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Generic and Subtribal Classification of American Vernonieae

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ABSTRACT

Robinson, Harold. Generic and Subtribal Classification of American Vernonieae. *Smithsonian Contributions to Botany,* number 89, 116 pages, 1999.—The Vernonieae in America is herein defined to exclude the Liabeae and *Pseudostifftia* (Moquinieae), and to include elements sometimes placed in the Heliantheae (*Trichospira*) or Lactuceae (*Stokesia*). Pollen, style bases, raphids, inflorescence form, involucre, anther appendage, and chemistry are some characters used in the reclassification. Tables 1–12 indicate the distribution of these characteristics in most American genera. *Vernonia* s.s., with type A pollen, is typified by *V. noveboracensis* (L.) and occurs in the Bahamas, eastern North America, south to central Mexico and has two species in temperate South America. All other species previously placed in *Vernonia* need to be removed from the genus, a process that is nearly complete for neotropical species. Most American Vernonieae seem to form a single related subgroup in the tribe. Subtribes included in the related subgroup are the Lychnophorinae ($x=15$, 17, 18) and Centratherinae ($x=16$) with type A pollen and furoheliangolides; Piptocarphinae ($x=17$) with type A pollen, deciduous inner involucre, and sometimes opposite leaves; Vernoniinae ($x=17$), many with glanduliferous anther appendages (including the *Lepidaploa* complex mostly with echinolophate pollen); and the newly proposed subtribes Sipolisiinae with type A pollen, armed receptacles, and carbonized achenes; Chrestinae with echinolophate pollen; and Leiboldiinae ($x=19$) with type A pollen, large heads, and a modified callus at the top of the achene. Of uncertain relationship to the preceding related subgroup are *Stokesia* ($x=7$), the Elephantopodinae ($x=11$, 13), and the Rolandrinae ($x=8$) with echinolophate pollen; three genera with type E pollen (*Pacourina, Acilepidopsis,* and *Mesanthophora*); and the Trichospirinae with type A pollen and flattened bicornute achenes. Ten subtribes are recognized, plus four unplaced generic groups. Three of the subtribal names, Leiboldiinae, Chrestinae, and Sipolisiinae are validated in the treatment. The genus *Caatinganthus* of eastern Brazil, a possible relative of the Elephantopinae, is described as new. A list of the 76 accepted genera of Vernonieae, native or introduced in the New World, is provided, and a complete list of names of American Vernonieae is given with an indication of their present taxonomic dispositions and geographical distributions. Fifteen new combinations are provided.

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Contents

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Introduction

The present paper is derived from text and illustrations originally prepared for presentation at the International Compositae Conference, Royal Botanic Gardens, Kew, in July–August 1994 and for subsequent publication in the Symposium volume. The paper is expanded in the present version to include validation of new subtribes, illustrations of selected genera, scanning electron photomicrographs of pollen (Figures 1–8), illustrations of various neotropical Vernonieae (Figures 9–18), tables of the subtribes and genera of Vernonieae (Tables 1–12), a description of a new species of *Caatinganthus* H. Rob. (Figures 19, 20), a list of the Western Hemisphere genera of the Vernonieae with their synonyms, authors, and places of publication (Appendix I), and a complete as possible list of the species of American Vernonieae with accepted taxonomic dispositions and geographic distribution (Appendix II).

The treatment of the Vernonieae by Bentham in Bentham and Hooker f. (1873) presented a pattern common in traditional concepts of Asteraceous tribes, namely a large core genus, *Vernonia* Schreb., and various satellite genera based mostly on variations in pappus and obvious features of the inflorescence. Some of the primary characters used by Bentham in the treatment of the tribe involved congestion of the heads, number of florets in the heads, surface of the receptacle, and presence or absence and texture of tails on the bases of the anther thecae. The 1873 treatment suffered from the comparatively few characters used at the time, the excessively paraphyletic nature of the core genus, *Vernonia,* the artificial delimitation of many of the segregate genera, and the failure to intercalate the segregate genera into the related parts of the core genus. The 1873 treatment had a brief mention of potentially useful pollen structure that was first used in the taxonomy of the tribe by Steetz (1864). The Bentham classification was accepted almost without change by Hoffmann (1890–1894), differing only in the addition of the genus *Gorceixia* Baker (1882) and the transfer of *Gongrothamnus* Steetz ex Peters from the Senecioneae to the synonymy of *Vernonia.* This classification, based on Bentham in Bentham and Hooker f. and adopted by Hoffmann, was accepted as traditional by most workers in the tribe for the next ninety years.

The review of the Vernonieae by Jones (1977) provided the most recent basis for revisional studies in the tribe using pollen, chromosome numbers, and chemistry. This work was part of a series of studies by Jones and various coauthors (1973–1986), and various students (Chapman and Jones, 1978; Jones and Faust, 1978; Coile and Jones, 1981, 1983; Keeley and various coauthors, 1978–1980; B.L. King, 1986; Kirkman, 1981; MacLeish, 1984–1987; MacLeish and Schumacher, 1984; G.L. Smith, 1981, 1982; and Stutts, 1980, 1981, 1983, 1988). Some of these studies, and work of other recent authors, emphasized trichomes (Faust and Jones, 1973; Pope, 1983), underground systems (Menezes et al., 1979); anatomy (Magalhães and Alencastro, 1973; Alencastro, 1978; Carlquist, 1964; Petriella, 1966), pollen (Stix, 1960; C.E. Smith, 1969; Kingham, 1976; Jones, 1979b, 1981a; Keeley and Jones, 1977b, 1979; Bolick, 1983; Isawumi et al., 1996), presence of latex (Lewinsohn, 1991), chromosome numbers (Jones, 1974, 1979a; Keeley, 1978; Dematteis, 1996), and nomenclatural details (Nicolson, 1991; Jeffrey and Hind, 1994; Grant, 1994). Jones (1977), Harborne and Williams (1977), and Robinson, Bohlmann, and King (1980) presented some early apparent correlations of chemical data with classification or geography, and the extensive subsequent studies of secondary metabolites were summarized by Bohlmann and Jakupovic (1990). Floral dimorphism in the African *Vernonia biafrae* Oliv. & Hiern was noted by Ayodele (1995). Economic value of *Stokesia* L'Her. was discussed by Gunn and White (1974) and in *Centrapalus galamensis* Cass. by Ayorinde et al. (1990), Perdue (1989), and Perdue and various coauthors (1986, 1989, 1993). Also see literature listed

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on the web site AGRICOLA under the headings *Vernonia galamensis, V. anthelmintica* L., and other sources of vernolic acid. Possible medicinal value of terpenoids in *Gymnanthemum amygdalinum* (Del.) Sch. Bip. ex Walp. and use by wild Chimpanzees has been reviewed (Huffman, 1991; Jisaka et al., 1992a, 1992b; Ohigashi et al., 1991).

Most papers about the tribe have emphasized particular geographic areas: United States (Clonts and McDaniel, 1978; Gleason, 1906, 1922, 1923b; Urbatsch, 1977), Mexico and Central America (Blake, 1926, 1932, 1936; Carvajal, 1981; Elias, 1975; Jones, 1973, 1976, 1979b; B.L. King and Jones, 1975; Jones and Stutts, 1981; Keeley, 1987; McVaugh, 1984; Robinson and Funk, 1987; Robinson and Reed, 1973; Rzedowski and Calderón, 1995a, 1995b; Turner, 1981–1994), West Indies (Adams, 1971; Borhidi, 1992; Ekman, 1914; Keeley, 1978, 1982; Stutts and Muir, 1981; Urbatsch, 1989), Colombia, Venezuela, and Guayana (Aristeguieta, 1963; Badillo, 1981–1989; Cuatrecasas, 1956; Pruski, 1992, 1996; Robinson, 1992e; Stutts, 1981), Peru (Dillon, 1982, 1984; Jones, 1980), Bolivia (Gleason, 1923a); Brazil (Baker, 1873, 1882; Barroso, 1957, 1959, 1960–1961, 1969, 1970; Cabrera and Vittet, 1961; Cabrera and Klein, 1980; Duarte, 1974; Esteves, 1981, 1992, 1993, 1994; Hind, 1993, 1994; Jones, 1981b, 1981c, 1982a; Leitão Filho and Semir, 1979; Lobo, 1982; MacLeish, 1984–1987; Matzenbacher and Mafioleti, 1994a, 1994b; Philipson, 1938b; Schultz-Bipontinus, 1863; Semir, 1991; G.L. Smith, 1982; Soares Nunes, 1982; Stutts, 1983, 1988), Paraguay (Cabrera, 1995), Argentina (Cabrera, 1944, 1974, 1978; Ariza-Espinar, 1994), Africa (Burtt, 1950; Gilbert, 1986; Gilbert and Jeffrey, 1988; Isawumi, 1984–1995; Isawumi et al., 1996; Jeffrey, 1988; Kalanda, 1981, 1982, 1986; Kalanda and Lisowski, 1981; Lisowski, 1987, 1992; Lebrun, 1985; Philipson, 1938a; Pope, 1986a, 1986b, 1992; C.E. Smith, 1971; Steetz, 1864; Wild, 1977, 1978; Wild and Pope, 1977–1978), Madagascar (Humbert, 1960), Thailand (Koyama, 1984), Malay or Indo-Malesia (Koster, 1935).

