involved possess no basic differences from the typical *Liabum* of the West Indies, except perhaps a tendency to be more strongly trinervate. The groups are not recognized here even as subgenera.

A more complex situation is found in the generic segregate *Oligactis* Cassini, which was resurrected by Robinson and Brettell (1974b). The genus *Liabum* was distinguished from *Oligactis* in the latter work by the mostly nonscented habit, the trinervate rather than pinnate leaf venation, the subumbellate rather than corymbose or thyrsoid inflorescence, and the achenes without glands. Since 1974, the styles in *Liabum* have been seen to differ by the usually short zone of the upper shaft bearing hairs. The latter character finds its greatest exceptions in *L. igniarium* of Colombia and Ecuador and in *L. solidagineum* of Peru and Bolivia. Exceptions to the achene pubescence and leaf venation were not known at the

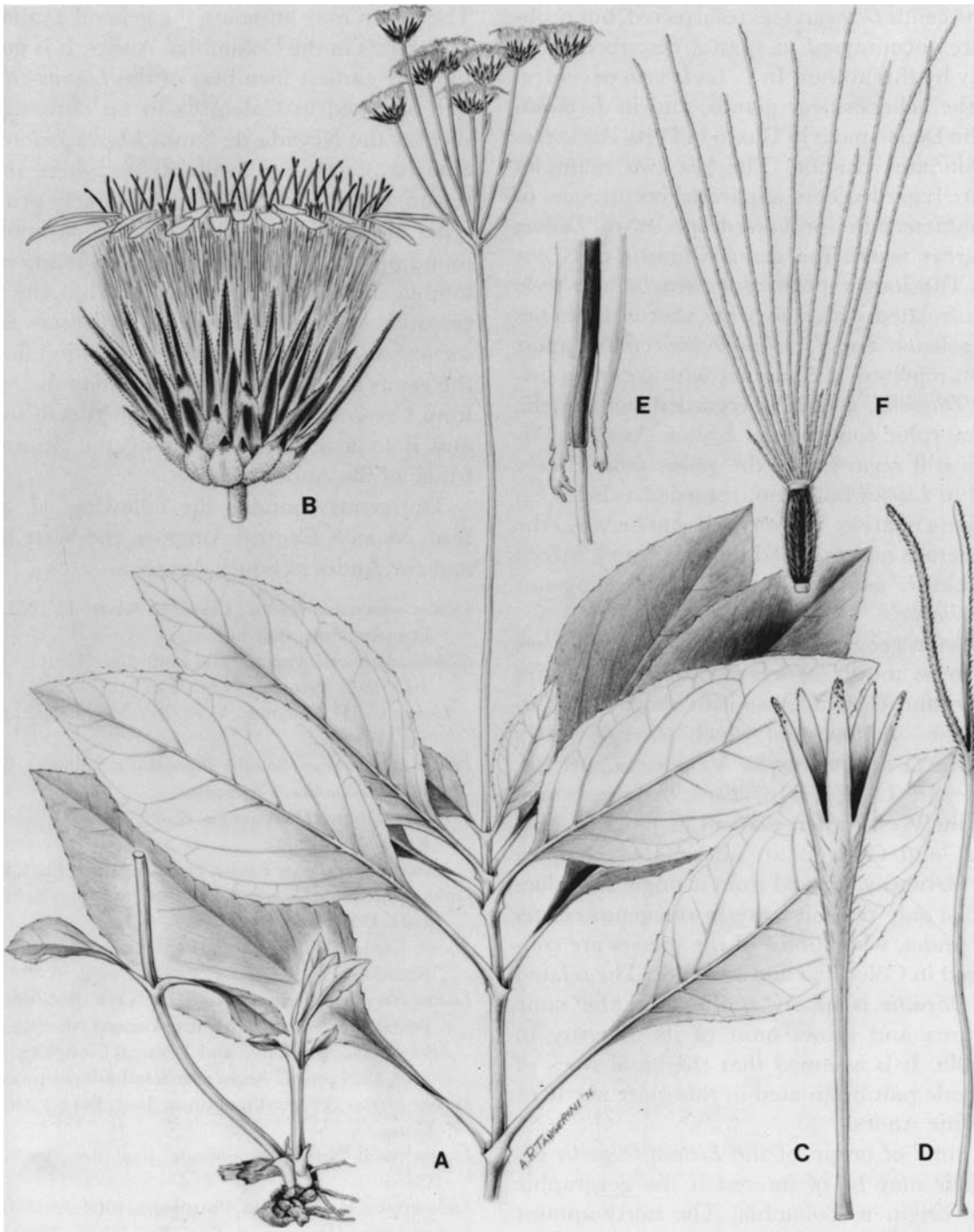


FIGURE 7.—*Liabum umbellatum* (L.) Schultz-Bipontinus: A, habit,  $\times \frac{1}{2}$ ; B, head,  $\times 3\frac{1}{2}$ ; C, disk corolla,  $\times 10$ ; D, disk style,  $\times 10$ ; E, bases of anther thecae,  $\times 35$ ; F, achene,  $\times 9$ .

time the genus *Oligactis* was resurrected, but problems are encountered in species described more recently by this author. In *L. sandemanii* of central Peru, the achenes bear glands, and in *L. diehlii* from the Department of Cuzco in Peru, the leaves have pinnate venation. The last two examples cited are regarded here as parallel occurrences of the characters in specialized species of *Liabum* from areas where the genus *Oligactis* does not occur. The longer pubescent area on the style shaft correlated with somewhat shorter branches in *L. igniarium* and *L. solidagineum* remains most likely to represent a character with common origin in *Oligactis*, and it is regarded here as the pleiomorphic condition in *Liabum*. As such, *Oligactis* is still regarded as the genus most closely related to *Liabum* but is not regarded as being an immediate relative. The phyletic gap between the two genera is no less broad than the gap between the species *L. solidagineum* and *Oligactis* subgenus *Andromachiopsis*.

The wide geographical distribution of *Liabum* seems to be mostly of recent origin. The entire Mexican and Central American range is due to one species, *L. bourgeauii*, which is very closely related to *L. asclepiadeum* of Venezuela and Colombia and *L. ferreyrii* of Peru. As mentioned above, the West Indian element in Jamaica, Hispaniola, and Cuba is an interrelated complex that is obviously derived from a single introduction. The only real diversity in the genus occurs in the Andes, where most of the species are concentrated in Colombia and Ecuador. The related genus *Oligactis* is nearly confined to the same latter area and shows most of its diversity in Colombia. It is assumed that the basal stock of the generic pair originated in this more northern part of the Andes.

The time of origin of the *Liabum-Oligactis* generic pair may be of interest if the geographic area of origin is Colombia. The northernmost Andes are the most recently elevated part of the range. Both the diversity within the generic pair and the phyletic gap between them and other genera would indicate that a considerable time period is involved in the evolution of the group.

The group may antedate the general availability of habitats in the Colombian Andes. It is possible that the earliest members of the *Liabum-Oligactis* line occurred in Colombia in an outlying area such as the Nevada de Santa Marta before suitable habitats were available elsewhere in that region, but it is notable that the likely primitive types of *Liabum* such as *L. igniarium* are not now found on Santa Marta or north of southern Colombia. It should also be noted that the lower elevation species of *Liabum*, *L. acuminatum* and *L. amplexicaule*, by all indications, are specialized in the genus and have recently extended their range from Colombia or Ecuador in the north to Peru and Bolivia in the south along the Amazonian fringe of the Andes.

The genus contains the following 37 species from Mexico, Central America, the West Indies, and the Andes of South America.

- Liabum acuminatum* Rusby, Descr. S. Amer. Pl., 161, 1920. Ecuador, Peru, Bolivia.
- Liabum amplexicaule* Poeppig and Endlicher, Nov. Gen. et Sp., 3:43, 1843. Ecuador, Peru.
- Liabum ulei* Hieronymus, Verh. Bot. Ver. Brand., 68:206, 1907 [1906].
- Liabum asclepiadeum* Schultz-Bipontinus, Linnæa, 20:521, 1847. Colombia, Venezuela.
- Liabum caliense* Hieronymus, Engl. Bot. Jahrb., 28:623, 1901.
- Liabum subumbellatum* Rusby, Descr. S. Amer. Pl., 159, 1920.
- Liabum barahonense* Urban, Arkiv. Bot. (Stockh.), 23A(11):85, 1931. Dominican Republic.
- Liabum barclayae* H. Robinson, Phytologia, 34(3):286, 1976. Ecuador.
- Liabum bourgeauii* Hieronymus in Ule, Verh. Bot. Ver. Prov. Brand., 48:208, 1907. Mexico, Central America.
- Allendea lanceolata* Llave and Lexarza, Nov. Veg. Descr., 1:10, 1824 [not *L. lanceolatum* Schultz-Bipontinus].
- Liabum crispum* Schultz-Bipontinus, Jour. Bot., 1:236, 1863. Cuba.
- Liabum cubense* Schultz-Bipontinus, Jour. Bot., 1:236, 1863. Cuba.
- Liabum diehlii* H. Robinson, Phytologia, 46(2):99, 1980. Peru.
- Liabum eggersii* Hieronymus, Engl. Bot. Jahrb., 28:624, 1901. Ecuador, Peru.
- Liabum eriocaulon* Poeppig and Endlicher, Nov. Gen. et Sp., 3:43, pl. 249, 1843. Peru, Bolivia.
- Liabum jalcatum* Rusby, Descr. S. Amer. Pl., 161, 1920. Colombia.

- Liabum ferreyrii* H. Robinson, Phytologia, 34(3):287, 1976. Peru.
- Liabum floribundum* Lessing, Linnaea, 6:702, 1831. Ecuador. Peru.
- Liabum grandiflorum* (Humboldt, Bonpland, and Kunth) Lessing, Linnaea, 6:701, 1831. Ecuador.
- Andromachia grandiflora* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp., ed folio, 4:77, 1818.
- Liabum weberbaueri* Muschler, Engl. Bot. Jahrb. 50, Beibl., 3:78, 1913.
- Liabum amplexans* Blake, Journ. Wash. Acad. Sci., 17:292, 1927.
- Liabum igniarium* (Humboldt, Bonpland, and Kunth) Lessing, Linnaea, 6:698, 1831. Colombia. Ecuador.
- Andromachia igniaria* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp., ed folio, 4:77, 1818.
- Liabum bonplandii* Cassini, Dict. Sci. Nat., 26:206, 1823.
- Liabum lehmannii* Hieronymus, Engl. Bot. Jahrb., 19:61, 1894.
- Liabum kingii* H. Robinson, Phytologia, 34(3):288, 1976. Ecuador.
- Liabum macbridei* H. Robinson, Phytologia, 34(3):290, 1976. Peru.
- Liabum melastomoides* (Humboldt, Bonpland, and Kunth) Lessing, Linnaea, 6:699, 1831. Colombia.
- Andromachia melastomoides* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp., ed folio, 4:79, 1818.
- Liabum nigro-pilosum* Hieronymus, Engl. Bot. Jahrb., 29:59, 1900. Ecuador.
- Liabum nudicaule* H. Robinson, Phytologia, 35(1):37, 1976. Peru.
- Liabum oblanceolatum* Urban and Ekman, Arkiv. Bot. (Stockh.), 23A(11):89, 1931. Dominican Republic.
- Liabum ovatifolium* Urban, Arkiv. Bot. (Stockh.), 23A(11):86, 1931. Dominican Republic.
- Liabum poiteaui* (Cassini) Urban, Arkiv. Bot. (Stockh.), 23A(11):87, 1931. Haiti.
- Andromachia poiteaui* Cassini, Bull. Soc. Philom., 1817:184, 1817.
- Liabum polycephalum* Urban, Arkiv. Bot. (Stockh.), 23A(11):88, 1931. Haiti.
- Liabum saloyense* Domke in Diels, Bibl. Bot., 116:168, 1937. Colombia. Ecuador.
- Liabum sandemanii* H. Robinson, Phytologia, 35(6):488, 1977. Peru.
- Liabum selleanum* Urban, Arkiv. Bot. (Stockh.), 23A(11):86, 1931. Haiti.
- Liabum solidagineum* (Humboldt, Bonpland, and Kunth) Lessing, Linnaea, 6:700, 1831. Peru, Bolivia.
- Andromachia solidaginea* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp., ed. folio, 4:78, 1818.
- Liabum fulvotomentosum* O. Kuntze, Rev. Gen., 3(2):163, 1898.
- Liabum acutifolium* Cuatrecasas, Collect. Bot., Barcinone, 3:299, 1953.
- Liabum steinbachii* H. Robinson, Phytologia, 35(6):489, 1977. Bolivia.
- Liabum stipulatum* Rusby, Descr. S. Amer. Pl., 160, 1920. Colombia, Ecuador.
- Liabum subcaule* Rydberg, North Amer. Flora, 34(4):290, 1927. Haiti, Dominican Republic.
- Liabum domingense* Rydberg, North Amer. Flora, 34(4):291, 1927.
- Liabum trianae* H. Robinson, Phytologia, 34(3):291, 1976. Colombia.
- Liabum umbellatum* (L.) Schultz-Bipontinus, Jour. Bot., 1:236, 1863. Jamaica.
- Amellus umbellatus* L., Syst. Nat. ed., 10:1225, 1759.
- Starkea umbellata* (L.) Willdenow, Sp. Pl., 3:2216, 1804.
- Liabum broenei* Cassini, Dict. Sci. Nat., 26:203, 1823.
- Liabum vargasii* H. Robinson, Phytologia, 34(3):292, 1976. Peru.
- Liabum wrightii* Grisebach, Mem. Amer. Acad., n. ser., 8:515, 1862. Cuba.
- Liabum longipes* Urban, Fedde. Rep. Sp. Nov., 26:115, 1929.
- Liabum wurdackii* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado" Bot., ser. B., 20:2, 1965. Peru.

Rydberg (1927) has provided a partial treatment of the species north of South America, but there have been considerable changes since that time. The Ecuadorian species have been treated by Robinson (1978a), and some additional distinctions of species are mentioned by Robinson (1976c).

## Microliabum

### FIGURE 8

- Microliabum* Cabrera, Bol. Soc. Argent. Bot., 5:211, 1955.
- Liabellum* Cabrera, Not. Mus. La Plata, 17(84):76, 1954 [not *Liabellum* Rydberg, 1927]. [Type-species: *Liabellum humile* Cabrera.]
- Angelianthus* H. Robinson and Brettell, Phytologia, 28(1):48, 1974.

Annual herbs to 10 cm tall, unbranched or sparsely branched; stems covered with appressed white tomentum and hirsute with coarse minutely gland-tipped purple hairs; internodes short to ~1 cm long. Leaves opposite, sometimes congested at base of plant; bases of leaf pairs fused into short sheath, without distinct petioles; lamina elliptical to subrhomboid, faintly trinervate,

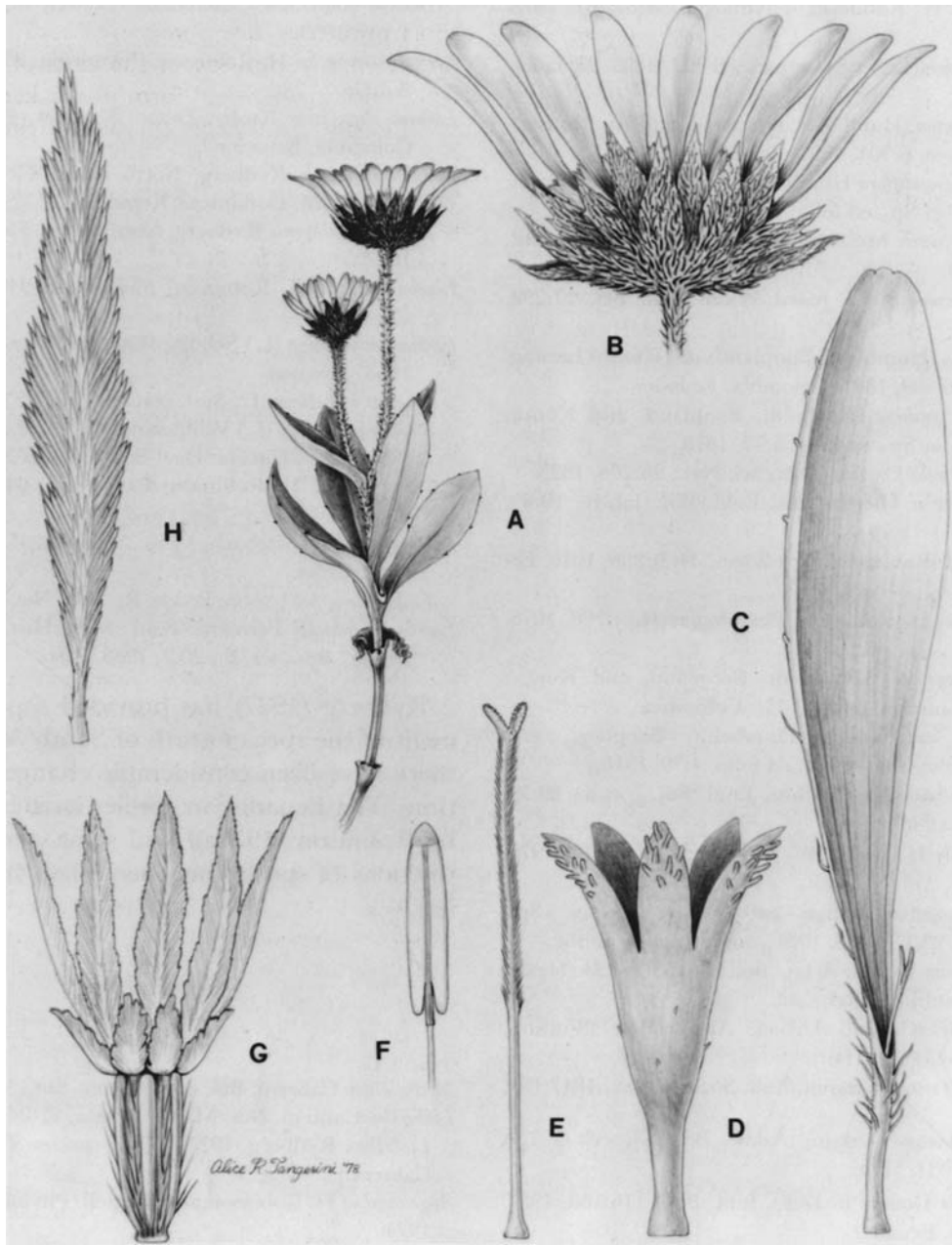


FIGURE 8.—*Microliabum humile* (Cabrera) Cabrera: A, habit,  $\times 1$ ; B, head,  $\times 3\frac{1}{2}$ ; C, ray corolla,  $\times 13$ ; D, disk corolla,  $\times 16$ ; E, disk style,  $\times 16$ ; F, anther,  $\times 16$ ; G, achene,  $\times 16$ ; H, element of inner pappus,  $\times 35$ .

entire to subdentate, acute at tip, green and smooth above, glabrous to coarsely pilose, white-tomentose below. Heads single on slender peduncles or scapes, broadly campanulate. Involucral

bracts  $\sim 10$ – $20$  in  $\sim 2$  series, subequal, ovate to broadly lanceolate, apex acute, hirsute with purple glandular hairs on outer surface; receptacle flat to slightly convex, foveolate, without chaff.