Some studies during the last 30 years have dealt with the limits of the Vernonieae. It was recognized that *Llerasia* Triana was not a synonym of *Vernonia* but was an older name for an Andean genus of the tribe Astereae (Cuatrecasas, 1970). Confusion between the Vernonieae and Eupatorieae was dealt with by Robinson (1977a, 1977b). *Liabum* Adans. and its relatives were once treated as members of the Vernonieae (Cassini, 1823, 1825, 1830), then long treated as part of the Senecioneae (Bentham in Bentham and Hooker f., 1873; Hoffmann, 1890–1894). They were returned to the Vernonieae (Nash, 1976) but are now generally accepted as members of the distinct tribe Liabeae (Rydberg, 1927; Robinson and Brettell, 1973b, 1974; Robinson, 1983d; Bremer, 1994). The description in the Vernonieae of *Pseudostifftia* (Robinson, 1979d) from Brazil was followed by the addition of the related *Moquinia* DC. (Gamerro, 1990) and then by the transfer of both genera to the new tribe Moquinieae by Robinson (1994a). The South African *Hoplophyllum* DC., traditionally placed in the Vernonieae, was shown by Karis (1992) to be related to *Eremothamnus* Hoffm. *Eremothamnus* and *Hoplophyllum* were placed by Robinson (1992c, 1994a) in the tribe Eremothamneae, which is most closely related to the Arctoteae. *Corymbium* L. of South Africa (Weitz, 1989) is now also regarded as not a member of the Vernonieae, especially on the basis of chemistry (Bohlmann and Jakupovic, 1990), but it remains unplaced tribally. Some elements added to the tribe or confirmed as members of the tribe are *Stokesia* L'Her. and *Trichospira* H.B.K. *Stokesia* was sometimes compared with the Lactuceae because of the ligulate form of most of the florets in its heads (Cronquist, 1955), but it has usually been properly placed in the Vernonieae (Bentham and Hooker f., 1873; Hoffmann, 1890–1894; Jones, 1977). *Trichospira* was placed in the Vernonieae by Cassini (1819) but was placed in the Heliantheae in traditional treatments of the Asteraceae (Bentham and Hooker f., 1873; Hoffmann, 1890–1894). It was transferred to the Vernonieae by Robinson and Brettell (1973a) and was included in that tribe by Dillon (1982), a disposition supported in general in the pollen study by Bolick (1983). The most interesting additions to the tribe were the various synonyms of *Distephanus* Cass. (*Gongrothamnus* Steetz, *Newtonia* Hoffm., and *Antunesia* Hoffm.) that were rather consistently placed in the Senecioneae in the traditional systems of classification (Bentham and Hooker f., 1873; Hoffmann, 1890–1894, 1893) because of their yellow florets and trinervate leaves. The placement in the Vernonieae is discussed fully by Robinson and Kahn (1986). A recent DNA study suggests that the Hawaiian *Hesperomannia* is a member of the tribe (Kim et al., 1998).

A DNA study of the tribe (Keeley, 1994) has produced a preliminary strict consensus tree of various New and Old World species of *Vernonia* s.l. The study stated that the hypothesized division between Old and New World Vernonieae (Jones, 1977, 1979a, 1979b, 1981a; Robinson et al., 1980; Jeffrey, 1988) is not supported by the cpDNA data. The cpDNA study claimed to support the suggestions by the same previously cited authors (Jones, 1977, 1979a, 1981; Robinson et al., 1980; Robinson and Funk, 1987; Jeffrey, 1988) that *Vernonia* s.l. is paraphyletic or possibly polyphyletic. Some seeming violations of the hemispheric monophyly in the authors' published tree are not supported by fully resolved phyletic results. The strikingly anomalous elements in the study are the Old World and widely adventive *Cyanthillium patulum* (Aitch.) H. Rob. (as *Vernonia chinensis*) positioned among species of the New World *Vernonia* s.s. and *Vernonanthura* H. Rob., and members of the New World *Lepidonia-Stramentopappus* group in a position between various African groups. Keeley and Jansen (1994) concluded that the subdivision of *Vernonia* s.l. into segregate genera is premature.

The publications of Robinson and various coauthors (1973–1999) about the Vernonieae initially included only descriptions of new species, but the aim has increasingly been to produce a full generic revision of the tribe with description of new genera and restoration of some older genera that had been placed in synonymy. As mentioned in the study of *Di-*

stephanus (Robinson and Kahn, 1986), the subdivision of *Vernonia* was considered inevitable as early as the initial study of subtribes by Robinson, Bohlmann, and King (1980). An attempt at a complete generic revision of the neotropical members of the tribe is presented herein. Partial results of the series of studies were included in the review by Bremer (1994). The 76 genera presently recognized in the Americas are listed with synonyms in Appendix I.

During the segregation of various neotropical genera from *Vernonia,* the overall pattern of relationships has become clearer, but some of the characters used in earlier papers of the series to distinguish subtribes and genera have needed refinement. Examples can been noted below in the review of subtribes under the relationships and generic limits of *Lessingianthus* H. Rob. and under the delimitation of the Piptocarphinae.

In other cases, during the present series of studies, generic distinctions have followed already known alignments of characters. The limits of the genus *Vernonia* s.s., which have finally been recognized, were precisely anticipated by Gleason in his key subgrouping and treatment of species 89–123 in the treatment of *Vernonia* s.l. in the North American Flora (1922).

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Relationships of the Vernonieae

The tribe is considered closest to the tribes Lactuceae and Liabeae (Robinson, 1983d), but some variations in this relationship have been proposed recently using cpDNA and cladistics (Jansen et al., 1988, 1991; Bremer et al., 1992). The Vernonieae is believed to have originated in the Eastern Hemisphere (Bremer, 1994) where the most divergent element of the tribe, the yellow-flowered and trinervate-leaved *Distephanus* occurs. The Eastern Hemisphere is also where almost all the Vernonieae with $x=9$ or 10 occur. The higher chromosome numbers found in the Western Hemisphere Vernonieae follow the pattern of higher numbers in members of groups invading new geographical areas. This is the view accepted herein for all Vernonieae except perhaps *Trichospira.*

If it is true that the Vernonieae arose in Africa or Asia, they were orginally geographically closer to the Lactuceae and remote from the strictly neotropical Liabeae. It is the Lactuceae that often show a style form more closely similar to that of the Vernonieae, and it is the Lactuceae that show a similar pattern of lophate pollen, apparently reverting commonly to type A pollen. As noted by Lewinsohn (1991), the Vernonieae sometimes even have latex like the Lactuceae and most Liabeae.

Even though most Western Hemisphere Vernonieae are undoubtedly derived from Eastern Hemisphere ancestors, one Western Hemisphere genus, *Trichospira,* may be a relict of an even more remote ancestry. The flattened, bicornute, echinate achenes of the latter genus are unlike anything else seen in the Vernonieae, Liabeae, or Lactuceae. If there is an older American ancestral element of the Vernonieae, the origin and relationship of the tribe could be closer to the Western Hemisphere Liabeae. The majority of American Vernonieae would still be interpreted as introductions or reintroductions from the Eastern Hemisphere.

Distinguishing Features of the Vernonieae

Perennial or rarely annual herbs to shrubs, small trees, or vines, with decumbent to xylopodial bases, rarely with latex. Hairs simple, monoseriate, T-shaped, stellate, or glandular. Leaves usually alternate, more rarely opposite or ternate, sometimes in basal rosette, sessile or petiolate. Leaf blades usually pinnately veined, rarely trinervate, margins entire to lobed or spiny, often with glandular dots. Inflorescence cymose or with cymose branches, often scorpioid or seriate cymose, more rarely glomerulate or syncephalous and simultaneously flowering or spiciform. Heads discoid, sometimes with outer rows flowering on one day and remaining florets flowering on following day, homogamous, 1–200-flowered, florets usually bisexual and fertile; involucral bracts few to many, in 1 to about 12 series, usually closely imbricated, sometimes with expanded foliose or colored tips, inner bracts persistent or deciduous; receptacle flat to convex, glabrous, or with awns, pales, or partitions, rarely with achenes completely immersed. Corollas reddish to purplish or white, rarely yellowish, tubular or rarely ligulate to bilabiate, tube short to elongate, lobes 3, 4, or 5, usually longer than throat, rarely divided to base of limb, usually narrowly oblong to linear, glabrous to villous outside, limb rarely pubescent inside; anther bases usually calcarate, with or without sterile appendages, endothecial cells subquadrate, with polarized thickenings, apical appendage not constricted at base, with or without glands; style base immersed in nectary, with or without basal enlargement or differentiated basal ring; style branches spreading laterally, slender, acute, with continuous stigmatic surfaces inside extending almost to tip, with outer surface and upper style shaft bearing long sweeping hairs. Achene terete to triangular or obcompressed, usually 10-ribbed, sometimes 3–5-angled, rarely dimorphic, densely setuliferous or glanduliferous to glabrous, often with idioblasts, rarely slightly winged, usually with raphids, very rarely carbonized; pappus usually with capillary bristles, usually with outer series of squamellae, sometimes totally squamiform or coroniform, persistent to deciduous. Pollen 37–80 µm in diameter (in fluid) tricolporate to triporate, echinate and sublophate, or echinolophate to lophate without spines or perforated tectum. Characteristic secondary metabolites being highly oxygenated germacranolides and simple acetylenes (polyines). Diterpenes, phenyl propanes, and p-hydroxyacetophenone derivatives absent.

Members of the Vernonieae can be distinguished from most Eupatorieae in the field by the lateral rather than radial spreading of the style branches (Robinson, 1984). Most Vernonieae have alternate leaves and long corolla lobes, whereas most Eupatorieae have opposite leaves and corolla lobes rarely much longer than wide. Many traditional characters, chromosome number data of Jones (1974, 1979a) and Keeley (1978), and much of the secondary metabolite data summarized by Bohlmann and Jakupovic (1990) are used in the present classification. The structural characters include the base of the plant, phyllotaxy, leaf venation, hair types, shape of the inflorescence, persistence of the inner involucral bracts, surface of the receptacle, number of involucral bracts and florets, color and shape of the corolla, pubescence of the corolla, length of corolla lobes, form of anther bases, anther appendages, basal node of the style, sweeping hairs on the outside of the style branches and upper style shaft, shape and dimorphism of achene, achene wall structure, raphids, upper callus of the achene, pappus structure, and form of pollen. These characters require the following brief comments.

BASE OF PLANT.—The present study is mostly based on herbarium material, and the bases have not been consistently available for study. Nevertheless, the stem bases in *Vernonia* s.s. and *Acilepidopsis* H. Rob. seem distinctive in their rather decumbent nature. They completely lack the xylopodia that are common in many other members of the tribe, especially many savanna species of *Vernonanthura.*

PHYLLOTAXY.—Members of the Vernonieae are almost all alternate leaved. As one exception in Africa, some species of *Bothriocline* Oliver ex Benth. have opposite or ternate leaves. In the Neotropics, most species with opposite leaves belong to the Piptocarphinae, *Critoniopsis* Sch. Bip., *Joseanthus* H. Rob., or *Piptocarpha* R. Br. Opposite leaves occur in one localized Colombian forma of *Lepidaploa canescens* (Robinson, 1981b), and *Lepidaploa verticillata* Proctor ex Adams, of Jamaica has ternate, opposite, and alternate leaves.

LEAF VENATION.—Most members of the tribe have pinnately veined leaves. The most important exception is *Distephanus* of the Eastern Hemisphere, a genus increasingly regarded as a pleisiomorphic element in the tribe (Bremer, 1994). Keeley and Turner (1990) note the trinervate foliose bracts in the inflorescence of the Brazilian *Hololepis* DC.

HAIR TYPES.—Trichomes in the tribe have been studied repeatedly (Faust and Jones, 1973; Pope, 1983; Isawumi, 1984, 1989), and Jeffrey (1988) used the presence or absence of T-shaped hairs as a key character distinguishing major groups of *Vernonia* in Africa. Stellate hairs are found in such neotropical genera as *Ekmania* Gleason, *Piptocarpha,* and *Critoniopsis* of the Piptocarphinae. The present series of studies includes description of some extreme serial T-shaped hairs in *Quechualia* H. Rob., but it has been more concerned with various types of hairs occurring inside of corollas (Figures 13D,E; 14E,G) (Robinson, 1993b).

SHAPE OF THE INFLORESCENCE.—The tribe is notable for one of the most striking exceptions to cymose inflorescences in the Asteraceae in the genus *Pithecoseris* Mart. (Figure 16A). The cymose condition in most of the tribe attains an extreme condition that has been referred to as scorpioid cymose (Figure 12A), but a term, seriate cymose, has been introduced in the present series of studies for the majority of the so-called scorpioid cymes in the tribe that are not scorpioid (Robinson, 1987c, 1988b, 1990b; Figure 11A). The latter forms of inflorescence seem to be almost restricted to neotropical members of the tribe. An instance of apparent developmental conversion of a seriate cyme to a spiciform cyme has been seen in *Lessingianthus* (Robinson, 1988b). The cymose form of the whole inflorescence in *Vernonia* s.s. versus the restriction of the strongly cymose form to branches, as in *Vernonanthura* (Robinson, 1992b), was anticipated in the key to *Vernonia* s.l. by Gleason (1922).

PERSISTENCE OF INNER INVOLUCRAL BRACTS.—In the neotropical Vernonieae, the Piptocarphinae mostly show obviously deciduous inner involucral bracts. Other subtribes, such as the Vernoniinae, usually show involucral bracts widely spreading and persistent with age.

SURFACE OF THE RECEPTACLE.—Most members of the Vernoniinae have an unornamented receptacle surface that is considered pleisiomorphic. The occurrence of pales is somewhat erratic; it occurs in *Bolanosa* A. Gray of Mexico, one Guatemalan species of *Lepidonia* S.F. Blake, and a group of genera in Brazil herein placed in the new subtribe Sipolisiinae. The latter group has both pales and long bristles that seem to be developmentally equivalent in spite of their different structure. *Blanchetia* DC. has thin partitions enclosing the bases of its achenes, whereas *Albertinia* Spreng. has deep holes in the receptacular surface that enclose the full lengths of the achenes. It is questionable whether the structures in *Trichospira* are pales or whether the structures are remnant involucral bracts in reduced compound heads.

NUMBER OF BRACTS AND FLORETS.—The number of florets in the heads varies from one to many hundred. The ratio of involucral bracts to florets also may vary in significant ways, such as nearly 1 to 1 in typical *Vernonia* and in *Lepidonia,* but 2 to 1 in many members of the *Lepidaploa* complex. Marked reductions in flower number, as in *Vernonia angustifolia* Michx., *V. fasciculata* Michx., and *Chrysolaena* H. Rob., and marked increases in involucral bracts, as in *Echinocoryne* H. Rob., may drastically alter the ratio.

COLOR AND SHAPE OF THE COROLLA.—Most members of the tribe have purplish to white corollas. The occurrence of yellow corollas is apparently restricted to the Eastern Hemisphere genus *Distephanus,* which is also notable for its distinctive leaf venation. Varying degrees of zygomorphy are found in scattered nearctic and neotropical members of the tribe, *Stokesia, Dipterocypsela* S.F. Blake, *Mattfeldanthus* H. Rob. and R.M. King, and the Elephantopinae.

PUBESCENCE OF THE COROLLA.—The pubescence varies from glabrous or with hairs simple, multicellular, and T-shaped to stellate. One useful character in the present study has been the various types of hairs inside the corolla in *Dasyandantha* H. Rob., *Dasyanthina* H. Rob. (Figure 13D,E,I), and *Quechualia* (Figure 14E,G, Robinson, 1993b).