Flowers yellow. Ray flowers 10–18; tubes hirsute; limbs narrowly elliptical, with tinge of red, with few to many short hairs on outer surface; style branches elongate, not spiralled. Disk flowers ~15; corollas glabrous below, tubes expanding gradually into throat; lobes with large stomates near margin, with numerous short glandular hairs on outer surface and with cluster of stout non-glandular hairs near tip; anther collars with annular thickenings on walls; thecae pale, not digitate at base; median endothelial cells oblong, sclerified shield mostly with weak irregular coiled ornamentation, often with long uncinat extension on lower end; appendages smooth, with shortly oblong to subquadrate cells; style base with prominent node, branches short, ~0.5 mm long. Achenes prismatic, obovate, with mostly 8 shallow costae with long setae, intercostal areas glabrous, cells of achene wall with elongate raphids; carpopodium with narrow rim of small, thin-walled, firm, subquadrate cells in ~2–3 rows; pappus distinctly biseriate, short outer squamae positioned over furrows of achene, inner easily deciduous, broadly winged by fused spreading lateral cells, lanceolate to oblanceolate, apices of cells simple. Pollen grains ~35  $\mu\text{m}$  in diameter, with spines unevenly dispersed, with distinct internal columellae.

*Microliabum* was described by Cabrera (1954, as *Liabellum*) during a period in the history of the tribe when genera were based exclusively on pappus characters. In the case of *Microliabum*, the distinction was the broad lamellate form of the inner pappus segments, a form resembling the outer pappus segments in width. Though segments of the outer series are sometimes broad in other genera of the Liabeae, the inner segments, when present, are always capillary. The pappus difference, the comparatively short anther bases, and the small size of the plants provide ample distinction for the species, which is specialized for higher elevations in the southern Andes. Nevertheless, critical examination indicates close relationship to the more robust species from lower elevations in the same area of the southern Andes, which until recently were placed in *Liabum*. Both *Microliabum* and the related species have the same

prominent costae on the achene, a prominent short outer pappus, a very deciduous inner pappus, elongate raphids in the cells of the achene wall, and an identical form of thickenings in the short endothelial cells. In spite of the similarity, the separation seems best, and a separate generic name, *Austroliabum*, has been provided for the related group.

The genus *Microliabum* was originally known from only Jujuy in northern Argentina but since has been collected farther south in the Province of Salta. It is likely to be found farther north, also, in adjacent southern Bolivia.

The original illustration of the genus by Cabrera (1954) shows a plant with strictly rosulate leaves and strap-shaped inner pappus segments without a stipitate base. Material seen from the Province of Salta has a slight elongation to the vegetative stem, and the segments of the inner pappus are oblanceolate with a long narrow base (see Figure 8). It is possible that more than one species is involved, but this cannot be confirmed, since the herbarium at Tucuman has refused to send the type specimen from Jujuy on loan and has not replied to requests for information on details of the plant. Except for the kindness of Dr. Zardini at the Universidad Nacional de La Plata, who arranged for the loan of a fragment of some Salta material, the genus would have been completely unavailable for this study. It is hoped that further material will be collected of this inadequately known genus.

The genus is monotypic with the species as follows.

*Microliabum humile* (Cabrera) Cabrera, Bol. Soc. Argent. Bot., 5:211, 1955. Argentina.

*Liabellum humile* Cabrera, Not. Mus. La Plata, 17(84):78, 1954.

*Angelianthus humilis* (Cabrera) H. Robinson and Brettell, Phytologia 28(1):48, 1974.

## *Oligactis*

### FIGURE 9

*Oligactis* (Humboldt, Bonpland, and Kunth) Cassini, Dict. Sci. Nat., 36:16, 1825.

*Andromachia* sect. *Oligactis* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp., ed. folio. 4:79, 1818. [Lectotype: *Andromachia volubilis* Humboldt, Bonpland, and Kunth.]

Scandent shrubs and vines, sparsely branching. Stems terete to strongly hexagonal, tomentose to glabrescent, apparently without milky sap. Leaves opposite, with or without nodal disks; petioles with or without wings, sometimes included in perfoliate leaf base; blade ovate to narrowly linear, base cuneate to rounded or slightly cordate, sometimes confluent into petiole wings, margins of blade never angulate, subentire to serrate, upper surface flat to slightly bullate, densely tomentose below, pinnately veined. Inflorescence terminal on branches or axillary, paniculate with spiciform to corymbose branches; pedicels less than 5 cm long, thinly to densely tomentose. Heads narrowly to broadly campanulate; 16–55 involucre bracts in 4–5 series, ovate to lanceolate, tips obtuse to narrowly acute, outer surface puberulous to hirsute; receptacle with lacinate chaff or prominent ridges. Flowers yellow. Rays 3–18 in 1 series; corolla with tube narrow, glabrous, or puberulous above, limb short, elliptical, glabrous; style branches not spiralled. Disk flowers 3–34, corollas narrowly funnelform, tube slender, sometimes slightly swollen and sparsely puberulous at base of throat, lobes without evident stomates, tips plain or with crests; filament of anther smooth; cells of anther collar with weak annulate thickenings on walls; anther thecae pale, digitate at base, median endothelial cells oblong with oval or strap-shaped sclerified bands, with a single thickening on the transverse walls; anther appendages oblong-ovate, smooth or papillose, with short-oblong to subquadrate cells; nectary short, not or scarcely lobed; style base with distinct node; style branches of disk flowers elongate, linear, 1.0–1.5 times as long as the hispidulous upper portion of the shaft (longer in subgenus *Andromachiopsis*), tips narrowly obtuse, tapering in some species. Achenes prismatic with 5–8 ribs, bearing contorted setae and small

glands, cells of achene wall with quadrate raphids; carpodium short and distinct, usually annuliform with small subquadrate cells in 3–5 series, walls of cells moderately thickened; pappus with 20–35 rather persistent inner setae often with broadened tips, with teeth of setae appearing mucronate-tipped in Hoyer's solution; with outer series of 7–20 short setae or squamellae. Pollen grains 25–35  $\mu\text{m}$  in diameter, with spines rather unevenly dispersed, with distinct internal columellae grouped under spines.

The relationship of *Oligactis* to *Liabum* is discussed under the latter genus.

*Oligactis* is divided into two subgenera, which have distinctive, scarcely overlapping distributions. The less-specialized scandent subgenus *Andromachiopsis*, having heads in corymbose panicles, usually more than 18 flowers per head, and foliar disks on the nodes, is centered in Ecuador with extensions into southern Colombia. Three species have been found in northern Peru. Most of the species are restricted to elevations above 2000 m, but *O. asplundii* from the Pacific slope of the Ecuadorian Andes is found as low as 1200 m. One species, *O. cusalaguensis*, has distinctive perfoliate leaves.

The subgenus *Oligactis* is the most specialized element of the genus, with more scandent plants bearing heads in subglomerate, spiciform, or racemose branches in an axillary or terminal position. The anther appendages are unique in the tribe by the projecting cell-ends on the surfaces. The heads often have about 10 flowers and sometimes have as few as six flowers, three of each type. The subgenus occurs primarily in northern and central Colombia and extends into Venezuela, Panama, and Costa Rica. In most species, the leaves are ovate to narrowly elliptical, but *O. garcia-barrigae* has narrowly linear leaves (Robinson, 1980a).

### Key to the Subgenera of *Oligactis*

- Inflorescence axillary or terminal, with a subglomerate, spiciform, or racemose arrangement of heads; heads usually with 6–10 flowers; anther appendages with papillose surfaces ..... subgenus ***Oligactis***

Inflorescence terminal, with a corymbose arrangement of heads; heads with ~18–50 flowers; anther appendages smooth subgenus **Andromachiopsis**

The genus contains approximately 12 species, which are disposed in the subgenera as follows.

*Oligactis* subgenus *Oligactis*

- Oligactis garcia-barrigae* H. Robinson, *Phytologia*, 46(2):100, 1980. Colombia.
- Oligactis latifolia* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):57, 1974. Colombia.
- Liabum volubile* var. *latifolium* Hieronymus, *Engl. Bot. Jahrb.*, 28:622, 1901.
- Liabum latifolium* (Hieronymus) Cuatrecasas, *Fedde Rep. Spec. Nov.*, 55:129, 1953.
- Oligactis mikanioides* (Blake) H. Robinson and Brettell, *Phytologia*, 28(1):57, 1974. Colombia.
- Liabum mikanioides* Blake, *Journ. Wash. Acad. Sci.*, 17:294, 1927.
- Oligactis sessiliflora* (Humboldt, Bonpland, and Kunth) H. Robinson and Brettell, *Phytologia*, 28(1):58, 1974. Colombia, Venezuela.
- Andromachia sessiliflora* Humboldt, Bonpland, and Kunth, *Nov. Gen. et Sp.*, ed. folio, 4:79, 1818.
- Oligactis apodocephala* Cassini, *Dict. Sci. Nat.*, 36:17, 1825 [nom. superfl.].
- Liabum sessiliflora* (Humboldt, Bonpland, and Kunth) Lessing, *Linnaea*, 6:703, 1831.
- Liabum tovarense* Badillo, *Bol. Soc. Venez. Cienc. Nat.*, 10:314, 1946.
- Oligactis valeri* (Standley) H. Robinson and Brettell, *Phytologia*, 28(1):58, 1974. Costa Rica, Panama.
- Liabum valeri* Standley, *Publ. Field Mus. Nat. Hist. Chicago, bot. ser.*, 18:1490, 1938.
- Oligactis volubilis* (Humboldt, Bonpland, and Kunth) Cassini, *Dict. Sci. Nat.*, 36:17, 1825. Colombia, Venezuela.
- Andromachia volubilis* Humboldt, Bonpland, and Kunth, *Nov. Gen. et Sp.*, ed. folio, 4:80, 1818.
- Liabum volubile* (Humboldt, Bonpland, and Kunth) Lessing, *Linnaea*, 6:704, 1831.
- Liabum biattenuatum* Rusby, *Descr. S. Amer. Pl.*, 159, 1920.
- Liabum boyacense* Cuatrecasas, *Not. Fl. Colomb.*, 6:36, 1944; *Rev. Acad. Colomb.* 6:61, 1944.
- Liabum meridense* Badillo, *Bol. Soc. Venez. Cienc. Nat.*, 10:314, 1946.
- Oligactis biattenuata* (Rusby) H. Robinson and Brettell, *Phytologia*, 28(1):57, 1974.
- Oligactis boyacensis* (Cuatrecasas) H. Robinson and Brettell, *Phytologia*, 28(1):57, 1974.

*Oligactis* subgenus *Andromachiopsis*

- (H. Robinson and Brettell, *Phytologia*, 28(10):58, 1974)
- Oligactis asplundii* H. Robinson, *Phytologia*, 35(3):200, 1977. Ecuador.

- Oligactis coriacea* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1): 58, 1974. Colombia, Ecuador, Peru.
- Liabum coriaceum* Hieronymus, *Engl. Bot. Jahrb.* 29:58, 1900.
- Liabum scandens* Domke in Diels, *Bibl. Bot. no.*, 116:167, 1937.
- Liabum granatensis* Cuatrecasas, *Fedde Rep. Sp. Nov.* 55:128, 1953.
- Oligactis granatensis* (Cuatrecasas) H. Robinson and Brettell, *Phytologia*, 28(1):58, 1974.
- Oligactis scandens* (Domke) H. Robinson and Brettell, *Phytologia*, 28(1):59, 1974.
- Oligactis coriacea* var. *granatensis* (Cuatrecasas) H. Robinson, *Phytologia*, 35(3):201, 1977.
- Oligactis cusalaguensis* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):58, 1974. Ecuador.
- Liabum cusalaguense* Hieronymus, *Engl. Bot. Jahrb.*, 29:55, 1900.
- Oligactis ecuadoriensis* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):58, 1974. Ecuador.
- Liabum ecuadoriense* Hieronymus, *Engl. Bot. Jahrb.* 19:60, 1894.
- Oligactis ochracea* (Cuatrecasas) H. Robinson and Brettell, *Phytologia*, 28(1): 58, 1974. Peru.
- Liabum ochraceum* Cuatrecasas, *Collect. Bot. Barcinone*, 3:302, 1953.
- Oligactis pastoensis* (Cuatrecasas) H. Robinson and Brettell, *Phytologia*, 28(1):58, 1974. Colombia.
- Liabum pastoense* Cuatrecasas, *Not. Fl. Colomb.*, 6:36, 1944; *Rev. Acad. Colomb.*, 6:62, 1944.
- Oligactis pichinchensis* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):59, 1974. Ecuador.
- Liabum pichinchense* Hieronymus, *Engl. Bot. Jahrb.*, 29:56, 1900.
- Liabum hallii* Hieronymus, *op. cit.*, 57.
- Oligactis hallii* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):58, 1974.

Incertae sedis

- Oligactis nubigena* (Humboldt, Bonpland, and Kunth) Cassini, *Dict. Sci. Nat.*, 36:16, 1825. Ecuador?
- Andromachia nubigena* Humboldt, Bonpland, and Kunth, *Nov. Gen. et Sp.*, ed. folio, 4:79, 1818.
- Liabum nubigenum* (Humboldt, Bonpland, and Kunth) Lessing, *Linnaea*, 6:704, 1831.