The glabrous corollas in the typical Vernoniinae contrast with the pubescent corollas in most members of the *Lepidaploa* complex of the same subtribe.

COROLLA LOBES.—The corolla lobes of the Vernonieae are erect when mature or sometimes distorted, especially in members of the Piptocarphinae, but they are rarely rolled strongly backward as in most Mutisieae. The lobes are usually longer than the throat but are unusually short in a few neotropical examples. The lobes are separated to the base of the limb in *Joseanthus* (Figure 15E) and *Cuatrecasanthus* H. Rob., and they are shorter than the throat in *Cololobus* H. Rob. (Figure 10C). The only other such short lobes on a disciform corolla in the tribe are, as illustrated, in a paleotropical species from Socotra, described by Jeffrey (1971). The veins of the lobe are distally strongly thickened in many members of the tribe and may form a thickened shield in such genera as *Mattfeldanthus.* Other genera, such as *Chrysolaena,* have characteristically thinner veins. The interior of the lobe is filled with sometimes obvious longitudinal ducts in *Vernonanthura* and *Trepadonia* (Robinson, 1994c).

ANTHER BASES.—The bases of the anthers in the tribe are usually calcarate or spurred, with the pollen-bearing anther thecae extending below the point of attachment to the filament. The actual point of attachment may be obscure because of the way the anther collar lies between the spurs. This spurred condition is found in most members of the subfamily Cichorioideae, but in the Elephantopinae and in *Xiphochaeta* Poeppig. the bases are shorter than the anther collars. Traditionally, *Piptocarpha* has been distinguished in the tribe by having tails, or sterile extentions on the basal ends of the thecae, but the true distinction seems to be the sclerified and often sharply pointed nature of those tails. Tails as long or longer occur in many other genera of the tribe, such as *Distephanus* (Robinson and Kahn, 1986), *Vernonanthura* (Robinson, 1992b), and *Critoniopsis* (Robinson, 1993a). The distinctive *Acilepidopsis* actually has anther tails as sharp and sclerified as those of *Piptocarpha,* and blunt sclerified tails are seen in *Hololepis.*

APICAL ANTHER APPENDAGES.—The apical appendages of the anther vary from thin-walled to very thick-walled. The latter condition is rather characteristic of the Piptocarphinae and Lychnophorinae, and occurs in such unplaced genera as *Acilepidopsis* and *Pacourina* Aubl. Only the appendages with thin-walled cells, such as those of the Vernoniinae, bear glands. One gland seen on the anther of a *Piptocarpha triflora* (Aubl.) Benn. ex Baker seemed anomalous in that genus, and it was placed oddly on the edge of the theca.

BASAL NODE OF THE STYLE.—The character has been used extensively in the Vernonieae of both Hemispheres. *Distephanus* is distinct in having a greatly enlarged node (Robinson and Kahn, 1986), whereas Isawumi (1993) noted the complete lack of a node in *Baccharoides* Moench correlated with a high, sheathing nectary. In the Neotropics, a basal stylar node seems characteristically lacking in the Lychnophorinae and Centratherinae among others. The node is usually present in the Piptocarphinae but is lacking in the generic group of *Piptocoma* Cass. (including *Pollalesta* H.B.K.) and *Ekmania.* A node is usually present in the Vernoniinae, but there have been separate reductions in such genera as *Chrysolaena* (Robinson, 1988c) and *Lessingianthus* (Robinson, 1988b), where there is at least one exception (in *L. regis*).

SHAPE AND DIMORPHISM OF THE ACHENE.—The peripheral achenes are strongly obcompressed in *Dipterocypsela* and *Heterocypsela* H. Rob., and lateral margins of the former appear winged. The achenes of *Pithecoseris* and the type species of *Lychnophoriopsis* Sch. Bip. are described as biformed (Baker, 1873), the inner differing in shape, pubescence, fertility, or shape and persistence of the pappus. The heteromorphism of the achenes, like that described from *Lychnophoriopsis heterotheca* Sch. Bip. has not been seen in any other members of the genus (Robinson, 1992d).

ACHENE WALL.—The most interesting character seen in the tribe is carbonization of the inner wall of the achene in four genera herein placed in the Sipolisiinae. The character was once thought to be restricted to the Eupatorieae and Heliantheae. Such carbonization also occurs in the *Blepharispermum* group that has been erroneously placed in the Heliantheae on the basis of the character (Eriksson, 1991).

The presence or absence of setulae (twin-hairs) or glands (short-stalked capitate glands) is a character of some genera. Glands have not been seen in *Lessingianthus,* although they are common in the related *Lepidaploa.* Hind (1993) stated that glands were present in *L. myrsinites* H. Rob., but reexamination of material indicates that the structure Hind saw must be what are referred to herein as idioblasts or resin cells. The latter are differentiated cells in the outer surface of the achene and are not the trichomes called glands herein.

RAPHIDS.—The shape of the raphids in the wall of the achene is theoretically an excellent character in neotropical Vernonieae, but the crystals are often hard to see. The shape also can be mistaken if quadrate forms are viewed from the side or if the seam between two joined subquadrate cystals is not noticed. The raphids are short in typical Vernoninae, such as *Vernonia* and *Cololobus* (Figure 10G). The shape varies in a few genera, such as *Chresta* Vell. ex DC., of the Chrestinae, but in the *Lepidaploa* complex of the Vernoniinae, elongate raphids correlate closely with rhizomatous crests on the lophate pollen and distinguish *Lepidaploa* and its most closely related genera from *Aynia* H. Rob., *Pseudopiptocarpha* H. Rob., *Harleya* S.F.

Blake, and most *Lessingianthus.* Some genera, such as *Stenocephalum* Sch. Bip., seem to characteristically lack raphids, and raphids appear to be lacking in members of the *Sipolisia* group that have carbonized achene walls. Elongate raphids occur in a few other neotropical groups not directly related to the *Lepidaploa* complex, such as *Dasyandantha, Dasyanthina* (Figure 13H), and *Quechualia* (Figure 14K) of the Vernoniinae and *Chresta*.

UPPER CALLUS OF THE ACHENE AND PAPPUS STRUCTURE.—The *Lepidonia* group of the Vernoniinae is notable for a progressive reduction of the upper achene callus (Figure 9I) (Robinson and Funk, 1987). The reduction series can be interpreted as loss of an outer layer bearing the pappus followed by loss of an inner ring. An expanded callus appears to be responsible for the pappus collar seen in *Struchium* P. Brown. A capillary pappus with an outer series of short bristles or squamellae is considered pleisiomorphic in the tribe. A recurring variation has an outer series that grades into the inner series without clear distinction. The bristles can be short in *Lepidonia* and *Lessingianthus,* but genera have not been based on that character alone in either the traditional or present classifications. Vernonieae with a pappus flattened (*Stilpnopappus* Mart. ex DC., *Xiphochaeta*), twisted (*Lychnophora* Mart.), with reduced number of segments (*Ekmania, Piptocoma* Cass., *Elephantopus* L.), or with only fused outer sheath or collar (*Gorceixia* Baker, *Huberopappus* Pruski, *Struchium*) have traditionally been distinguished at the generic level.

POLLEN.—The pollen in the Vernonieae is one of the most useful characters available, and it is inexplicable that taxa would be described at this time without detailed description of the pollen. It seems no accident that the use of pollen in the taxonomy of the tribe goes back to the work of Steetz in 1864. Some pollen variation in the tribe was reviewed by Stix (1960), but the pollen types cited herein follow mostly Keeley and Jones (1977b, 1979) and Jones (1979c, 1981a). The majority of the important pollen characters can be observed with any compound light microscope. Only the rhizomate versus baculate form of the lophate crests requires SEM for confirmation. A recent integration of pollen into a generic survey is in the review of the tribe in the Guianas (Robinson, 1992e). Tricolporate echinolophate variants are discussed in the treatment of *Lepidaploa* (Robinson, 1990b).

Fractured pollen grains revealed a significant character of the Vernonieae that differs from the related Liabeae. In the Vernonieae, the spines of echinate grains have a single solid columella or baculum centered under each spine (Figure 1B). In the Liabeae, the columellae under the spines are either hollow or form a cluster around an open center (Figure 1C,D). As illustrated in TEM sections by Skvarla et al. (1977), the Lactuceae also have open centers under the spines.