There is no available treatment of the genus, but Robinson (1978a) has provided a key to the Ecuadorian species, and the two species from Venezuela have been treated by Aristeguieta

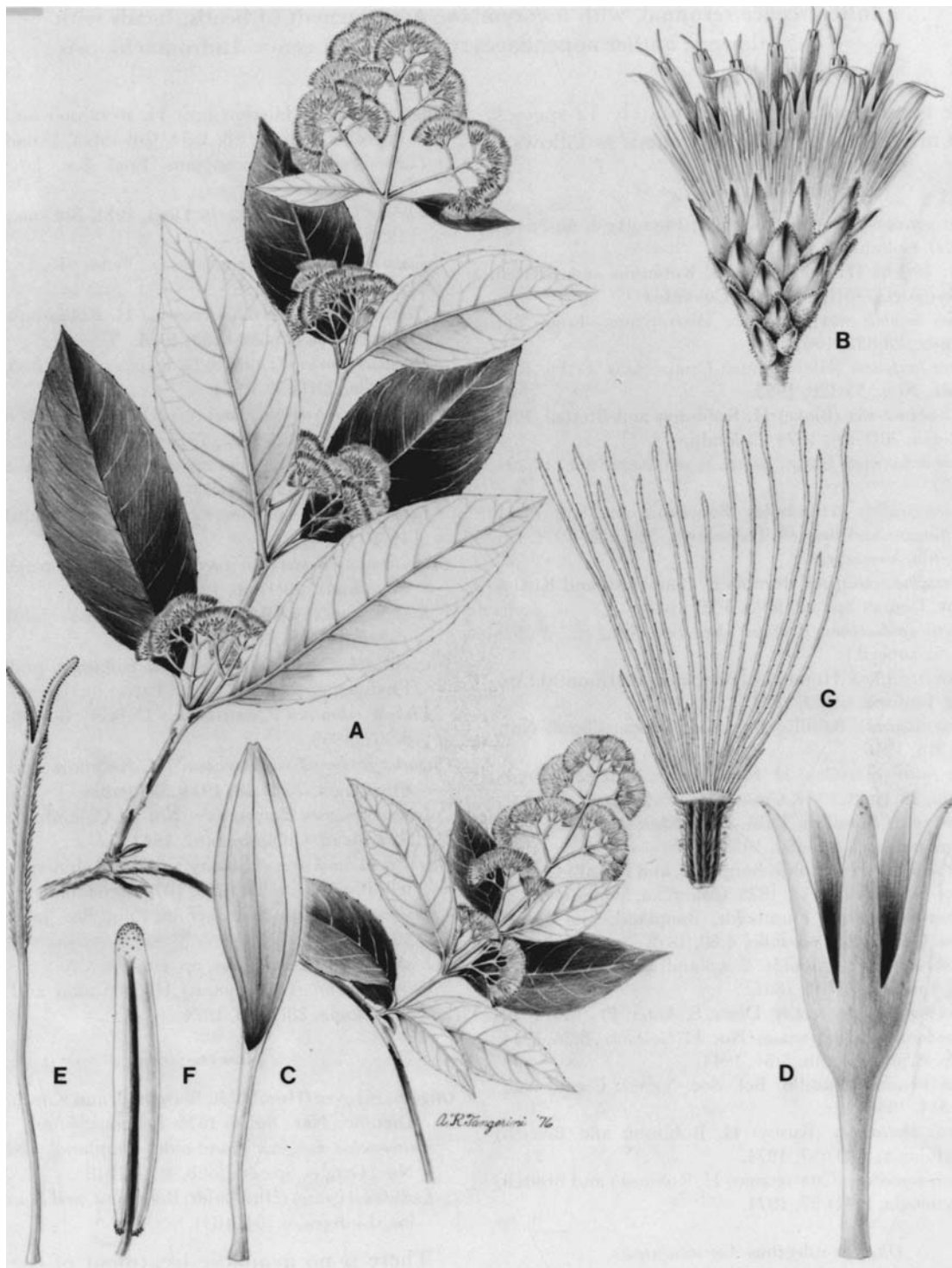


FIGURE 9.—*Oligactis volubilis* (Humboldt, Bonpland, and Kunth) Cassini: A, habit,  $\times \frac{1}{2}$ ; B, head,  $\times 7$ ; C, ray corolla,  $\times 13$ ; D, disk corolla,  $\times 13$ ; E, disk style,  $\times 13$ ; F, anther,  $\times 25$ ; G, achene,  $\times 13$ .

(1964). Additional comments of value can be found in Cassini (1825:16–18) and in Steyermark (1957:1151).

### *Sinclairia*

FIGURE 10

*Sinclairia* Hooker and Arnott, *Bot. Beech. Voy.*, 433, 1841.

[Type-species: *Sinclairia discolor* Hooker and Arnott; originally monotypic.]

*Sinclairiopsis* Rydberg, *North Amer. Flora*, 34(4):292, 1927.

[Type-species: *Liabum klattii* B.L. Robinson and Greenman; originally monotypic.]

*Megaliabum* Rydberg, *North Amer. Flora*, 34(4):293, 1927.

[Type-species: *Vernonia andrieuxii* DeCandolle.]

Erect to scandent subshrubs, shrubs, or vines, sparingly branched. Stems terete to slightly hexagonal, with sparing often evanescent arachnoid tomentum, with milky sap. Leaves opposite or ternate, often defoliated at anthesis, without nodal disks or sheaths, petioles distinct, narrow, not noticeably winged; blade ovate to suborbicular or triangular, base broadly cuneate to truncate, margin remotely mucro-denticulate to coarsely irregularly dentate, upper surface smooth to slightly roughened, with or without coarse hairs, thinly to densely whitish pubescent below, strongly trinervate at or near base. Inflorescence terminal or partly axillary, corymbose to thyrsoid paniculate with corymbose branches, with few to many heads, pedicels 0.1–4.0 cm long, hirtellous to white-tomentose. Heads narrowly to broadly campanulate; 18–45 involucre bracts in 3–5 series, unequal, oblong to lanceolate, tips broadly rounded to narrowly acuminate, outer surface subglabrous to densely tomentose; receptacle plane, sometimes with minute spines, glabrous or with minute hairs. Flowers yellow. Rays when present 4–25 in 1 series; corolla with tube narrow, limb broadly to narrowly elliptical, sometimes obsolete, glabrous to minutely puberulous, minutely bilobed at tip; style branches elongate, not spiralled. Disk flowers 5–30; corollas narrowly funnelform, tube narrow, moderately expanding at base of throat, glabrous below, becoming densely puberulous above, lobes with stomates

near margins, sometimes piliferous at tip; filament smooth, anther collar with few or no subquadrate cells below, sometimes with unsclerified lower cells, walls without obvious annular thickenings; thecae pale, minutely crenulate at base; median endothelial cells oblong, with oval to strap-shaped sclerified shields, shields spirally ornamented with 1 to many nodes at lower end; appendages oblong, 1–2 times as long as wide, smooth, cells elongate with mostly oblique end walls; nectary with irregular crenulations or lobules; style base usually without nodular expansion; style branches elongate, 10–15 times as long as wide, often less than 1/2 as long as hispidulous upper part of shaft. Achenes prismatic, ~8–10 ribbed, up to 2.5–7.0 mm long, glabrous to densely setuliferous, cells of achene wall with elongate raphids; carpopodium short-cylindrical or annuliform, prominent, with ~15 rows of minute subquadrate cells, cell walls slightly thickened, densely beaded; pappus of 30–40 persistent setae, mostly 5–8 mm long, 13–15 mm long in 3 species, tips not or slightly thickened, teeth simple, outer pappus with series of 15–20 short, narrow, usually squamiform setae. Pollen grains 33–50  $\mu\text{m}$  in diameter, with spines rather unevenly dispersed, with usually a few large internal columellae grouped under spines.

*Sinclairia* and *Liabellum* together form a distinctive element of the tribe that is nearly restricted to Mexico and Central America and shows considerable diversity in that area. The diversity was the basis of four genera recognized by Rydberg (1927), two of which are not recognized here. Both of the Rydberg segregates synonymized here had heads with involucre bracts more obviously graduated and more acute than in typical *Sinclairia*. The genus *Megaliabum* had a normal short outer pappus but was notable for its coarse leaves and large heads. *Megaliabum* included *S. andrieuxii* and *S. pringlei*, and the more recently described *S. moorei* would belong to the group. The genus *Sinclairiopsis* was distinguished by the lack of an outer pappus series and had heads of intermediate size with acute involucre bracts. The single species included in *Sinclairiopsis*, *S. klattii*, is notable

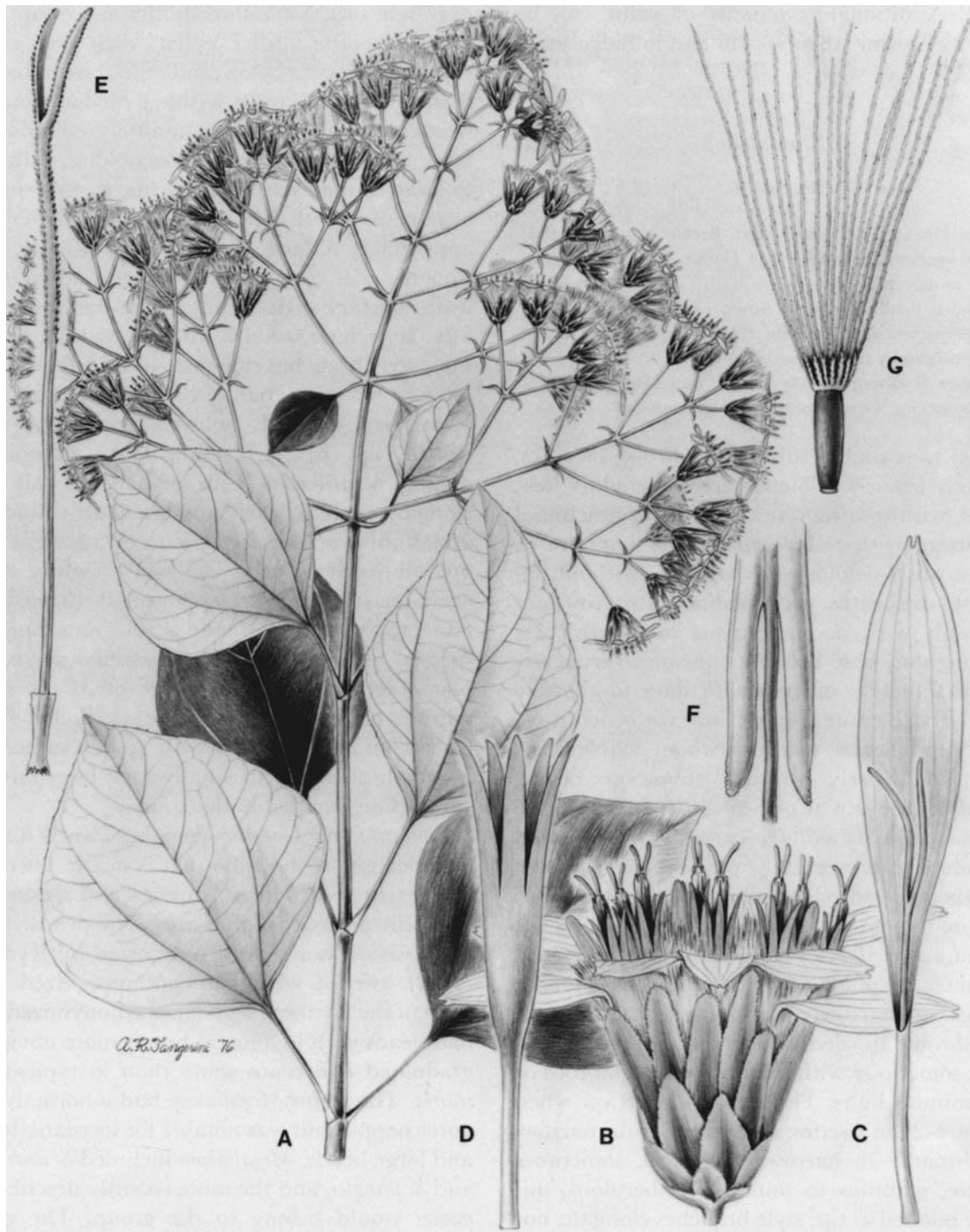


FIGURE 10.—*Sinclairia discolor* Hooker & Arnott: A, habit,  $\times \frac{1}{2}$ ; B, head,  $\times 3\frac{1}{2}$ ; C, ray corolla,  $\times 8$ ; D, disk corolla,  $\times 8$ ; E, disk style,  $\times 10$ ; F, bases of anther thecae,  $\times 35$ ; G, achene,  $\times 8$ .

for the lack of leaves at the time of anthesis, but this trait is developed to some extent in other members of *Sinclairia*. The seasonal foliage is reminiscent of the situation in *Pachythamnus* King and Robinson of the Eupatorieae and *Pittocaulon* Robinson and Brettell in the Senecioneae, both from the same geographic area. It is also a habit shared by many plants of other families such as *Cnidocolus* in the Euphorbiaceae.

*Sinclairia* has a few traits that are rather distinctive in the tribe. The presence of discoid heads in many species is a character found elsewhere in the Liabeae only in the closely related *Liabellum*. A character not found in any other genera of the tribe is the tendency for ternate leaves. Such leaves are not an absolute characteristic of any species, but they occur commonly in many members of the genus, including some material seen of *S. (Megaliabum) pringlei*. Unenlarged or slightly enlarged style bases are found in the subtribe only in *Sinclairia* and *Liabellum*, whereas elongate nectaries occur only in *Sinclairia*. The anther collar of *Sinclairia* is unique in the tribe by the nonquadrate or unsclerified basal cells.

The distinctly petiolate and totally nonstipulate nature of the leaves in *Sinclairia* prove to be one of the most useful characteristics of the genus. This feature distinguishes the genus completely from the closely related *Liabellum* in which the leaves are all sessile or lobed from the base or even perfoliate. Of the other genera of the Liabeae reaching Central America in at least Costa Rica, *Liabum* usually has a nodal disk or a petiolar wing continuing across the node, and *Munnozia* often has either a winged petiole or a nodal lobe. The closest approach to the *Sinclairia* type of leaf insertion in a member of the Liabeae in Central America is in *Oligactis*, which is distinguished by its pinnately veined leaves.

*Sinclairia polyantha* has been known from Panama as far east as the Cerro Jeffe area, and there has been some suspicion that the genus occurred in the adjacent part of South America. Recently, an old collection of the species has been seen from the Departamento de Caldas in Colombia, *Sneidern 524C*, La Selva, 1600–1900 m “I 8 1946.”

The genus contains ~25 species, which are almost entirely restricted to Mexico and Central America. The species are as follows.

- Sinclairia adenotricha* (Greenman) Rydberg, North Amer. Flora, 34(4):300, 1927. Mexico.  
*Liabum adenotrichum* Greenman, Field Mus. Publ. Bot., 2:349, 1912.
- Sinclairia andrieuxii* (DeCandolle) H. Robinson and Brettell, Phytologia, 28(1):60, 1974. Mexico, Guatemala.  
*Vernonia andrieuxii* DeCandolle, Prodr., 5:16, 1836.  
*Liabum andrieuxii* (DeCandolle) Benth. and Hooker f. ex Hemsley, Biol. Centr. Amer., Bot., 2:231, 1881.  
*Megaliabum andrieuxii* (DeCandolle) Rydberg, North Amer. Flora, 34(4):293, 1927.
- Sinclairia andromachioides* (Lessing) Schultz-Bipontinus ex Rydberg, North Amer. Flora, 34(4):298, 1927. Mexico.  
*Vernonia andromachioides* Lessing, Linnaea, 6:397, 1831.  
*Liabum andromachioides* (Lessing) Benth. and Hooker f. ex Hemsley, Biol. Centr. Amer., Bot., 2:231, 1881.
- Sinclairia blakei* H. Robinson and Brettell, Phytologia, 28(1):60, 1974 [non *Sinclairia hypoleuca* (Greenman) Rydberg]. Mexico.  
*Vernonia hypoleuca* DeCandolle, Prodr., 5:27, 1836.  
*Liabum hypoleucum* (DeCandolle) Blake, Proc. Biol. Soc. Wash., 39:144, 1926.
- Sinclairia brachypus* Rydberg, North Amer. Flora, 34(4):299, 1927. Guatemala.
- Sinclairia broomeae* H. Robinson [as *broomei*], Phytologia, 33(4):287, 1976; correction, Phytologia, 41(1):47, 1978. Mexico.
- Sinclairia caducifolia* (B.L. Robinson and Bartlett) Rydberg, North Amer. Flora, 34(4):299, 1927. Mexico.  
*Liabum caducifolium* B.L. Robinson and Bartlett, Proc. Amer. Acad., 43:59, 1907.
- Sinclairia deamii* (B.L. Robinson and Bartlett) Rydberg, North Amer. Flora, 34(4):299, 1927. Guatemala, Belize, Honduras, El Salvador.  
*Liabum deamii* B.L. Robinson and Bartlett, Proc. Amer. Acad., 43:60, 1907.  
*Liabum subglandulare* Blake, Contr. U.S. Nat. Herb., 24:31, 1922.
- Sinclairia subglandularis* (Blake) Rydberg, North Amer. Flora, 34(4):298, 1927.
- Sinclairia deppeana* (Lessing) Rydberg, North Amer. Flora, 34(4):300, 1927. Mexico.  
*Andromachia deppeana* Lessing, Linnaea, 6:401, 1831.  
*Liabum deppeanum* (Lessing) Hemsley, Biol. Centr. Amer., Bot., 2:232, 1881.
- Sinclairia dimidia* (Blake) H. Robinson and Brettell, Phytologia, 28(1):61, 1974. Guatemala.  
*Liabum dimidium* Blake, Journ. Wash. Acad. Sci., 22:385, 1932.
- Sinclairia discolor* Hooker and Arnott, Bot. Beech. Voy., 433.