The present series of studies of the Vernonieae have shown a number of isolated examples of lophate pollen apparently reverting to type A pollen within genera or within well-defined generic groups (*Cyrtocymura* H. Rob., *Eirmocephala* H. Rob., *Lessingianthus, Lepidaploa*). These examples and the overall pattern of distribution of pollen types in the tribe indicate that the lophate forms are pleisiomorphic. The comparatively complex lophate pollen forms occur throughout the diversity of the tribe, in both Hemispheres, and it is considered impossible that they have independently and repeatedly re-evolved from the comparatively simple type A pollen. It is personally believed from these studies that the lophate forms of pollen in the Vernonieae and the related Lactuceae have a common origin, and that the type A pollen in both tribes is probably derived repeatedly by some sort of reversion. The Lactuceae have a similar mixture of pollen types that have been difficult to interpret systematically (Tomb, 1977).

Although the type A pollen is apparently a reversion from lophate forms, it has become fixed in some groups of the neotropical Vernonieae, such as the Lychnophorinae, Piptocarphinae, and the *Vernonia-Vernonanthura* element of the Vernoniinae. The result of the common reversion of lophate pollen to type A is that the co-occurrence of such pollen in different groups of the Vernonieae may have little phyletic significance. The co-occurrences of any of the basically different forms of lophate grains seem to be far more phyletically significant. There is no evidence in the neotropical Vernonieae of type A pollen reverting to lophate forms, but the pollen variation in Old World *Distephanus* involves a lophate form that differs from type A only in the continuity of different parts of the exine (Robinson and Kahn, 1986), and changes seem likely in both directions in that genus.

The type A pollen shows some variation in size, usually being about 40 μm in diameter, as measured in fluid or Hoyer's solution, but being 50–60 μm in diameter in *Lepidonia* (Robinson and Funk, 1987) and *Lessingianthus cephalotes* (DC.) H. Rob. and about 45 μm in diameter in *L. glaziovianus* (Baker) H. Rob. (Robinson, 1988b). The type A pollen grains may show apical patterns of spines similar to the lophate patterns in type C and type G grains (Robinson, 1987c). In fact, careful examination of the whole surface of the grain shows a patterned distribution of spines that is referred to herein as sublophate. A few taxa, such as *Bishopalea* H. Rob. (Figure 1E), have spines strongly oriented in muri, but the perforated tectum is continuous between the muri as in other type A grains. The unique pollen of *Orthopappus* Gleason looks like an unusual type A under the light microscope, and it is best classified in that category, but the surface actually consists of dense irregular muri with narrow gaps between (Figure 1F). These type A grains all differ from the pattern with evenly distributed spines of truly echinate grains seen in other tribes.

The echinolophate pollen types of most neotropical Vernonieae are tricolporate with orderly patterns of lacunae or areoles at the poles. The perforated tectum is restricted to the muri, often not in contact with the footlayer at the sides of the muri. The colpi are the primary organizational feature of the grains. Type C grains have single polar lacunae (Figure 4A), whereas types B (Figure 2B), D (Figure 4F), G (Figure 4E), and the

Aynia type (Figure 3B) lack them. Of the last four types, the lacunae converging on the poles in the first three are aligned with the colpus, whereas the lacunae at the poles in the *Aynia*-type are aligned with the intercolpus. The crests of these echinolophate grains retain a perforated tectum. The attachment of the crests to the footlayer is by stout baculae in genera such as *Lessingianthus* (Figures 2C, 3A), *Aynia* (Figure 3D), and *Pseudopiptocarpha,* but the baculae form a horizontal rhizome that is weakly attached to the footlayer in other members of the *Lepidaploa* complex (Figure 4B,D). The rhizomate character cannot be seen with the compound microscope, but its presence is sometimes evident by the ease with which the crests are stripped from the grains in pollens of that type (Figure 4C).

There are a few lophate pollen types, such as those in the Vernoniine genera *Struchium* (Figure 5C,D) and *Heterocypsela* (Figure 5E,F), which have both polar lacunae and crosswalls in the colpi above and below the pores. The columellae of the muri are short and irregular (Figure 5F). These pollens occur in groups characterized by tricolporate grains, and the grains differ from triporate types cited below by their simple polar lacunae.

Additional types of pollen in the Vernonieae are triporate. These triporate pollen types can be differentiated by the indefinite patterns formed by the two or more series of lacunae surrounding the poles. The colpi are usually obscured or lacking, and the pores are located in lacunae scarcely differing in form from the lacunae that do not contain pores. The triporate grains of this type are most common in Vernonieae native to the Eastern Hemisphere, such as the widely adventive *Cyanthillium* Blume. Two groups with echinolophate triporate pollen are the pantropical Elephantopiinae (Figure 7A–E) and the neotropical Rolandrinae (Figures 7F, 8A,B). Genera with triporate pollen that do not have spinules or a perforated tectum are *Pacourina* (Figure 8C,D), *Acilepidopsis,* and *Mesanthophora* H. Rob. (Figure 8E,F). The *Pacourina* type nonechinate triporate pollen was cited by Jones (1981a) as type E, and it was cited from only paleotropical members of *Vernonia* s.l. The three neotropical genera with type E pollen all seem to have only remote relationship to other neotropical Vernonieae.

SECONDARY METABOLITES.—Differences in sesquiterpene lactones and flavonoids between American and paleotropical species were mentioned by Jones (1977) and Harborne and Williams (1977). The flavonoids of American species are more complex, consisting of both flavones and flavonols.

The summary by Bohlmann and Jakupovic (1990) cited other more recent literature on the subject. Their summary also mentioned primarily terpenoid secondary metabolites of systematic interest. The 5-alkylcoumarins seemed restricted to the distinctive paleotropical group, including *Cyanthillium, Ethulia* L.f., *Bothriocline* (including some reported as *Erlangea* Sch. Bip.), and *Volkensia* O. Hoffm. A distinctive neotropical genus with possible paleotropical relationships, *Acilepidopsis,* lacks the specialized sesquiterpene lactones seen in other neotropical groups, and it is the only member of the tribe known with phenylpropanes (lignanes). Furoheliangolides show a significant distribution in subtribes recognized herein as Lychnophorinae, Centratherinae, and Sipolisiinae, but they are lacking in the Vernoniinae and Piptocarphinae. The Vernoniinae, Piptocarphinae, and Rolandrinae, in contrast, are noted for the presence of glaucolides and related sesquiterpene lactones. Bohlmann and Jakupovic (1990) concluded that *Chresta* should be rejected from its traditional position in the Lychnophorinae because of the presence of glaucolides, a rejection that is reenforced in this study by examination of pollen and anther appendages.

CHROMOSOME NUMBER.—The principal sources of chromosome numbers continue to be Jones (1974, 1979a) and Keeley (1978), but some more recent counts were cited by Keeley and Turner (1990). Some new reports with karyological details and a review of other sources were provided by Ruas et al. (1991). Papers cited by Ruas et al. included Cabrera (1944), Coleman (1968), Hunter (1964), Jones (1968, 1970, 1974, 1977, 1982b), Jones and Duncan (1966), Keeley (1978), Keeley and Jones (1977a), Powell et al. (1974), Sundberg et al. (1986), and Turner (1981). A basic pattern of $x=9$ or 10 for paleotropical Vernonieae and $x=16$ or 17 for American Vernonieae was first mentioned by Jones (1977). *Stokesia* has been the most notable exception, but a few other apparent exceptions were mentioned by Keeley and Turner (1990). The *Leiboldia/Lepidonia* group seems distinct in its count of $n=19$. Ruas et al. (1991) emphasized the different numbers reported for many species, especially the $n=17$ ($2n=34$) and $n=20$ ($2n=40$) that have been reported from two members of *Chrysolaena* (*C. flexuosa* Sims and *C. platensis* (Spreng.)) and one superficially *Chrysolaena*-like species of *Lessingianthus* (*L. simplex* Less.). Dematteis (1996) found a consistent base of $x=10$, based on three species, for what is herein recognized as *Chrysolaena.*

Summary of the Subtribes and Genera of the Neotropical Vernonieae

The idea of two centers of distribution for *Vernonia* s.l. has been reviewed by Jones (1977), Harborne and Williams (1977), and Keeley and Turner (1990), and the idea is generally extended herein to the satellite genera as well. Although most of the American members of the Vernonieae seem to form a related group, it will be seen in the following treatment that not all elements placed in *Vernonia* s.l. result from a single introduction into the Americas. The division is not a simple one that allows *Vernonia* s.l. to be divided into two large, defined genera only on the basis of hemisphere. Nevertheless, *Vernonia* in the restricted sense, with the type in eastern North America, is wholly part of the major derived group in the Western Hemisphere. Thus, none of the elements called *Vernonia* in the Eastern Hemisphere are *Vernonia,* and they must all be transferred to other genera. The present study places the majority of American species from outside of eastern North America in other genera, but the process remains incomplete for Eastern Hemisphere species that do not belong to *Distephanus* (Robinson and Kahn, 1986) or *Baccharoides* (Robinson, 1990a; Isawumi, 1993, 1995a) or genera treated by Robinson (1999b).

When the present series of studies began, the members of the tribe were thought to have extensive reticulating evolution, but this opinion has changed. At present, intergeneric hybridization in neotropical Vernonieae is considered very limited.

The first regional use of the new generic concepts was in the Guiana review of Robinson (1992e). The recognized neotropical groups are as follows. The subtribes are arranged according to characters in the following key (modified from Robinson, 1996).

Key to the Subtribes and Genera of the Neotropical Vernonieae

1\. Achenes not all flattened, usually cylindrical, not bicornute.
  2\. Pollen tricolporate; $n=20$, 19, 17, or 16.
    3\. Characteristic sesquiterpene lactones glaucolides.
      4\. Upper callus of achenes partially or completely vestigial; $n=19$ .... LEIBOLDIINAE
      4\. Upper callus of achene not vestigial, sometimes enlarged; $n=20$, 17, or 16.
        5\. Inflorescence cymose, with heads separate.
          6\. Inner involucral bracts persistent; leaves rarely opposite; lobes of corollas not strongly recurved .... VERNONIINAE
          6\. Inner involucral bracts deciduous; leaves sometimes opposite; lobes sometimes strongly recurved .... PIPTOCARPHINAE
        5\. Inflorescence glomerulose to spiciform, with congested heads .... CHRESTINAE
    3\. Characteristic sesquiterpene lactones include furoheliangolides, with or without glaucolides or guaianolides.
      7\. Receptacles of heads without spines or pales; walls of achenes without phytomelanins.
        8\. Corollas with many prominent stipitate glands; heads solitary at tips of branches .... CENTRATHERINAE
        8\. Corollas without obvious stipitate glands; heads often congested in complexes or glomerules .... LYCHNOPHORINAE
      7\. Receptacles of heads with spines or pales; walls of achenes usually with phytomelanins .... SIPOLISIINAE
  2\. Pollen usually triporate; $n=13$, 11, 8.
    9\. Pollen echinolophate, usually with perforated tectum on crests.
      10\. Heads with four florets; corollas often zygomorphic, with 5 lobes; dilactones often present ... ELEPHANTOPODINAE
      10\. Heads with single florets; corollas not zygomorphic, with 4 or 5 lobes; dilactones lacking .... ROLANDRINAE
    9\. Pollen psilolophate, crests of muri smooth or nearly smooth, without perforated tectum .... ***Acilepidopsis*** and ***Pacourina*** groups
1\. Achenes flattened and bicornute with divergent apical projections or horns .... TRICHOSPIRINAE

LEIBOLDIINAE subtribus nov.—Type: *Leiboldia* Schltdl. ex Gleason

FIGURE 9; TABLE 1

Plantae fruticosae; bracteae involucri interdum granditer appendiculatae; receptacula paleata vel non paleata; flores 100–120 in capitulo; thecae antherarum base non appendiculatae, cellulis appendicibus antherarum incrassatis; achenia 4–5 angulata glabra idioblastifera, callo apicale variabiliter vestigiale; setae pappi facile deciduae plerumque abbreviatae. Grana pollinis typis A in diametro 50–60 µm. Chromosomatum numerus $n=19$.

The characteristic sesquiterpene lactones are glaucolides (Bohlmann and Jakupovic, 1990).

INCLUDED GENERA.—*Leiboldia* (1 sp.), *Lepidonia* (7 sp.), *Stramentopappus* H. Rob. & Funk (1 sp.).

DISCUSSION.—The three genera, *Leiboldia, Lepidonia,* and *Stramentopappus,* are most notable for the series of reductions in the upper callus of the achene (Figure 9I). *Leiboldia* has the outer circle under the uniseriate, capillary pappus unsclerified, leaving an inner sclerified ring. *Stramentopappus* has the outer zone of the callus expanded to bear many rows of shortened pappus bristles, but the inner ring is retained. In *Lepidonia* the pappus is like *Stramentopappus,* but the inner ring is lost and the callus is completely unsclerified. The chromosome number of $n=19$ is also distinctive and is now known from three members of the subtribe (Keeley and Turner, 1990). In all members of the subtribe except *Leiboldia,* the achenes are turbinate above, and the achene walls are densely covered with idioblasts. The type A pollen is unusual for its size. The involucral bracts of *Lepidonia* have the largest appendages in the neotropical Vernonieae. The type species of the genus *Lepidonia* has a paleaceous receptacle. Only *Leiboldia* in the subtribe has a basal stylar node.

VERNONIINAE Lessing, Synopsis 146. 1832.—Type: *Vernonia* Schreb., nom. cons.

FIGURES 2–5; 10–14; TABLES 2–6

Mostly trees or shrubs, glabrous to densely pubescent. Leaves alternate except in some plants of two species. Inflorescence monocephalic to paniculate, cymose to thyrsoid with cymose branches. Heads with 6–120 florets; involucral bracts persistent, with little or no appendage, often apically mucronate; receptacle plain, awned, paleaceous, or deeply pitted. Corollas usually regular, rarely zygomorphic, sometimes with hairs inside, usually 5-lobed; anther bases with or without tails; apical appendage often with glands, without thickened cell walls except sometimes at border; style base usually with node; branches with usually sharply pointed hairs. Achenes prismatic or obcompressed, rarely dimorphic or laterally winged; pappus usually double with short outer series and capillary inner series, sometimes all elements capillary of various lengths, rarely reduced to corona or massive collar. Pollen tricolporate, type A or echinolophate, 37–80 µm in diameter. Chromosome number usually $n=17$. Characteristic sesquiterpene lactones being glaucolides (Bohlmann and Jakupovic, 1990).

INCLUDED GENERA.—*Vernonia* (22 sp.), *Vernonanthura* (68 sp.), *Cololobus* (3 sp.), *Trepadonia* (1 sp.), *Lessingianthus* (103 sp.), *Aynia* (1 sp.), *Pseudopiptocarpha* (2 sp.), *Harleya* (1 sp.), *Lepidaploa* (142 sp.), *Mattfeldanthus* (2 sp.), *Echinocoryne* (6 sp.), *Stenocephalum* (5 sp.), *Chrysolaena* (9 sp.), *Xiphochaeta* (1 sp.), *Struchium* (1 sp.), *Cyrtocymura* (6 sp.), *Eirmocephala* (3 sp.), *Dasyanthina* (2 sp.), *Quechualia* (4 sp.), *Heterocypsela* (1 sp.), *Dipterocypsela* (1 sp.), *Stilpnopappus* (20 sp.), *Blanchetia* (1 sp.), *Irwinia* G.M. Barroso (1 sp.), *Albertinia* (1 sp.).

DISCUSSION.—The subtribe is considerably reduced herein from the concept of Robinson et al. (1980), especially in the restriction of the subtribe to American species. The genera retained herein in the subtribe fall into numerous subgroups that include the typical element, the *Lepidaploa* complex, *Dasyanthina/Quechualia* with hairs inside the corolla, *Dipterocypsela/Heterocypsela* with obcompressed outer achenes, *Stilpnopappus* with broadened pappus segments, *Blanchetia/Irwinia* with heterotrichous stems and broadened pappus segments, and *Albertinia* with achenes recessed in the receptacle.

Typical Vernoniinae (Table 2) have essentially glabrous corolla lobes and type A pollen. *Vernonia,* with a decumbent stem base and a wholly cymose inflorescence, occurs in Eastern North America, the Bahamas, and south to central Mexico. Two temperate South American species, *V. echioides* Less. and *V. incana* Less., show the basic characters of *Vernonia* and are retained there. Still, the latter two are individually distinctive, and they would not be taken as each other's closest relatives at first glance. The other three genera of the subgroup have thyrsoid inflorescences with only the branches cymose, a distinction that was noted as early as in the treatment in the North American Flora by Gleason (1922). *Cololobus* (Figure 10A–I) of coastal Brazil has the shortest disk corolla lobes in the subfamily (Robinson, 1994c). The widely distributed *Vernonanthura* (Robinson, 1992b) and *Trepadonia* of Peru (Robinson, 1994c) often show distinctive resin ducts in the lamina of the corolla lobes. *Vernonanthura* often has distinct basal tails on the anthers, a condition not seen in other members of the immediate *Vernonia* group. *Trepadonia* is a vine primarily distinguished by the pyramidally thyrsoid inflorescences with racemiform branches.