1841. Mexico, Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica.
- Liabum discolor* (Hooker and Arnott) Bentham and Hooker f. ex Hemsley, *Biol. Centr. Amer., Bot.*, 2:232, 1881.
- Sinclairia glabra* (Hemsley) Rydberg, *North Amer. Flora*, 34(4):297, 1927. Mexico.
- Liabum glabrum* Hemsley, *Biol. Centr. Amer., Bot.*, 2:232, 1881.
- Liabum glabrum* var. *hypoleucum* Greenman, *Proc. Amer. Acad.*, 32:294, 1897.
- Sinclairia hypoleuca* (Greenman) Rydberg, *North Amer. Flora*, 34(4):297, 1927.
- Sinclairia hypochlora* (Blake) Rydberg, *North Amer. Flora*, 34(4):301, 1927. Mexico, Guatemala.
- Liabum hypochlorum* Blake, *Contr. Gray Herb., n.s.*, 53:27, 1918.
- Sinclairia klattii* (B.L. Robinson and Greenman) H. Robinson and Brettell, *Phytologia*, 28(1):61, 1974. Mexico.
- Liabum klattii* B.L. Robinson and Greenman, *Amer. Journ. Sci., ser. 3*, 1:156, 1895.
- Sinclairiopsis klattii* (B.L. Robinson and Greenman) Rydberg, *North Amer. Flora*, 34(4):293, 1927.
- Sinclairia liebmanni* (Klatt) Schultz-Bipontinus ex Rydberg, *North Amer. Flora*, 34(4):300, 1927. Mexico.
- Liabum liebmanni* Klatt, *Leopoldina*, 23:146, 1887.
- Sinclairia moorei* (H. Robinson and Brettell) H. Robinson and Brettell, *Phytologia*, 28(1):61, 1974. Mexico.
- Liabum moorei* H. Robinson and Brettell, *Phytologia*, 27(4):252, 1973.
- Sinclairia pittieri* Rydberg, *North Amer. Flora*, 34(4):300, 1927. Costa Rica.
- Sinclairia platylepis* (Schultz-Bipontinus ex Klatt) Rydberg, *North Amer. Flora*, 34(4):296, 1927. Mexico.
- Liabum platylepis* Schultz-Bipontinus ex Klatt, *Leopoldina*, 23:146, 1887.
- Sinclairia polyantha* (Klatt) Rydberg, *North Amer. Flora*, 34(4):299, 1927. Guatemala, Belize, Costa Rica, Panama, Colombia.
- Liabum polyanthum* Klatt, *Bull. Soc. Roy. Bot. Belg.*, 31:209, 1892.
- Liabum tonduzii* B.L. Robinson, *Proc. Bost. Soc. Nat. Hist.*, 31:270, 1904.
- Sinclairia tonduzii* (B.L. Robinson) Rydberg, *North Amer. Flora*, 34(4):298, 1927.
- Sinclairia pringlei* (B.L. Robinson and Greenman) H. Robinson and Brettell, *Phytologia*, 28(1):61, 1974. Mexico.
- Liabum pringlei* B.L. Robinson and Greenman, *Proc. Amer. Acad.*, 32:49, 1896.
- Megaliabum pringlei* (B.L. Robinson and Greenman) Rydberg, *North Amer. Flora*, 34(4):294, 1927.
- Sinclairia sericolepis* (Hemsley) Rydberg, *North Amer. Flora*, 34(4):301, 1927. Mexico.
- Liabum sericolepis* Hemsley, *Biol. Centr. Amer., Bot.*, 2:232, 1881.
- Sinclairia similis* (McVaugh) H. Robinson and Brettell, *Phytologia*, 28(1):62, 1974. Mexico.
- Liabum simile* McVaugh, *Contr. Univ. Mich. Herb.*, 9:468, 1972.
- Sinclairia sublobata* (B.L. Robinson) Rydberg, *North Amer. Flora*, 34(4):297, 1927. Guatemala, El Salvador, Honduras, Nicaragua.
- Liabum sublobatum* B.L. Robinson, *Proc. Amer. Acad.*, 51:539, 1916.
- Sinclairia tajumulcensis* (Standley and Steyermark) H. Robinson and Brettell, *Phytologia*, 28(1):62, 1974. Guatemala.
- Liabum tajumulcense* Standley and Steyermark, *Publ. Field Mus. Nat. Hist., Chicago, bot. ser.*, 23:27, 1943.
- Sinclairia vagans* (Blake) H. Robinson and Brettell, *Phytologia*, 28(1):62, 1974. Guatemala.
- Liabum vagans* Blake, *Brittonia*, 2:354, 1937.

Most of the species of *Sinclairia* can be identified using the key by Rydberg (1927), and the Guatemalan species have recently been treated by Nash (1976). Greenman (1897) provided an older key of some interest to the Mexican species of *Liabum* that included 10 species of *Sinclairia*.

#### PARANEPHELIINAE, new subtribe

Paranepheleinae, subtribus nov. Plantae rosuliformes vel breviter caulescentes perennes; folia pinnatinervata vel leniter trinervata. Capitula sessilia vel in pedunculo elongato saepe solitaria; corollae disci in tubis valde elongatae; antherae pallidae; thecae base non denticulatae, cellulis endothelialibus in partibus scleroideis non contiguus ovalis vel taeniatis in parietibus transversalibus paucae noduliferis; rami stylosum elongati interdum spiraliter contorti; raphides achaeiorum elongatae. Grana pollinis regulariter spinulifera, spinis intus fere vel omnino caveata.

Type genus: *Paranephelius* Poeppig and Endlicher.

The subtribe is restricted to the central Andes in Peru, Bolivia, and northernmost Argentina. The subtribe contains the following two genera.



## *Paranephelius*

### FIGURE 11

*Paranephelius* Poeppig and Endlicher, Nov. Gen. et Sp., 3:42, pl. 248, 1843. [Type-species: *Paranephelius uniflorus* Poeppig and Endlicher; originally monotypic.]

*Liabum* sect. *Paranephelius* (Poeppig and Endlicher) Benth and Hooker f., Gen. Pl., 2(1):436, 1873.

Perennial acaulescent or shortly caulescent herbs, single or in clusters, with distinct tap-root and often with prominent fusiform lateral roots; sometimes with milky sap. Leaves in rosette or rather congested, petiolate or sessile with petioliform bases, usually narrowly winged, not sheathing; blade ovate to oblanceolate, crenate to pinnately lobed, trinervate to pinnately veined, smooth to prominently bullate, glabrous to pilose above, whitish tomentose below. Inflorescence with 1 or a few clustered sessile heads. Heads broadly campanulate; involucre bracts 40–50 in about 4 series, slightly to strongly unequal, oblong to lanceolate, outer bracts digitately lobed to blunt or acute, inner bracts acute to acuminate, outer surface white-tomentose to pilose; receptacle with high ridges enclosing bases of achenes, without chaff. Flowers yellow. Ray flowers ~20–35, in 1 series, corolla with tube hirsute above, limbs linear with sparse to dense tomentum on abaxial surface, style branches spiralled. Disk flowers ~20–35, corollas mostly 15–23 mm long, narrowly funnelform, not abruptly expanded at base of throat, tube very long, upper tube and most of throat puberulous; lobes with stomates along distal margin, glabrous or with a few stipitate glands near tip; walls of cells of anther collars not strongly annulated; anther thecae pale, not digitate at base, median endothelial cells elongate, oblong with strap-shaped to oval sclerified shields, attenuate and often uncinuate at upper and lower ends; appendages smooth, cells mostly short-oblong with mostly truncate end walls; nectary short, cylindrical, unlobed; style base scarcely noduliferous, not or scarcely narrowed above into shaft of style; style branches slender, elongate, up to 5 mm long, abaxial hairs not or scarcely extending below bases of branches

onto shaft of style. Achenes when mature 4–5 mm long, prismatic with ~10 ribs, glabrous or with sparse setae or tomentum, cells of achene walls containing elongate raphids; carpodium a narrow rim of ~3–5 rows of rather small, subquadrate cells, cell walls slightly thickened, porose; pappus with 45–80 capillary setae, 1–2 cm long in 2–3 series, with a few shorter, often finer-tipped, outer setae, without distinct outer series, teeth of setae simple. Pollen grains 35–45  $\mu\text{m}$  in diameter, spines mostly evenly dispersed, without columellae or with 1–3 slender strands.

The sessile rosette of *Paranephelius* is a habit shared by a number of other genera of Asteraceae in the Andes, most notably *Werneria* and a few species of *Senecio* such as *S. macrorrhizus* Weddell and *S. werneroides* Weddell in the Senecioneae and a number of species of *Hypochaeris* in the Lactuceae. The members of the Senecioneae can be distinguished from *Paranephelius* most easily by the single series of equal involucre bracts, which are often partially fused in *Werneria*. Closer examination will also show truncate style branches in the disk flowers, short-lobed, glabrous, disk corollas, and narrowed appendages on the anthers. *Hypochaeris* is readily distinguished by the ligulate corollas and by the plumose setae of the pappus.

The fusiform lateral roots seen on many species of *Paranephelius* are unique in the tribe but are approached in form by roots of many genera specialized for similar habitats. Such roots have not been seen in some species of the genus, such as *P. ferreyrii*, and are comparatively sparse or lacking in *P. ovatus*, but the apparent differences may be more the result of faulty collecting of underground parts of the plants.

*Paranephelius* is the only genus in the tribe with tomentum on the outer surfaces of the ray corollas. Such tomentum was lacking in *P. ovatus* according to Weddell (1855–1857). The latter species does show only slight tomentum on the rays of most specimens, but tomentum is apparently present in all the species of the genus. On younger rays the tomentum is usually dense, but it may

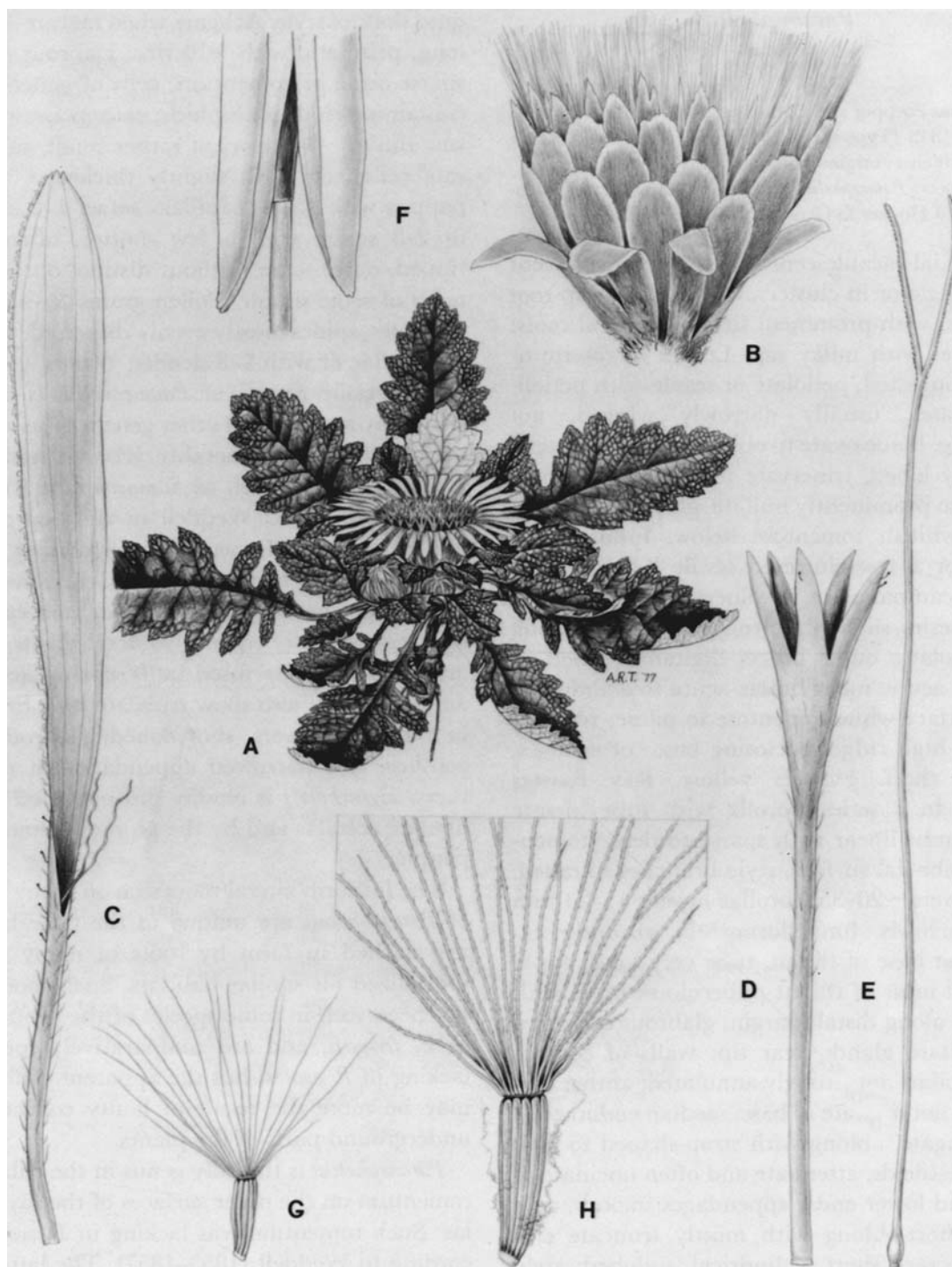


FIGURE 11.—*Pavanephelus uniflorus* Poeppig & Endlicher: A, habit,  $\times \frac{1}{2}$ ; B, head,  $\times 3\frac{1}{2}$ ; C, ray corolla,  $\times 10$ ; D, disk corolla,  $\times 10$ ; E, disk style,  $\times 10$ ; F, bases of anther thecae,  $\times 50$ ; G, achene,  $\times 2\frac{1}{2}$ ; H, achene,  $\times 5$ .

not be obvious on the fully expanded mature corollas.

The achenes of *Paranephelius* are larger than those of most other members of the tribe and are present in mature form in a number of collections. The latter feature is not seen in specimens of most other Liabeae. Because of the habitat of the genus and the size of the achenes, it is suspected that achenes of *Paranephelius* have a longer viability than those of other members of the tribe.

The following seven species are recognized from Peru, Bolivia, and Argentina.

*Paranephelius asperifolius* (Muschler) H. Robinson and Brettell, *Phytologia*, 28(1):59, 1974. Bolivia, Argentina.

*Liabum asperifolium* Muschler, *Engl. Bot. Jahrb.* 50, Beibl., 3:78, 1913.

*Paranephelius bullatus* A. Gray ex Weddell, *Chlor. And.*, 1:214, 1855. Peru.

*Paranephelius ferreyrii* H. Robinson, *Phytologia*, 35(3):235, 1977. Peru.

*Paranephelius jelskii* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):59, 1974. Peru.

*Liabum jelskii* Hieronymus, *Engl. Bot. Jahrb.*, 36:499, 1905.

*Paranephelius ovatus* Weddell, *Chlor. And.*, 1:214, pl. 37b, 1855. Peru, Bolivia.

*Liabum ovatum* (Weddell) J. Ball, *Journ. Linn. Soc.*, 22:46, 1885.

*Paranephelius uniflorus* Poeppig and Endlicher, *Nov. Gen. et Sp.*, 3:42, pl. 248, 1843. Peru, Bolivia.

*Liabum uniflorum* (Poeppig and Endlicher) Schultz-Bipontinus, *Flora*, 36:34, 1853.

*Paranephelius wurdackii* H. Robinson, *Phytologia*, 35(3):236, 1977. Peru.

Distinctions of many of the species are discussed by Robinson (1977b), but no key has been prepared.

### *Pseudonosseris*

#### FIGURE 12

*Pseudonosseris* H. Robinson and Brettell, *Phytologia*, 28(1):59, 1974. [Type-species: *Liabum striatum* Ferreyra.]

Perennial acaulescent or short-stemmed herbs usually in clusters, with distinct tap root, with milky sap. Leaves opposite, sometimes in rosettes, sessile, oblanceolate, base slightly auriculate, margin crenate to deeply lobed, pinnately veined,

upper surface rugose to nearly smooth, white-tomentose below. Inflorescence scapose or subsca-pose, with sparse alternate branches above. Heads broadly campanulate; involucre bracts ~40 in ~4 series, unequal, lanceolate, outer bracts narrowly acute, inner bracts long-attenuate, pilose to stipitate-glandular on outer surface; receptacle weakly alveolate, subglabrous. Flowers yellow or reddish. Ray flowers 15–20 in 1–2 series, corolla with tube puberulous, limbs linear, usually yellow (reddish in *P. szyszylowiczii*); style branches elongate, not spiralled. Disk flowers 25–55, narrowly funnelform, not abruptly expanded at base of throat, tube long, upper tube and lower throat hirsute; lobes with stomates along margins, glabrous or with single glands distally on outer surface, walls of cells of anther collars not strongly annulated; anther thecae pale, not digitate at base, shields of median endothelial cells oval with nodular thickenings at upper and lower ends; appendages shortly ovate to oblong, 1–1½ times as long as wide, smooth, cells rather elongate with truncate or oblique end walls; nectary short, not lobed; style base with a large node tapering into the broad shaft; style branches slender, ~3–4 mm long, filiform, tapering distally, hispidulous surface not or scarcely extending onto upper part of shaft. Achenes prismatic, obovate, slightly narrowed below, with ~10 strong ribs, sparsely setuliferous, cells of achene wall containing elongate raphids; carpopodium short-cylindrical, with rather large cells in 5–10 series, walls of cells noduliferous; pappus with 25–30 somewhat persistent inner setae in a single series, with outer series of short, narrow, squamiform setae, teeth of setae simple. Pollen grains 35–45 µm in diameter, spines evenly dispersed, without columellae or with minute tenuous columellae under spines.

The usually subrosulate habit, the long tubes of the disk corollas, the long slender branches of the disk styles, and the elongate raphids of the achene wall are all consistent with the assumed relationship of *Pseudonosseris* with *Paranephelius*. The occurrence at generally lower elevations, the presence of latex, the erect branching inflorescences, the simple low-alveolate surface of the

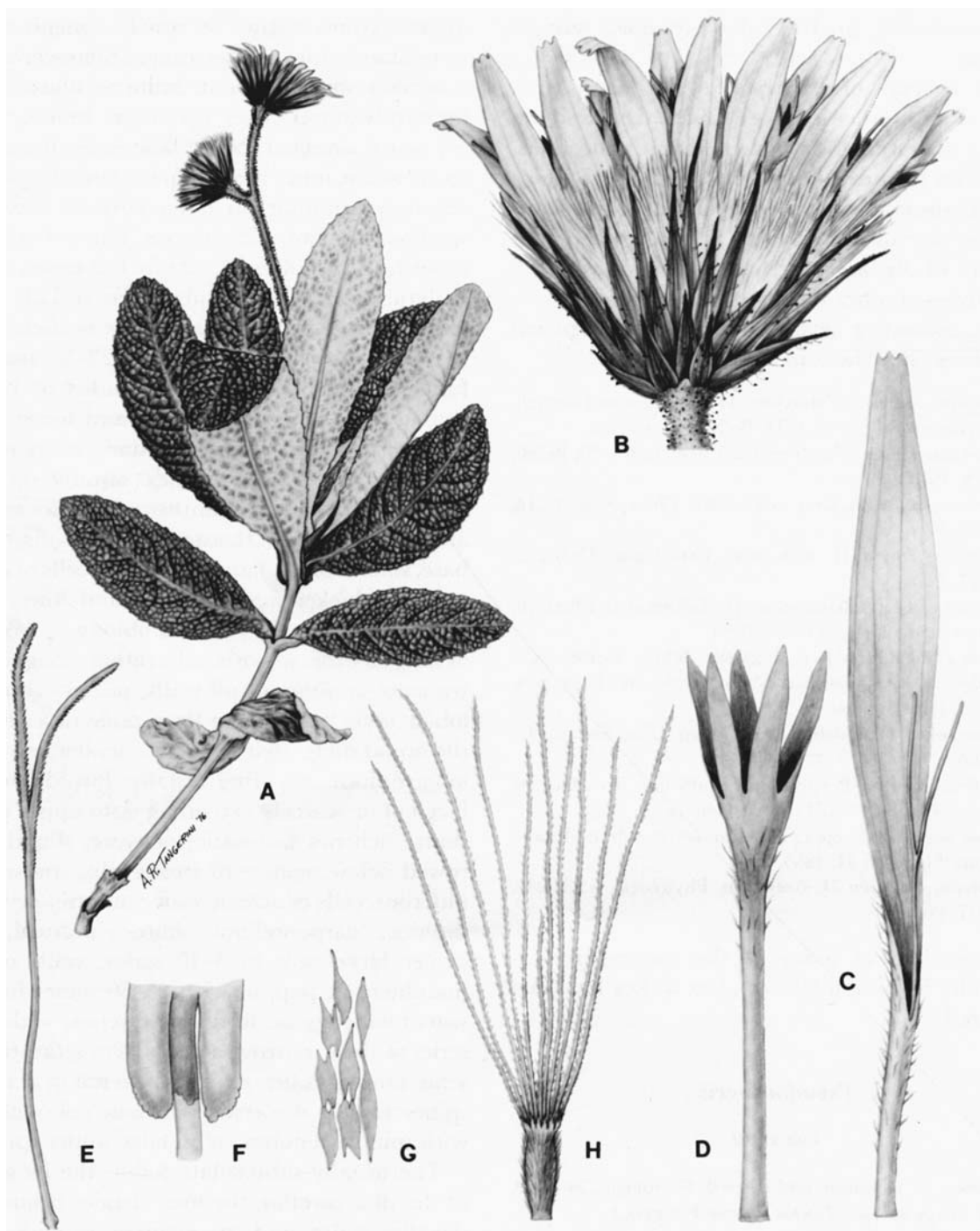


FIGURE 12.—*Pseudonosyris discolor* (Muschler) Robinson & Brettell: A, habit,  $\times \frac{1}{2}$ ; B, head,  $\times 3\frac{1}{2}$ ; C, ray corolla,  $\times 8$ ; D, disk corolla,  $\times 8$ ; E, disk style,  $\times 8$ ; F, bases of anther thecae,  $\times 35$ ; G, median endothelial cells,  $\times 400$ ; H, achene,  $\times 8$ .

receptacle, and the more differentiated outer series of the pappus would all indicate a less specialized condition of *Pseudonoseresis* in the subtribe. Nevertheless, similarities between all three of the widely separated species of *Pseudonoseresis* indicate that they are more closely related to one another than any are to *Paranephelium* and that they are not simply relicts of an older stock of the subtribe.

In *Pseudonoseresis*, the leaves all have blades continuing to the base and forming auricles at the node, and the venation is strictly pinnate. The inflorescence always has a lax alternate branching with long-stalked glands on the pedicels and involucre, and the involucre is multiseriate with narrow, often attenuate bracts. The two northern species have lobed leaves and achenes with heavily corticated ribs, in contrast to the more southern *P. discolor*. One species, *P. szyszyłowiczii*, has reddish or reddish-orange flowers.

All three species of *Pseudonoseresis* are found in Peru, but they are from widely separated localities; *P. discolor* is from Puno near the Bolivian border, *P. szyszyłowiczii* is from the eastern slope of the Andes in the Dept. of Amazonas, and *P. stricta* is from the coastal range in Lambayeque.

The three species are as follows.

- Pseudonoseresis discolor* (Muschler) H. Robinson and Brettell. *Phytologia*, 28(1):60, 1974. Peru.  
*Onoseris discolor* Muschler. *Engl. Bot. Jahrb.* 50, Beibl., 3:94, 1913 [non *Liabum discolor* Humboldt, Bonpland, and Kunth].  
*Liabum lanatum* Ferreyra, *Bol. Soc. Peru. Bot.*, 1:17, 1948.  
*Pseudonoseresis striata* (Cuatrecasas) H. Robinson and Brettell, *Phytologia*, 28(1):60, 1974. Peru.  
*Liabum striatum* Cuatrecasas, *Collect. Bot., Barcinone*, 3:306, 1953.  
*Pseudonoseresis szyszyłowiczii* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):60, 1974. Peru.  
*Liabum szyszyłowiczii* Hieronymus, *Engl. Bot. Jahrb.*, 36:503, 1905.

### MUNNOZIINAE, new subtribe

Munnoziinae, subtribus nov. Plantae herbaeae perennes vel raro annuae interdum subscandentes vel procumbentes; folia saepe in marginis angulatae plus minusve trinervatae vel palmatinervatae. Capitula solitaria aut in paniculo dis-

posita; corollae disci in faucibus saepe abrupte expansae; antherae plerumque nigrescentes, thecis base non denticulatis, cellulis endothecialibus in partibus scleroideis plerumque contiguus; rami stylorum breves; raphides achaeniorum quadratae. Grana pollinis regulariter vel irregulariter spinosa, spinis intus columellatis vel variabiliter caveatis.

Type genus: *Munnozia* Ruiz and Pavon.

The subtribe can be divided into two groups, each containing two genera. *Chrysactinium* and *Munnozia* have tomentum on their stems and leaves as in most Liabeae but have pollen grains with regularly dispersed spines. *Erato* and *Philoglossa* have large stiff hairs on their stems and leaves and have pollen with irregularly dispersed spines. The subtribe is mostly South American, but three species reach Costa Rica. The four genera are as follows.

### *Chrysactinium*

FIGURE 13

- Chrysactinium* (Humboldt, Bonpland, and Kunth) Weddell, *Chlor. And.*, 1:212, 1856.  
*Andromachia* sect. *Chrysactinium* Humboldt, Bonpland, and Kunth, *Nov. Gen. et Sp.*, ed. folio, 4:77, 1818. [Lectotype: *Andromachia acaulis* Humboldt, Bonpland, and Kunth.]

Small perennial herbs; without reports of milky sap. Leaves opposite, in basal rosettes, or crowded on short stems, sessile with cuneate or petioliform bases; blades obovate, trinervate from near basal fourth, entire to dentate, green above with or without pilosity or arachnoid pubescence, tomentose below. Inflorescence with long unbranched erect peduncles bearing solitary heads, peduncles covered with arachnoid pubescence, with scattered purplish hairs. Heads broadly campanulate. Involucral bracts 40–60 in ~4 series, strongly unequal, narrowly ovate to lanceolate, tips sharply acute to acuminate, outer surface glabrous to glabrescent; receptacle with chaff prominent, narrowly lanceolate. Flowers yellow. Rays 30–60, tubes of corollas puberulous, limbs narrowly elliptical to linear, glabrous, slightly trilobed at tips; style branches elongate, not spi-

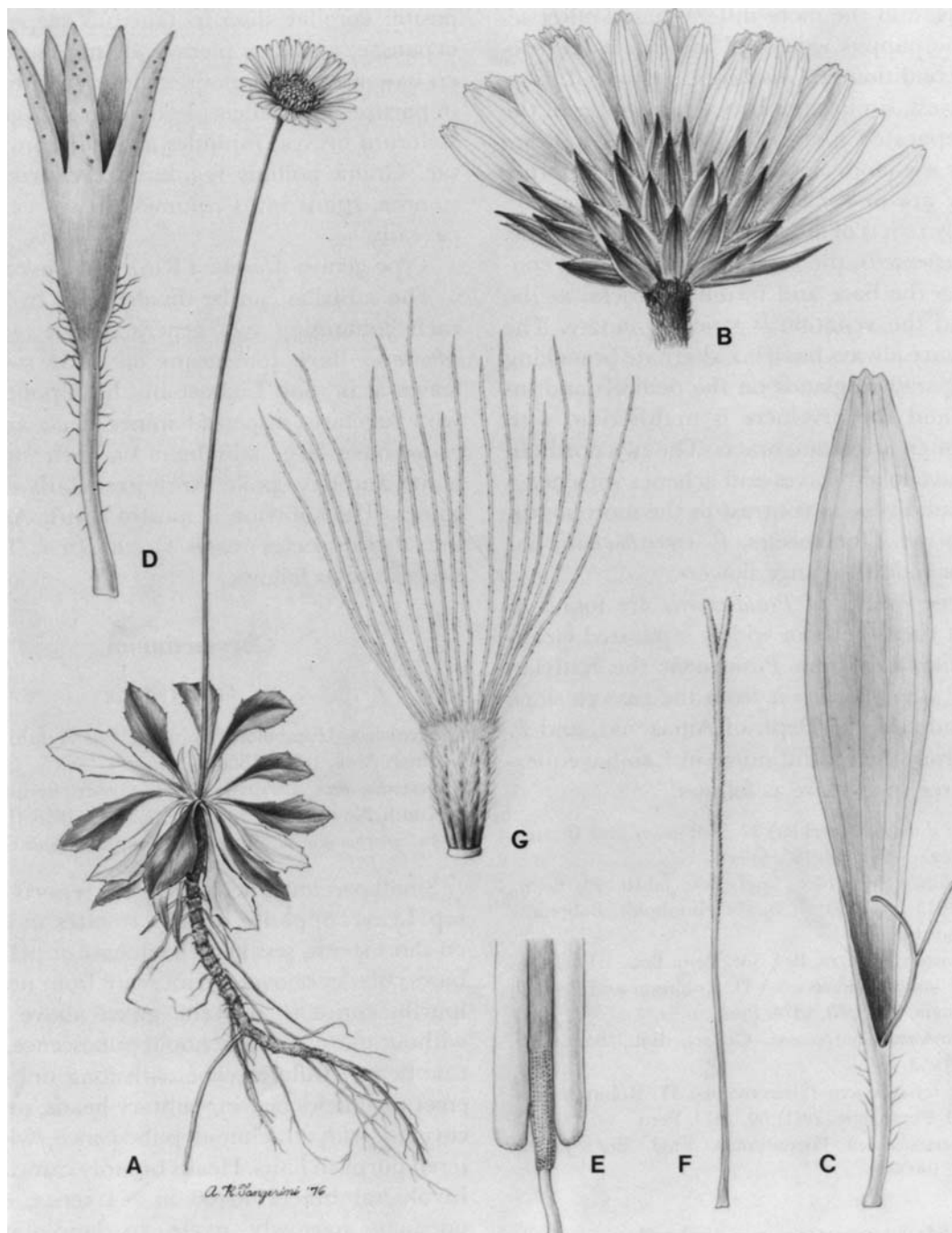


FIGURE 13.—*Chrysactinium acaule* (Humboldt, Bonpland, and Kunth) Weddell: A, habit,  $\times \frac{1}{2}$ ; B, head,  $\times 2\frac{1}{2}$ ; C, ray corolla,  $\times 8$ ; D, disk corolla,  $\times 13$ ; E, anther collar and bases of thecae,  $\times 45$ ; F, disk style,  $\times 13$ ; G, achene,  $\times 13$ .

ralled. Disk flowers 50–100?; upper tube and lower throat of corolla hirsute on outer surface; throat rather abruptly expanded at base; lobes with stomates near margin, with only sessile, short-stalked glands on outer surface; cells of anther collar densely annulated, cross walls obscure; thecae all or partly black, not digitate at base; median endothelial cells oblong with simple broad oval or strap-shaped sclerified band, with single thickening on transverse wall; appendages smooth, cells rather elongate with truncate or oblique end walls; nectary not or slightly lobed; style base with distinct node; branches short, less than 1/2 as long as the hirtellous upper part of the shaft, with rounded tips. Achenes prismatic, puberulous, cells of achene wall containing small quadrate raphids; carpodium distinct, annuliform, with subquadrate to suboblong cells in 3–5 series, cell walls slightly thickened; pappus white, with 30–60 hispid slender-tipped capillary setae, fragile at base, teeth of setae simple, without shorter setae in outer series. Pollen grains 30–40  $\mu\text{m}$  in diameter, with spines regularly dispersed, with distinct columellae under spines.

The name "*Chrysactinium*" is unfortunately close to that of another asteraceous genus, *Chrysactinia* A. Gray of the Heliantheae (Pectidinae). The *International Code of Botanical Nomenclature* does not prohibit such names when the endings differ in gender, but such similar names would not have been chosen intentionally, especially for members of the same family.

The genus *Chrysactinium* is closely related to *Munnozia*, from which it is superficially most distinct in the reduced acaulescent habit with long-scapose heads. A more complete study shows that the habit does not accurately distinguish between the genera, some species of *Chrysactinium* having more elongate vegetative stems similar to those in some of the smaller species of *Munnozia* such as *M. ferreyrii*, *M. (Kastnera) nivea*, and *M. perfoliata*. The appearance of intergradation in habits, itself, is misleading, however, since the genera are completely distinct in a number of details that seem to indicate a significant phyletic gap. In *Chrysactinium*, the cells of the anther collar always have

dense annular thickenings, whereas none are seen in *Munnozia*, and the corolla lobes of *Chrysactinium* have only small sessile glands, never the longer hairs or glands usually present near the lobe tips in *Munnozia*. It is convenient that the pappus of *Chrysactinium* is pure white, whereas that in all species seen in *Munnozia* is darkened or discolored in some way, thus providing the most easily observed reliable distinction between the genera.

In *Chrysactinium*, as in *Munnozia*, the stout hairs or pilosity on the upper surface of the leaves has been used as a species character, and here, as in *Munnozia*, the character has been found unreliable. An apparently reliable species character is the greater length of the projections on the receptacle in *C. hieracioides* reported by Robinson (1978a), but the feature is of limited use, since it is usually hidden within the flowering heads, and specimens rarely have more than one or two heads. Hieronymus (1895) described the achenes of *C. longiradiatum* as glabrous, but this is presumed to be an error based on immature material. No glabrous achenes have been seen in the genus.

The following six species are known, ranging from central Ecuador south to central Peru.