The *Lepidaploa* complex (Table 3, 4) was initially distinguished in the present series of studies for a large element of the Vernoniinae with mostly echinolophate pollen. It was also notable for the many examples of scorpioid-cymose or seriate-cymose inflorescence branches even in some genera with type A pollen (Robinson, 1987c). The corollas also often bear long hairs. The complex proves to be subdivided into two groups, one including *Lessingianthus* and the other with *Lepidaploa.*

The *Lessingianthus* subgroup (Table 3) is most distinct in the strongly baculate crests of its echinolophate pollen (Figures 2C, 3A,D). The four genera also have mostly subquadrate raphids in the achene wall. The pollen types can usually be distinguished from those of the *Lepidaploa* subgroup by the details of their lophate pattern. Type B pollen is in almost all of *Lessingianthus* (Figures 2A–D, 3A), and the *Aynia* type is in *Aynia* (Figure 3B–D), *Harleya,* and *Pseudopiptocarpha* (illustrated under an incorrect name in Diaz Piedrahita, 1985, see Robinson, 1994c). Glands have not been seen on the anther appendages of any of the four genera.

The large, mostly Brazilian genus *Lessingianthus* (Figure 11A–G) (Robinson, 1988b) generally contains robust plants, and it parallels rather closely the group called Lepidaploae macrocephalae by Baker (1873). The style base usually lacks a node, but there are some exceptions. The achene lacks glands in all observed species; the structures Hind (1993) cited as glands for *L. mysinites* H. Rob. were evidently those referred to herein as idioblasts.

An overview of the pollen structure and raphids aligns *Lessingianthus* with *Aynia, Pseudopiptocarpha,* and *Harleya* in a group slightly outside of the group with *Lepidaploa* and its closest allies. In comparision with *Lessingianthus,* glands occur on the achenes of *Aynia* (Robinson, 1988d) and *Pseudopiptocarpha* (Robinson, 1994c). *Harleya* lacks glands, but it has strongly bulging idioblasts that resemble glands. *Harleya,* with its coroniform pappus, and *Pseudopiptocarpha* are distinct in their heads with only 6–10 florets. The heads are in terminal clusters in the former genus and in axillary clusters in the latter genus.

Lessingianthus was originally defined (Robinson, 1988b) with no node at the base of the style, but a distinct node has been noted in *L. regis* (H. Rob.) H. Rob. (Robinson, 1994b) and *L. santosii* (H. Rob.) H. Rob. In addition, *Lessingianthus* often has heads that are not sessile, whereas *Lepidaploa* was initially defined by Robinson (1990b) as having all heads except the apical ones strictly sessile. Individual species recently added to *Lepidaploa* have distinctly pedunculate heads (Robinson, 1995). The new observations weaken two of the characters originally used to distinguish *Lepidaploa* from *Lessingianhus;* however, the shape of the raphids in the achene, not originally considered a distinction between *Lepidaploa* and *Lessingianthus,* has now proven to be important. Even so, all species of *Lessingianthus* have not been reexamined for this character, and some, such as *L. santosii,* have proved to have elongate raphids. Except for the pollen, the latter species would be placed with the superficially similar and possibly closely related *Vernonia almasensis* D.J.N. Hind in *Lepidaploa.* The pollen and raphids of *Lessingianthus regis* are typical for the genus in which it is placed, but *L. regis* has an extremely close morphological resemblance to *Lepidaploa spixiana* (Mart. ex DC.) H. Rob. (Robinson, 1994b).

Another element of *Lessingianthus* requiring reexamination is the subgenus *Oligocephalus* H. Rob. As noted in the discussion of the chromosome numbers, one of the species, *L. simplex,* has distinctive numbers that are like those of species of *Chrysolaena,* which *L. simplex* superficially resembles and with which it was once classified in *Vernonia* subsection *Scorpioides* series *Flexuosae* (Jones, 1979c).

The majority of *Lessingianthus* is expected to remain unchanged in future studies, but some of the small elements mentioned above need to be reviewed, and some taxonomic refinements probably will be needed. Some small new genera are probably required. *Mattfeldanthus* has *Lessingianthus* type baculae in the pollen combined with *Lepidaploa* type raphids in the achene, but the genus is grouped in the following discussion with *Lepidaploa.*

The *Lepidaploa* subgroup (Table 4) has echinolophate pollen with crests or muri termed in these studies as rhizomiform (Figure 4B–D). The baculae are distorted or mostly fused with each other into a horizontal structure that is weakly attached to the footlayer. The structure cannot be observed properly with a compound microscope, but the way that the crests often peel off the footlayer can be seen. In this subgroup, all the genera have elongate raphids except *Stenocephalum,* where no raphids seem to occur. Numerous genera are recognized in the subgroup. The largest, *Lepidaploa* (Robinson, 1990b) is widely distributed from Mexico and the Antilles south through the Andes to Brazil and Argentina. The Brazilian *Mattfeldanthus* (H. Rob. & King, 1979) has peripheral florets with unequal inner lobes. The Brazilian *Echinocoryna* (Robinson, 1987b) has greatly increased numbers of pointed involucral bracts. *Stenocephalum* has only 4–7(–10) florets in the heads and apparently lacks raphids in the achenes. The mostly Brazilian *Chrysolaena* (Robinson, 1988c) has a reduced stylar node and usually has numerous glands on the anther. The northern South American aquatic, *Xiphochaeta* (Robinson, 1992d), has paleaceous pappus segments, shortened anther bases, a style base with no node, and a vestigial achene base. *Cyrtocymura* (Figure 12A–F) and *Eirmocephala* (Robinson, 1987c) usually have scorpioid-cymose inflorescence branches and have the most significant reversions of pollen to type A in the complex. The now pantropical *Struchium* has a large, thick, coroniform pappus and a corolla with three or four lobes, and it has a reported chromosome number of $n=16$ (Mathew and Mathew, 1988).

The small *Dasyanthina* (Figure 13A–I) and *Quechualia* (Figure 14A–K) group (Table 5) (Robinson, 1993b) is notable for hairs inside the corolla. The raphids in the achene are elongate but small.

The Colombian *Dipterocypsela* and Brazilian *Heterocypsela* (Figure 5) were initially compared by Robinson (1979d), but they were not then considered immediate relatives because of differences of inflorescence form and pollen. The heteromorphic achenes, with the outer series being strongly obcompressed, and the extreme density of the subquadrate raphids in the achenes indicate that the two genera are closely related. Both have glanduliferous anther appendages.

The mostly Brazilian *Stilpnopappus* group (Table 5), containing only *Stilpnopappus* (including *Strophopappus* DC.) (Esteves, 1994), has a pappus of broadened lanceolate segments and has subquadrate raphids enclosed in thick-walled cells of the achene wall. The pollen varies from type A to the *Aynia* type. Setulae, glands, and idioblasts have been seen on the achenes. The group seems closest to the *Lessingianthus* subgroup of the *Lepidaploa* complex.

The Brazilian *Blanchetia-Irwinia* group (Table 6) includes the two closely related genera that have heterotrichous pubescence of mixed stellate and spreading, uniseriate, multiseptate hairs. The spreading hairs of *Blanchetia* are very coarse. The inner pappus segments are broadened and linear. *Blanchetia* is distinct in the more numerous florets in the heads and the presence of thin projecting partitions on the receptacle. There is no basal node on the style. The anther bases have no tails, and the pollen is type A.

Albertina of Brazil is considered a distinct group on the basis of the deep pits in the receptacle that enclose the whole bodies of the achenes. The raphids are subquadrate and the pollen is type A. The genus superficially resembles various members of the subtribe Lychnophorinae, but the style has a basal node.

PIPTOCARPHINAE H. Rob., King, & F. Bohlmann, Phytologia 46:426. 1980.—Type: *Piptocarpha* R. Br.