- Chrysactinium acaule* (Humboldt, Bonpland, and Kunth) Weddell, Chlor. And., 1:212, 1857. Ecuador.  
*Andromachia acaulis* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp., ed. folio, 4:77, 1818.  
*Liabum acaule* (Humboldt, Bonpland, and Kunth) Lessing, Linnaea, 6:696, 1831.  
*Liabum arthrothrix* Blake, Journ. Wash. Acad. Sci., 17:288, 1927.  
*Chrysactinium arthrothrix* (Blake) H. Robinson and Brettell, Phytologia, 28(1):49, 1974.  
*Chrysactinium amphothrix* (Blake) H. Robinson and Brettell, Phytologia, 28(1):49, 1974. Peru.  
*Liabum amphothrix* Blake, Journ. Wash. Acad. Sci., 17:290, 1927.  
*Chrysactinium caulescens* (Hieronymus) H. Robinson and Brettell, Phytologia, 28(1):50, 1974. Ecuador, Peru.  
*Liabum caulescens* Hieronymus, Engl. Bot. Jahrb., 36:500, 1905.  
*Liabum bicolor* Blake, Journ. Wash. Acad. Sci., 17:290, 1927.  
*Chrysactinium bicolor* (Blake) H. Robinson and Brettell, Phytologia, 28(1):49, 1974.  
*Chrysactinium hieracioides* (Humboldt, Bonpland, and Kunth)

- H. Robinson and Brettell, *Phytologia*, 28(1):50, 1974. Ecuador, Peru.
- Andromachia hieracioides* Humboldt, Bonpland, and Kunth, *Nov. Gen. et Sp.*, ed. folio, 4:77, 1818.
- Liabum hieracioides* (Humboldt, Bonpland, and Kunth) Lessing, *Linnaea*, 6:699, 1831.
- Chrysactinium longiradiatum* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):50, 1974. Ecuador.
- Liabum longiradiatum* Hieronymus, *Engl. Bot. Jahrb.*, 21:352, 1895.
- Liabum tenuius* Blake [as *tenuior*], *Journ. Wash. Acad. Sci.*, 17:289, 1927.
- Chrysactinium tenuius* (Blake) H. Robinson and Brettell, *Phytologia*, 28(1):50, 1974.
- Chrysactinium rosulatum* (Hieronymus) H. Robinson and Brettell, *Phytologia*, 28(1):50, 1974. Peru.
- Liabum rosulatum* Hieronymus, *Engl. Bot. Jahrb.*, 36:501, 1905.

The species occurring in Ecuador have been treated by Robinson (1978a).

### *Erato*

#### FIGURE 14

- Erato* DeCandolle, *Prodr.*, 5:318, 1836. [Type-species: *Erato polymnioides* DeCandolle; originally monotypic.]
- Munnozia* subg. *Erato* (DeCandolle) H. Robinson and Brettell, *Phytologia*, 28(1):56, 1974.

Coarse perennial herbs or subshrubs. Stems, stipule-like sheaths, both surfaces of leaves, and peduncles pilose or strigose with stiff bulbous-based hairs. Stems with milky sap, lengths of internodes variable without pattern. Leaves opposite; stipule-like bases broadly oblong, usually deeply emarginate; petioles unwinged; blades somewhat succulent with 5–9 radiating veins from base, margins of larger leaves coarsely toothed or serrate, upper surface green, lower surface pale green, without tomentum. Inflorescence cymose to subumbellate; peduncles elongate. Heads broadly campanulate. Involucral bracts 40–100 in ~4 series, unequal, broadly ovate to lanceolate, outer bracts fleshy at base, with obtuse herbaceous tips often tomentose at tip, margins densely ciliate with stiff hairs; receptacle foveolate with unlobed or slightly lobed puberulous ridges. Flowers yellow. Ray flowers 75–230, in 2–3 series, tubes usually puberulous above, limbs linear and

glabrous, deeply notched at tip, often 3-lobed; style branches elongate, not spiralled. Disk flowers 20–150; tube and lower throat of corolla hirsute on outer surface, throat abruptly expanded at base, lobes with large stomates near margin, strongly spiculiferous at tip; cells of anther collars not or weakly annulated on walls; thecae black, not digitate at base; median endothelial cells oblong with sparse minute thickenings mostly on vertical walls; appendages oblong (sometimes tapering in *E. polymnioides*), smooth, with basal cells rather elongate, apical cells shorter to subquadrate; nectary elongate, slightly lobed; style base with distinct node; style branches short, usually less than 1/2 as long as the hirtellous portion of the upper shaft, with obtuse to rounded apices. Achenes mostly 4-sided, glabrous or hispidulous, cells of achene wall with small quadrate raphids; carpodium distinct with large subquadrate cells in ~5 series, cell walls thin; pappus setae 25–50, capillary or short and awn-like, sordid white to brownish-red, strongly spreading and persistent or easily deciduous, scabrid with simple teeth. Pollen grains 30–40  $\mu\text{m}$  in diameter, with spines somewhat unevenly dispersed, with distinct stout internal columellae grouped under spines.

The genus *Erato* was originally placed in a position remote from other Liabaeae by DeCandolle (1836) and close to elements now included in *Baccharis* of the Astereae. The genus was first placed in *Liabum* by Bentham in Bentham and Hooker (1873), along with all other elements now placed in the Liabaeae that have a basically capillary pappus. *Erato* was placed in a broad concept of *Munnozia* in the generic revision of the tribe Liabaeae by Robinson and Brettell (1974b) but was restored to separate generic status during a study of the members of the tribe in Ecuador (Robinson, 1976d, 1978a). The position of the genus is obviously closest to *Philoglossa*, with which it shares the same type of stiff hairs on the stems and leaves. The achenes of both genera also share a reduced number of ribs or angles, four in *Erato* and two in *Philoglossa*.

*Erato* almost totally lacks the arachnoid pubes-



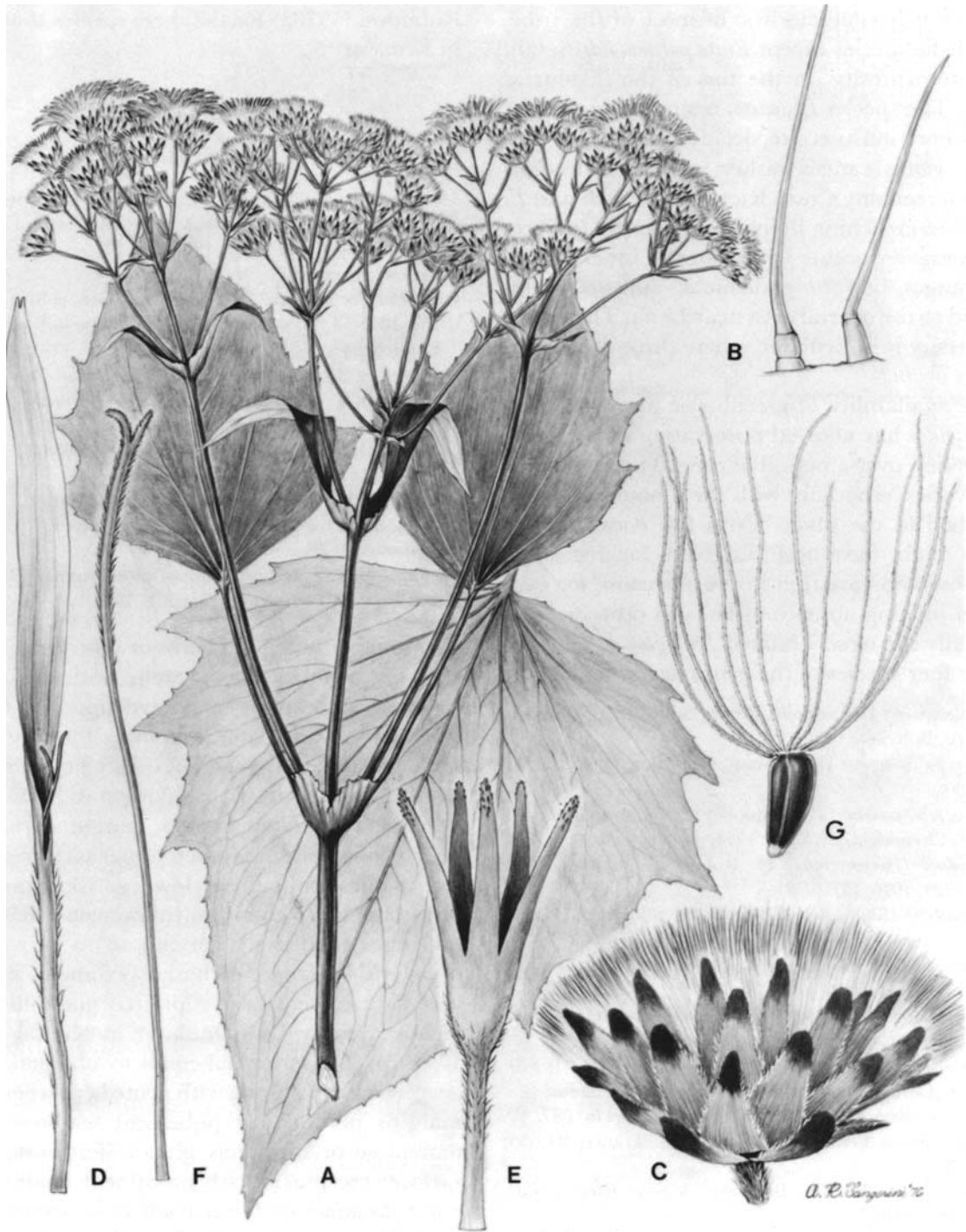


FIGURE 14.—*Erato polymnioides* DeCandolle: A, habit,  $\times \frac{1}{2}$ ; B, foliar hairs,  $\times 50$ ; C, head, post anthesis,  $\times 3\frac{1}{2}$ ; D, ray corolla,  $\times 10$ ; E, disk corolla,  $\times 10$ ; F, disk style,  $\times 10$ ; G, achene,  $\times 10$ .

cence that is characteristic of most of the tribe, but all the species except *Erato polymnioides* retain slight tomentosity on the tips of the involucre bracts. The species *E. sodiroi* is singularly distinct in the short, multiseriate, deciduous pappus awns.

The genus ranges rather widely, with *Erato vulcanica* reaching Costa Rica in the north and *E. polymnioides* reaching Bolivia in the south. In Peru, *E. polymnioides* occurs widely in the inner mountain ranges, but the endemic *E. stenolepis* is restricted to the coastal area near Lima. The center of diversity is in Ecuador, where three of the four species occur.

The availability of greenhouse plants of *Erato polymnioides* has allowed observation of the latex production over a period of time. The amount of latex varies, especially with the amount of water furnished to the plant. On a few occasions the plants might have been judged as lacking latex. The observed variation in *Erato* is cause for caution in judging absence of latex in other genera, especially the closely related *Philoglossa*.

The four species of the genus are as follows.

- Erato polymnioides* DeCandolle, Prodr., 5:318. 1836. Ecuador, Peru, Bolivia.  
*Liabum pallatangense* Hieronymus, Engl. Bot. Jahrb., 29:60, 1900.  
*Munnozia polymnioides* (DeCandolle) H. Robinson and Brettell, Phytologia, 28(1):56, 1974.  
*Erato sodiroi* (Hieronymus) H. Robinson, Phytologia, 34(4):379, 1976. Ecuador.  
*Erato stenolepis* (Blake) H. Robinson, Phytologia, 34(4):379, 1976. Peru.  
*Liabum stenolepis* Blake, Journ. Wash. Acad. Sci., 17:302, 1927.  
*Munnozia stenolepis* (Blake) H. Robinson and Brettell, Phytologia, 28(1):57, 1974.  
*Erato vulcanica* (Klatt) H. Robinson, Phytologia, 34(4):379, 1976. Costa Rica, Colombia, Venezuela, Ecuador.  
*Liabum vulcanicum* Klatt, Engl. Bot. Jahrb., 8:47, 1887.  
*Liabum anatina* Benoist, Bull. Soc. Bot. France, 84:633, 1938.  
*Liabum insigne* Badillo, Bol. Soc. Venez. Cienc. Nat., 10:313, 1946.  
*Munnozia anatina* (Benoist) H. Robinson and Brettell, Phytologia, 28(1):56, 1974.  
*Munnozia vulcanica* (Klatt) H. Robinson and Brettell, Phytologia, 28(1):57, 1974.

A key and descriptions have been provided by

Robinson (1978a) for the three species that occur in Ecuador.

## Munnozia

FIGURE 15

- Munnozia* Ruiz and Pavon, Fl. Peruv. Chil. Prodr., 108, 1794. [Lectotype: *Munnozia lanceolata* Ruiz and Pavon.]  
*Alibum* Lessing, Syn. Comp., 152, 1832. [Type-species: *Alibum liaboides* Lessing.]  
*Prionolepis* Poeppig and Endlicher, Nov. Gen. et Sp., 3:55, pl. 261, 1845. [Type-species: *Prionolepis silphioides* Poeppig and Endlicher.]  
*Liabum* subg. *Chrysastrum* Willdenow ex Schultz-Bipontinus, Flora, 36:37, 1853. [Lectotype: *Liabum sagittatum* Schultz-Bipontinus (= *Munnozia senecionidis* Benth.)]  
*Kastnera* Schultz-Bipontinus, Flora, 36:37, 1853. [Type-species: *Kastnera tenera* Schultz-Bipontinus.]  
*Chrysastrum* Willdenow ex Weddell, Chlor. And., 1:211, 1857 [in nota: nom. nud. in syn.]. [Type-species: *Chrysastrum sagittatum* Willdenow ex Weddell.]  
*Munnozia* subg. *Kastnera* (Schultz-Bipontinus) H. Robinson and Brettell, Phytologia, 28(1):57, 1974.

Annual or perennial herbs or subshrubs, low or creeping to subscandent. Stems with distinct internodes, with milky sap. Leaves opposite. Petiole bases often auriculate, sometimes forming nodal disk, not sheathing; petioles distinct, sometimes winged; blade with base rounded to hastate, trinervate or pinnately veined, margin serrulate to deeply lobed or pinnatisect, upper surface tomentose to pilose or glabrous, lower surface tomentose or rarely nearly glabrous. Inflorescence terminal, sparingly to densely corymbose to subcymose, often with ultimate dichasia; peduncles short to very long, tomentose to stipitately glanduliferous. Heads broadly campanulate; involucre bracts 17–70 in 2–4 series, subequal to unequal, outer bracts ovate to oblong with acute herbaceous tips, margins not densely pubescent, glabrescent to tomentose or stipitately glanduliferous on outer surface; receptacle with prominent chaff of lacinate squamae (without chaff in subgenus *Kastnera*). Flowers yellow (in 2 species with ray and sometimes disk corollas whitish, becoming lavender). Rays 6–70; corolla with upper tube often hirsute, limbs linear, usually with some hairs or glands, with short lobes at tip; style branches not

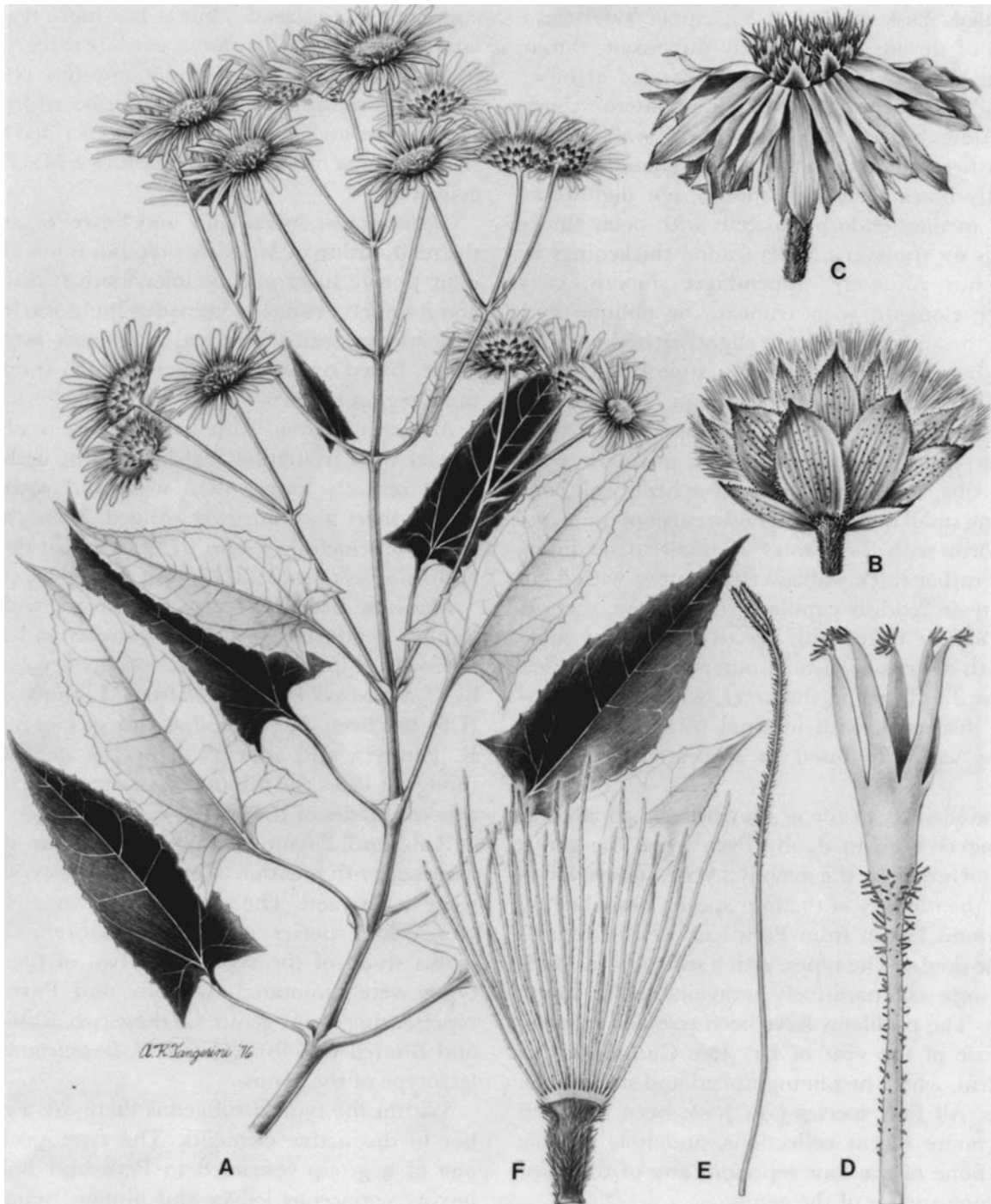


FIGURE 15.—*Mumozia senecionidis* Bentham: A, habit,  $\times \frac{1}{2}$ ; B, head, post anthesis,  $\times 2\frac{1}{2}$ ; C, older head showing receptacular chaff,  $\times 2\frac{1}{2}$ ; D, disk corolla,  $\times 7\frac{1}{2}$ ; E, disk style,  $\times 7\frac{1}{2}$ ; F, achene,  $\times 7$ .

spiralled. Disk flowers 9–85; upper tubes and bases of throats often densely pubescent, throat rather abruptly to bulbously expanded at base; lobes with large stomates along lateral veins, sometimes bearing stout hairs at tip; walls of cells of anther collars not strongly annulated; thecae usually black, pale in 3 species, not digitate at base; median endothelial cells with polar thickenings on transverse walls (radial thickenings in subgenus *Kastnera*); appendages smooth, cells rather elongate with truncate or oblique end walls; nectary short, not or slightly lobed; mature style base with distinct node; style branches of disk flowers short, usually less than 1/2 as long as the hirtellous portion of the upper shaft, with obtuse to rounded tips. Achenes prismatic with 6–10 ribs, setuliferous, cells of achene wall containing small quadrate raphids; carpopodium annuliform with 3–12 rows of small to medium-sized rather thick-walled cells; pappus with 5–55 sordid or reddish capillary inner setae, scabrid with simple teeth, with few to many outer setae or with a series of distinct outer squamae. Pollen grains 27–40  $\mu\text{m}$  in diameter, with spines regularly dispersed, with internal columellae under spines variously fused or separated from foot layer.

The identity of the genus *Munnozia* apparently has never been in doubt, even when the genus was included in the synonymy of *Liabum*; however, the identity of the four species described by Ruiz and Pavon from Peru has been in considerable doubt. The types, which still exist in Madrid, were comparatively unavailable for many years. The problems have been resolved recently because of the visit of Dr. Jose Cuatrecasas to Madrid, where he photographed and studied the types. All four species now have been matched with more recent collections, and it is notable that none of the four represent any of the most common species of the genus.

The species of Ruiz and Pavon most readily identified was *M. corymbosa*, which is represented by a duplicate at Paris and a small fragment obtained by S.F. Blake in the U.S. National Herbarium. The species is closely related to the

common *M. senecionidis*, but it has more densely lanate stem and leaf surfaces, cordate rather than hastate bases on the leaf blades, and disk corolla lobes lacking apical hairs. It appears to be the same as *Liabum eriocalyx* that Blake described from the same area of Peru on the basis of a MacBride collection.

*Munnozia venosissima* Ruiz and Pavon is also in the relationship of *M. senecionidis*, but it has abundant purple hairs and petioles toothed distally, and it sometimes has prominent stipuliform lobes. The species seems identical to *Liabum pulchrum* Blake, based on a MacBride collection from the same region in Peru.

*Munnozia trinervis* Ruiz and Pavon is also a species with triangular leaf blades but with the blade scarcely longer than wide and with the petiole short and narrowly winged. More recent collections include *Vargas 4109* from Cuzco (F), and *Killip and Smith 22247* from Ayacucho (US).

*Munnozia lanceolata* Ruiz and Pavon, with its solitary heads, has very short petioles and firm, narrowly elliptical blades. A specimen collected by *Hutchison and Wright 5928* from Huanuco, Peru (US) has been determined as this species by Dr. R. Ferreyra and appears to be the species, although it lacks the minute basal auricles seen on the leaf blades of the type.

Ruiz and Pavon (1794) described the genus *Munnozia* with mention of only two species, which were not named. The same authors later (1798) named four species. As noted by Cabrera (1960) in his study of the types, only two of the four types were annotated by Ruiz and Pavon as representing a new genus. Of these two, Robinson and Brettell (1974b) selected *M. lanceolata* as the lectotype of the genus.

Within the typical subgenus there are a number of distinctive elements. The type-species is one of a group restricted to Peru and Bolivia, having coriaceous leaves and pinnate venation. Most members of the genus have herbaceous or even membranaceous trinervate leaves. Two species, *M. jussieui* and *M. campii*, have flowers that are usually whitish, sometimes turning lavender. Apparently, rare yellow-flowered forms of *M. jus-*

*sieui* are known. Three species, *M. hastifolia*, *M. maronii*, and *M. subviridis*, characteristically have pale anther thecae, lacking the blackish color that is otherwise characteristic of the subtribe.

The subgenus *Kastnera* is a completely natural group originally distinguished because of the lack of chaff or projections on the receptacle. Subsequent investigation shows differences from other *Munnoziae* in the consistent lack of connation between the stipule-like lobes of paired leaves, in the strongly differentiated, often enlarged outer pappus elements, in the reduced number of inner pappus setae, and in the radial pattern of nodular thickenings on both transverse and vertical walls of the endothelial cells. In spite of these differences, the close relation and close similarity to other parts of *Munnozia* are evident, and separate generic status seems unnecessary and counterproductive. For others of a different opinion, it should be noted that the name "*Alibum* Lessing" would take precedence at the generic level.

In the revision of the tribe by Robinson and Brettell (1974b), the type-species of *Alibum*, *A.*

*liaboides* Lessing of Ecuador, was mistakenly regarded as the same as *M. lyrata* of Peru. On further examination, the two species prove thoroughly distinct, with *M. lyrata* not being a member of the subgenus *Kastnera*.

The subgenus *Kastnera* contains a number of species that are notable for their pinnately lobed or pinnatifid leaves. One of these, *M. annua*, has uniquely membranous and scarcely pubescent leaves, and it and *M. (Kastnera) nivea* are two of the few annuals in the tribe.

*Munnozia* is remarkable for the many taxonomically significant structural variations in the interior of the pollen wall (Robinson and Marticorena, in prep.). The pollen characters indicate that the *M. senecionidis*-*M. corymbosa* group is more closely related to the subgenus *Kastnera* than it is to the typical element of the genus. Other distinctive pollen types are seen in *M. lyrata* and *M. jussieui*.

The genus ranges from Costa Rica and Panama into Andean South America from Venezuela to Bolivia.

### Key to the Subgenera of *Munnozia*

- Receptacle with crests and projections; outer series of pappus with narrow segments; inner pappus bristles numerous; endothelial cells with nodular thickenings usually few or polarized; nodes of stem with stipuliform lobes often connecting between paired leaf bases ..... subgenus ***Munnozia***
- Receptacle without crests or projections; outer series of pappus often with rather broad segments; inner bristles 5-20, endothelial cells with radial thickenings; wings or lobes at bases of leaves never connecting across nodes ..... subgenus ***Kastnera***

The genus contains 40 known species, which are disposed in the subgenera as follows.

#### *Munnozia* subgenus *Munnozia*

- Munnozia affinis* (Blake) H. Robinson and Brettell, *Phytologia*, 28(1):54, 1974. Peru.
- Liabum affine* Blake, *Journ. Wash. Acad. Sci.*, 17:301, 1927.
- Munnozia angusta* (Blake) H. Robinson and Brettell, *Phytologia*, 28(1):54, 1974. Peru.
- Liabum angustum* Blake, *Journ. Wash. Acad. Sci.*, 17:295, 1927.
- Munnozia campii* H. Robinson, *Phytologia*, 35(1):38, 1976. Ecuador.
- Munnozia canarensis* (Cuatrecasas) H. Robinson and Brettell, *Phytologia*, 28(1):54, 1974. Ecuador.
- Liabum canarensis* Cuatrecasas, *Brittonia*, 8:46, 1954.
- Munnozia cardenasii* (Cabrera) H. Robinson and Brettell, *Phytologia*, 28(1):54, 1974. Bolivia.
- Liabum cardenasii* Cabrera, *Not. Mus. La Plata. Bot.*, 14:191, 1949.
- Munnozia chimboracensis* H. Robinson, *Phytologia*, 35(3):199, 1977. Ecuador.
- Munnozia convencionensis* (Cuatrecasas) H. Robinson and Brettell, *Phytologia*, 28(1):54, 1974. Peru.

- Liabum convencioneense* Cuatrecasas, Collect. Bot., Barcinone, 3:300, 1953.
- Munnozia corymbosa* Ruiz and Pavon, Syst. Veg. Peruv. Chil., 195, 1798. Peru.
- Liabum corymbosum* (Ruiz and Pavon) Schultz-Bipontinus, Flora, 36:34, 1853.
- Liabum eriocalyx* Blake, Journ. Wash. Acad. Sci., 17:297, 1927.
- Munnozia eriocalyx* (Blake) H. Robinson and Brettell, Phytologia, 28(1):54, 1974.
- Munnozia ferreyrii* H. Robinson, Phytologia, 34(4):381, 1976. Peru.
- Munnozia foliosa* Rusby, Bull. Torrey Bot. Cl., 54:312, 1927. Peru, Bolivia.
- Munnozia chrysanthemoides* Rusby, Bull. Torrey Bot. Cl., 54:313, 1927.
- Liabum herrerae* Cabrera, Rev. Univ. Cuzco, 33(87):119, 1945.
- Liabum foliosum* (Rusby) Ferreyra, Bol. Soc. Peru. Bot., 1:18, 1948.—Cabrera, Not. Mus. La Plata, Bot., 14:193, 1949.
- Munnozia herrerae* (Cabrera) H. Robinson and Brettell, Phytologia, 28(1):55, 1974.
- Munnozia fosbergii* H. Robinson, Phytologia, 34(4):382, 1976. Colombia.
- Munnozia gigantea* (Rusby) Rusby, Bull. Torrey Bot. Cl., 54:312, 1927. Peru, Bolivia.
- Liabum giganteum* Rusby, Bull. N.Y. Bot. Gard., 4:391, 1907.
- Munnozia glandulosa* (O. Kuntze) Rusby, Bull. Torrey Bot. Cl., 54:314, 1927. Bolivia.
- Liabum glandulosum* O. Kuntze, Rev. Gen., 3(2):163, 1898.
- Munnozia hastifolia* (Poeppig and Endlicher) H. Robinson and Brettell, Phytologia, 28(1):55, 1974. Colombia, Venezuela, Ecuador, Peru, Bolivia, Argentina.
- Liabum hastifolium* Poeppig and Endlicher, Nov. Gen. et Sp., 3:43, 1843.
- Heterotheca deltoidea* Klatt, Ann. Naturh. Hofmus. Wien, 9:358, 1894.
- Liabum laticiferum* Badillo, Bol. Soc. Venez. Cienc. Nat., 10:312, 1946.
- Munnozia hirta* (O. Kuntze) Rusby, Bull. Torrey Bot. Cl., 54:314, 1927. Bolivia.
- Liabum hirtum* O. Kuntze, Rev. Gen., 3(2):163, 1898.
- Munnozia jussieui* (Cassini) H. Robinson and Brettell, Phytologia, 28(1):55, 1974. Colombia, Ecuador [original citation by Cassini from Peru evidently in error].
- Andromachia jussieui* Cassini, Bull. Soc. Philom., 1817:184, 1817.
- Conyza stipulata* Vahl ex Cassini, loc. cit. [nom. nud. in syn.].
- Liabum jussieui* (Cassini) Cassini, Dict. Sci. Nat., 26:205, 1823.
- Liabum nonoense* Hieronymus, Engl. Bot. Jahrb., 29:59, 1900.
- Liabum nonoense* var. *microcephalum* Hieronymus, Engl. Bot. Jahrb., 28:625, 1901.
- Liabum tabanense* Cuatrecasas, Caldasia, 3:425, 1945.
- Munnozia nonoensis* (Hieronymus) H. Robinson and Brettell, Phytologia, 28(1):55, 1974.
- Munnozia tabanensis* (Cuatrecasas) H. Robinson and Brettell, Phytologia, 28(1):55, 1974.
- Munnozia karstenii* H. Robinson, Phytologia, 35(6):490, 1977. Colombia.
- Munnozia lanceolata* Ruiz and Pavon, Syst. Veg. Peruv. Chil., 196, 1798. Peru.
- Liabum lanceolatum* (Ruiz and Pavon) Schultz-Bipontinus, Flora, 36:34, 1853.
- Munnozia longifolia* Rusby, Bull. Torrey Bot. Cl., 54:313, 1927. Bolivia.
- Liabum hexagonum* Blake, Journ. Wash. Acad. Sci., 17:300, 1927.
- Munnozia lyrata* (A. Gray) H. Robinson and Brettell, Phytologia, 28(1):55, 1974. Peru.
- Liabum lyratum* A. Gray, Proc. Amer. Acad., 5:115, 1861.
- Munnozia maronii* (Andre) H. Robinson, Phytologia, 35(3):200, 1977. Bolivia.
- Andromachia maroni* Andre, Revue Horticole, 1887(21):496, 1887.
- Liabum corymbosum* Schultz-Bipontinus ex Klatt, Annal. Naturh. Hofmus. Wien, 9:363, 1894. [Not *L. corymbosum* (Ruiz and Pavon) Schultz-Bipontinus.]
- Munnozia klattii* H. Robinson and Brettell, Phytologia, 28(1):55, 1974.
- Munnozia olearioides* (Muschler) H. Robinson and Brettell, Phytologia, 28(1):55, 1974. Peru.
- Liabum olearioides* Muschler, Engl. Bot. Jahrb. 50, Beibl., 3:82, 1913.
- Munnozia oxyphylla* (Cuatrecasas) H. Robinson and Brettell, Phytologia, 28(1):55, 1974. Peru.
- Liabum oxyphyllum* Cuatrecasas, Collect. Bot., Barcinone, 3:303, 1953.
- Munnozia perfoliata* (Blake) H. Robinson and Brettell, Phytologia, 28(1):55, 1974. Colombia.
- Liabum perfoliatum* Blake, Journ. Wash. Acad. Sci., 17:291, 1927.
- Munnozia peruensis* (Cuatrecasas) H. Robinson and Brettell, Phytologia, 28(1):56, 1974. Peru.
- Liabum peruense* Cuatrecasas, Collect. Bot., Barcinone, 3:304, 1953.
- Munnozia pinnulosa* (O. Kuntze) H. Robinson and Brettell, Phytologia, 28(1):56, 1974. Bolivia.
- Liabum pinnulosum* O. Kuntze, Rev. Gen., 3(2):163, 1898.
- Munnozia deltoidea* Rusby, Bull. Torrey Bot. Cl., 54:315, 1927.
- Munnozia muricata* Rusby, Bull. Torrey Bot. Cl., 54:315, 1927.

- Munnozia rusbyi* (Britton) Rusby, Bull. Torrey Bot. Cl., 54:312, 1927. Bolivia.
- Liabum rusbyi* Britton, Bull. Torrey Bot. Cl., 19:263, 1892.
- Munnozia senecionidis* Benth. Pl. Hartweg., 134, 1844. Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia.
- Liabum sagittatum* Schultz-Bipontinus, Flora, 36:37, 1853.
- Liabum megacephalum* Schultz-Bipontinus, Flora, 36:38, 1853.
- Munnozia sagittata* Weddell, Chlor. And., 1:211, 1857.
- Chrysastrum sagittatum* Willdenow ex Weddell, loc. cit. [nom. nud. in syn.].
- Liabum hastatum* Britton, Bull. Torrey Bot. Cl., 19:263, 1892.
- Munnozia hastata* Weddell ex Britton, op. cit., 263 [nom. nud. in syn.; error for *M. sagittata* Weddell].
- Munnozia ariste-josephi* Rusby, Bull. Torrey Bot. Cl., 54:314, 1927.
- Munnozia attenuata* Rusby, Bull. Torrey Bot. Cl., 54:315, 1927.
- Munnozia strigulosa* Rusby, Bull. Torrey Bot. Cl., 54:317, 1927.
- Munnozia filipes* Rusby, Bull. Torrey Bot. Cl., 54:318, 1927.
- Munnozia laxiflora* Rusby, Bull. Torrey Bot. Cl., 54:319, 1927.
- Liabum isodontum* Blake, Journ. Wash. Acad. Sci., 17:298, 1927.
- Liabum taeniotrichum* Blake, Journ. Wash. Acad. Sci., 17:298, 1927.
- Munnozia isodonta* (Blake) H. Robinson and Brettell, Phytologia, 28(1):55, 1974.
- Munnozia megacephala* (Schultz-Bipontinus) H. Robinson and Brettell, Phytologia, 28(1):55, 1974.
- Munnozia sagittata* (Schultz-Bipontinus) H. Robinson and Brettell, Phytologia, 28(1):56, 1974 [nom. illeg.].
- Munnozia taeniotricha* (Blake) H. Robinson and Brettell, Phytologia, 28(1):56, 1974.
- Munnozia silphioides* (Poeppig and Endlicher) H. Robinson and Brettell, Phytologia, 28(1):56, 1974. Peru.
- Prionolepis silphioides* Poeppig and Endlicher, Nov. Gen. et Sp., 3:55, pl. 261, 1845.
- Liabum silphioides* (Poeppig and Endlicher) Blake, Journ. Wash. Acad. Sci., 17:301, 1927.
- Munnozia subviridis* (Blake) H. Robinson and Brettell, Phytologia, 28(1):56, 1974. Peru, Bolivia.
- Liabum subviride* Blake, Journ. Wash. Acad. Sci., 17:294, 1927.
- Munnozia trinervis* Ruiz and Pavon, Syst. Veg. Peruv. Chil., 195, 1798. Peru.
- Liabum trinerve* (Ruiz and Pavon) Schultz-Bipontinus, Flora, 36:34, 1853.
- Munnozia venosissima* Ruiz and Pavon, Syst. Veg. Peruv. Chil., 195, 1798. Peru.
- Liabum venosissimum* (Ruiz and Pavon) Schultz-Bipontinus, Flora, 36:34, 1853.
- Liabum pulchrum* Blake, Journ. Wash. Acad. Sci., 17:299, 1927.
- Munnozia pulchra* (Blake) H. Robinson and Brettell, Phytologia, 28(1):56, 1974.
- Munnozia wilburii* H. Robinson, Phytologia, 39(5):331, 1978. Costa Rica.

#### *Munnozia* subgenus *Kastnera*

- Munnozia acostae* (Chung) H. Robinson and Brettell, Phytologia, 28(1):54, 1974. Ecuador.
- Liabum acostae* Chung, Phytologia, 14(6):323, 1967.
- Munnozia annua* (Muschler) H. Robinson and Brettell, Phytologia, 28(1):57, 1974. Ecuador, Peru.
- Liabum annuum* Muschler, Engl. Bot. Jahrb. 50, Beibl., 3:84, 1913.
- Munnozia asplundii* H. Robinson, Phytologia, 34(4):380, 1976. Ecuador.
- Munnozia liaboides* (Lessing) H. Robinson, Phytologia, 35(1):38, 1976. Ecuador.
- Alibum liaboides* Lessing, Syn. Comp., 152, 1832.
- Liabum liaboides* (Lessing) Hieronymus, Engl. Bot. Jahrb., 19:63, 1894.
- Liabum alibum* Hieronymus, Engl. Bot. Jahrb., 28:627, 1901.
- Munnozia nivea* (Hieronymus) H. Robinson and Brettell, Phytologia, 28(1):57, 1974. Colombia, Ecuador, Peru.
- Liabum niveum* Hieronymus, Engl. Bot. Jahrb., 19:62, 1894.
- Liabum stuebelii* Hieronymus, Engl. Bot. Jahrb., 21:353, 1895.
- Munnozia pinnatipartita* (Hieronymus) H. Robinson and Brettell, Phytologia, 28(1):57, 1974. Ecuador.
- Liabum pinnatipartitum* Hieronymus, Engl. Bot. Jahrb., 29:62, 1900.
- Munnozia tenera* (Schultz-Bipontinus) H. Robinson and Brettell, Phytologia, 28(1):57, 1974. Colombia.
- Kastnera tenera* Schultz-Bipontinus, Flora, 36:38, 1853.
- Liabum tenerum* (Schultz-Bipontinus) Blake, Journ. Wash. Acad. Sci., 17:303, 1927.

There is no general treatment of the genus. The Ecuadorian species, including all but one of the members of subgenus *Kastnera*, have been treated by Robinson (1978a).

#### **Philoglossa**

##### FIGURE 16

- Philoglossa* DeCandolle, Prodr., 5:567, 1836. [Type-species: *Philoglossa peruviana* DeCandolle; originally monotypic.]
- Jaumeopsis* Hieronymus, Engl. Bot. Jahrb., 29:53, 1900 [nom.

nud.]: 28:619, 1901 [nom. nud.]. [Type-species: *Jaumea minuloides* Hieronymus; originally monotypic.]

Small erect, decumbent, or creeping herbs. Stems, stipule-like leaf bases, both surfaces of leaves, and peduncles pilose or strigose with stiff bulbous-based hairs. Stems with little or no milky sap, basal branch internodes of *P. peruviana* up to 18 cm long, followed by short internodes and leaves in false-whorls. Leaves opposite; stipule-like bases broadly oblong, usually deeply emarginate; petioles unwinged; blades herbaceous, ovate to elliptical, trinervate, margins serrulate to serrate, upper and lower surfaces green, without tomentum. Inflorescence from axils of normal leaves or from axils of leaves in false-whorls of 4 leaves. Heads solitary on slender and sometimes clustered peduncles, broadly campanulate; involucre bracts 20–30, unequal to subequal, oblong to oblong-lanceolate; outer bracts fleshy at base with obtuse herbaceous tips, margins densely ciliate with stiff hairs; receptacle without chaff, crests unlobed or slightly lobed. Flowers usually yellow, disk flowers red in 1 species. Ray flowers 21–70, tubes hirsute, limbs linear and glabrous, slightly notched at tip, bilobed; style branches elongate, not spiralled. Disk flowers 30–60; corolla tube and lower throat hirsute on outer surface; throat abruptly expanded at base, lobes with large stomates near margins, with spicules or stiff hairs at tip; walls of cells of anther collars without annulations; thecae black, not digitate at base; median endothelial cells subquadrate in series with numerous thickenings on lateral walls, transverse walls very faint; appendages smooth, with entire to denticulate margins, cells rather elongate with truncate or oblique end walls; nectary not or slightly lobed; style base not or scarcely enlarged; style branches short, less than 1/2 as long as the hirtellous portion of the upper shaft, with obtuse to rounded tips. Achenes compressed, with 2 ribs, mostly glabrous, sometimes hirtellous or winged on ribs, cells of achene wall containing small quadrate raphids, carpopodium poorly differentiated with many series of quadrate to short oblong cells, walls of cells scarcely thickened; pappus of small, usually deciduous

squamellae or awns, or lacking. Pollen grains 35–37  $\mu\text{m}$  in diameter, with spines rather unevenly disposed, with small or indistinct internal columellae.

*Philoglossa* was described originally by DeCandolle (1836) on the basis of material from near Lima, Peru, and was placed in the proximity of *Encelia* and *Rudbeckia*, members of the Heliantheae. The genus was later named but not validated by Hieronymus (1901) under the name "*Jaumeopsis*" based on material from Ecuador and Bolivia. Hieronymus also associated the genus with the Heliantheae-Helenieae series. Bentham and Hooker (1873) had placed *Philoglossa* in the Heliantheae in the subtribe Melampodiinae. Such a relationship was understandable, given the black anthers and the compressed achenes with reduced pappus. The position in the Melampodiinae seems to derive from the frequently incomplete fertilization or incomplete development of the central flowers, often given the appearance of a sterile disk. It was Sandwith (1956) who first cited the unpublished conclusions of S.F. Blake regarding the relationship of *Philoglossa* to *Liabum*, a position confirmed by Robinson and Cuatrecasas (1973) and Robinson and Brettell (1974b). The close relationship to *Erato*, with which it shares the distinctive pubescence and the reduced number of ribs on the achene, was not fully recognized until the study of the tribe Liabeae in Ecuador by Robinson (1978a).

The genus was originally credited with a single species (DeCandolle, 1836) and continued to be regarded as monospecific even after the description of a second species by Hieronymus (1900, 1901), which he failed to recognize as a *Philoglossa*. Sandwith (1956) described a new species and suggested that there were three species in the genus. Robinson and Cuatrecasas (1973) provided a summary of the genus with four species, but shortly afterward a fifth species was described (Robinson, 1976b).

The individual species show some distinctive characters, including the elongate internodes followed by false-whorls of four leaves and the spinose crested tips of the disk corolla lobes in *P.*



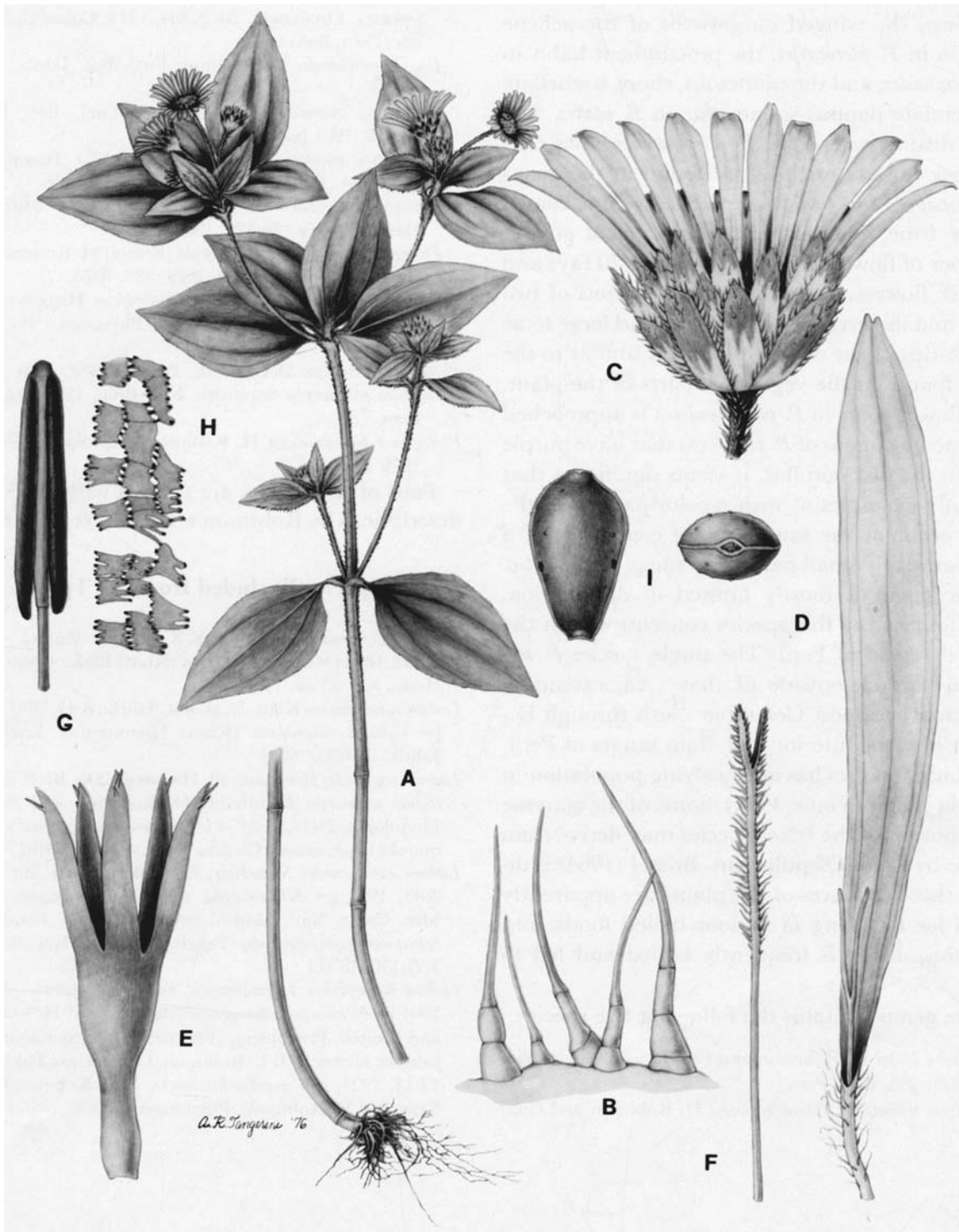


FIGURE 16.—*Philoglossa peruviana* DeCandolle: A, habit,  $\times \frac{1}{2}$ ; B, foliar hairs,  $\times 50$ ; C, head,  $\times 3$ ; D, ray corolla,  $\times 16$ ; E, disk corolla,  $\times 16$ ; F, disk style,  $\times 16$ ; G, anther,  $\times 20$ ; H, median endothelial cells,  $\times 400$ ; I, achenes, side and top views,  $\times 16$ .

*peruviana*, the winged outgrowths of the achene margin in *P. pterocarpa*, the procumbent habit in *P. mimuloides*, and the numerous, short, barbellate or lacinate pappus squamellae in *P. blakei*. The most distinctive species, *P. purpureodisca*, has purple disk flowers, such as are found in the genus *Chionopappus* but which are otherwise not known in the tribe. The last species also has a greater number of flowers in the head, up to 70 rays and 60 disk flowers, a well-developed pappus of two awns and intervening squamellae, and large setae on the tips of the disk corolla lobes similar to the hairs found on the vegetative parts of the plant. The flower color in *P. purpureodisca* is approached in some specimens of *P. peruviana* that have purple tips on the disk corollas. It seems significant that the only examples of such a color pattern in the tribe occur in the same area of coastal Peru, a comparatively small part of the range of the tribe.

The genus is mostly limited in distribution, with four of the five species concentrated in the coastal region of Peru. The single species *P. mimuloides* occurs outside of that area, extending from southernmost Colombia south through Ecuador into the interior mountain ranges of Peru. The latter species has one outlying population in Bolivia (Hieronymus, 1901). Some of the extreme distribution of the latter species may derive from its use by native populations. Bristol (1964) indicates that the leaves of the plants are apparently eaten for flavoring in various boiled foods, and the noncultivar is frequently boiled and fed to pigs.

The genus contains the following five species.

- Philoglossa blakei* H. Robinson and Cuatrecasas. *Phytologia*, 26(5):383. 1973. Peru.
- Philoglossa mimuloides* (Hieronymus) H. Robinson and Cuatrecasas. *Phytologia*, 26(5):384. 1973. Colombia. Ecuador. Peru. Bolivia.
- Jaunea mimuloides* Hieronymus, *Engl. Bot. Jahrb.*, 29:52. 1900.
- Jauneopsis mimuloides* Hieronymus, *Engl. Bot. Jahrb.*, 28:619. 1901 [nom. nud.].
- Jauneopsis mimuloides* forma *subintegrifolia* Hieronymus, *Engl. Bot. Jahrb.*, 28:619, 1901 [nom. nud.].
- Philoglossa peruviana* var. *sapida* Bristol. *Bot. Mus. Lfts. Harvard Univ.*, 20:326. 1964.
- Philoglossa mimuloides* var. *sapida* (Bristol) H. Robinson and Cuatrecasas. *Phytologia*, 26(5):385, 1973.
- Philoglossa mimuloides* forma *subintegrifolia* Hieronymus ex H. Robinson and Cuatrecasas. *Phytologia*, 26(5):385, 1973.
- Philoglossa peruviana* DeCandolle, *Prodr.*, 5:567. 1836. Peru.
- Philoglossa pterocarpa* Sandwith. *Kew Bull.*, 1956:292, 1956. Peru.
- Philoglossa purpureodisca* H. Robinson. *Phytologia*, 34(1):54. 1976. Peru.
- Four of the species are treated with a key and descriptions by Robinson and Cuatrecasas (1973).

### Species Excluded from the Tribe

- Liabum bolivianum* Klatt, *Ann. K.K. Naturh. Hofmus. Wien*, 9:362. 1894 [= *Gynoxys boliviana* (Klatt) Blake. *Contr. Gray Herb.*, n.s., 53:28, 1918].
- Liabum columbianum* Klatt, *Engl. Bot. Jahrb.*, 8:47, 1887 [1886] [= *Gynoxys columbiana* (Klatt) Hieronymus, *Engl. Bot. Jahrb.*, 28:630, 1901].
- Liabum erigeroides* Bentham, *Pl. Hartweg.*, 206. 1845; *Chrysactinium erigeroides* (Bentham) H. Robinson and Brettell. *Phytologia*, 28(1):50. 1974 [= *Orithrophium peruvianum* (Lamarck) Cuatrecasas. *Ciencia (Mex.)*, 21:22, 1961].
- Liabum eupatorioides* Muschler, *Engl. Bot. Jahrb.*, 50, Beibl., 3:83. 1913 [= *Schistocarpha sinforosi* Cuatrecasas. *Trab. Mus. Cienc. Nat., Madrid. ser. Bot.*, 29:43, 1935]. [Not *Schistocarpha eupatorioides* (Fenzl) O. Kuntze, *Rev. Gen. Pl.*, 3(2):170, 1898.]
- Liabum homogamum* Hieronymus, *Engl. Bot. Jahrb.*, 28:626. 1901 [= *Neomirandea homogama* (Hieronymus) H. Robinson and Brettell. *Phytologia*, 28(1):62. 1974]. [Synonyms: *Eupatorium hitchcockii* B.L. Robinson, *Contr. Gray Herb.*, n.s., 73:14, 1924; *Neomirandea hitchcockii* (B.L. Robinson) R.M. King and H. Robinson, *Phytologia*, 19:308, 1970.]

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