FIGURES 1A,B, 15; TABLE 7

Shrubs and trees, often many branched; pubescence often stellate or lepidote. Leaves alternate or often opposite. Inflorescence a terminal panicle or in axillary clusters. Heads with 1–11(–20) florets; inner involucral bracts deciduous. Corollas regular, without hairs inside except in *Dasyandantha;* anther bases often with tails, sometimes sclerified, apical appendages usually with thick-walled cells, glabrous; style base with or without node; style branches with often blunt-tipped hairs. Achenes prismatic, with 3–10 ribs or angles, glabrous or with setulae or glands, raphids mostly subquadrate; pappus capillary or linear sometimes twisted segments, or coroniform. Pollen type A (Figure 2A,B). Chromosome number usually n=17. Characteristic sesquiterpene lactones, glaucolides (Bohlmann and Jakupovic, 1990).

INCLUDED GENERA.—*Critoniopsis* (85 sp.), *Dasyandantha* (1 sp.), *Piptocarpha* (43 sp.), *Joseanthus* (3 sp.), *Cuatrecasanthus* (5 sp.), *Piptocoma* (including *Pollalesta* H.B.K.) (18 sp.), *Ekmania* (1 sp.), *Huberopappus* (1 sp.).

DISCUSSION.—The most significant feature of the subtribe was originally considered to be the blunt-tipped hairs of the style (Robinson et al., 1980), a feature noted previously by Cabrera (1944). Stellate to lepidote hairs also were emphasized. The blunt-tipped hair characteristic is now seen as only a weak trend. The most important character of the subtribe is now recognized to be the deciduous inner involucral bracts associated with comparatively few florets in the head. The deciduous inner bracts were recognized by many previous authors in their delimitation of *Vernonia* subgenus *Critoniopsis* (Baker, 1873). The shrubby or arborescent habit, the type A pollen, and the almost always subquadrate raphids of the achene also are important. More interestingly, almost all the opposite-leaved American Vernonieae belong to the subtribe in the genera *Critoniopsis, Joseanthus,* and *Piptocarpha.* The only consistently opposite-leaved genus is *Joseanthus* containing five species. The lobes of the corollas in many members of the group are recurved, whereas the lobes of most American Vernonieae are more or less erect.

Of the five genera of the Piptocarphinae having a basal node on the style, the most plesiomorphic genus seems to be *Critoniopsis* (including *Eremosis*) (Robinson, 1993a). *Dasyandantha* (Robinson, 1993b) differs most by the dense pubescence inside the corolla limb. *Piptocarpha* has sclerified tails on the anthers. *Joseanthus* (Figure 15A–E) and *Cuatrecasanthus* (Robinson, 1989a) have corolla lobes separate to the base of the limb, the former with 9–12 flowers and opposite leaves, and the latter with single-flowered heads and alternate leaves. The genera without a basal stylar node are the West Indian and the northern South American *Piptocoma* (Stutts, 1981), the Venezuelan *Huberopappus* (Pruski, 1992), and the Antillean *Ekmania*. The South American *Pollalesta* is accepted as congeneric with *Piptocoma* (Pruski, 1996). All the latter genera have reduced numbers of linear or contorted pappus segments or, in *Huberopappus,* have only an outer sheath. *Ekmania* has the most highly developed lepidote pubescence of the subtribe.

CHRESTINAE subtribus nov.—Type: *Chresta* Vell. ex DC.

FIGURES 6, 16; TABLE 8

Plantae perennes herbaceae vel suffruticosae, rosulatae vel caulescentes; pilis simplices vel T-formibus. Folia alterna. Inflorescentiae terminales vel axillares interdum scaposae corymbosae vel sphaerico-glomeratae vel spicatae, maturatione plerumque simultanea vel basifuga. Capitula angusta, bracteis involucri in seriebus paucis inaequales; receptacula inerma. Flores in capitulo 2–12; corollae regulares 5-lobatae, lobis interdum in celluis interioribus basilaribus seriale papillosis, tubis et lobis plerumque longe pilosis, pilis raro T-formibus, faucibus brevibus vel nullis; thecae antherarum base rotundatae, caudis brevibus vel nullis; appendices apicales obtusae vel emarginatae intus plerumque exaratae glabrae, parietibus cellularibus angustis; basi stylorum non nodati; rami stylorum breviter argute pilosuli. Achenia prismatica circa 10-costata, raro biformia in setulis et idioblastis plerumque obsita, raphidis subquadratis raro elongatis; series exteriores pappi breves, series interiores persistentes vel deciduae setiformes vel lineares vel lanceolatae. Grana pollinis in diametro 40–57 µm tricolporata plerumque echinolophata polariter areolata raro typis A.

The chromosome number of the subtribe is unknown. The characteristic sesquiterpene lactones are glaucolides, but furoheliangolides have been reported from the roots of *Chresta sphaerocephala* DC. (Bohlmann, Singh, Zdero, et al., 1982b).

INCLUDED GENERA.—*Chresta* (12 sp.), *Soaresia* Sch. Bip. (1 sp.), *Pithecoseris* (1 sp.).

DISCUSSION.—The genera of the Chrestinae are mostly restricted to Brazil and have traditionally been placed in the Lychnophorinae because of their congested heads. The chemical difference of having glaucolides was noted by Robinson, Bohlmann, and King (1980) and was the basis of the suggested exclusion of *Chresta* from the Lychnophorinae by Bohlmann and Jakupovic (1990). The exclusion is seconded herein on the basis of the lophate pollen (Figure 6A–C) and the anther appendages without thick-walled cells. In these three characteristics the Chrestinae resemble the Vernoniinae, and the subtribe seems to represent a lineage from near the point of divergence between the Lychnophorinae and the Vernoniinae.

Pithecoseris has been left in the Lychnophorinae until now for lack of examination, but its pollen and anther appendages align it with *Chresta. Pithecoseris* (Figure 16) is most notable for its strongly acropetal inflorescence maturation, a type of maturation highly anomalous in the Asteraceae. The form is also found in a smaller form in older heads of *Chresta martii* (DC.) H. Rob. *Soaresia* nom. cons. (*Bipontia*) is unusual in the venation of its leaves, neither pinnate nor trinervate, but so strongly ascending as to be nearly longitudinal. The pappus differs by its bristle-like awns.

Chresta is retained herein as in the broad interpretation of Robinson (1980c). The segregates recognized by MacLeish (1984a, 1985a, 1985b), namely *Argyrovernonia, Glazioviananthus,* and *Pycnocephalus,* all have various characteristics, such as reversion to type A pollen, broadened deciduous pappus segments, indeterminately elongate glomeruli, and sometimes elongate raphids in the achene, but these characteristics do not correlate and seem to violate close relationships. The broader concept is strongly recommended.

CENTRATHERINAE H. Rob., King, & F. Bohlmann. Phytologia 46:425. 1980.—Type: *Centratherum* Cass.

TABLE 9

Annual or short-lived perennial herbs, rarely shrubby; stems with T-shaped hairs, also with spreading multiseptate hairs in *Centratherum.* Leaves alternate. Heads terminal, mostly solitary, with 50–100 florets, subtended by dense cluster of foliose bracts below the appressed involucral bracts, involucre persistent; receptacle unarmed. Corollas with long-stalked glandular hairs, with five lobes; anther bases without tails, apical appendage glabrous, cells with little or no spiral thickening on walls; style base without node; branches with pointed hairs. Achenes terete to prismatic with 8–10 ribs, with glands and idioblasts, sometimes with setulae, raphids subquadrate; pappus of short bristles or lacking, deciduous. Pollen grains type A, 30–40 µm in diameter. Chromosome number $n=16$. Characteristic sesquiterpene lactones being furoheliangolides and guaianolides.

INCLUDED GENERA.—*Centratherum* (3 sp.), *Oiospermum* Less. (1 sp.).

DISCUSSION.—The solitary terminal heads subtended by foliose bracts, the many flowers in the heads, and the long-stalked glands on the corollas are distinctive. The chromosome number of $n=16$ and the furoheliangolides also help to distinguish the subtribe.

The subtribe contains only *Oiospermum* of Brazil, having achenes with slender reflexed tips on the setulae, and the widespread *Centratherum* Cass. (Kirkman, 1981), with glabrous to spiculiferous achenes. *Centratherum* is obviously neotropical in origin with recent introduction into Australia and the Philippines.

LYCHNOPHORINAE Benth. in Benth. & Hook. f., Gen. Pl. 2: 171. 1873.—Type: *Lychnophora* Mart.

FIGURES 17, 18; TABLE 10

Perennial herbs to shrubs and small trees; usually pubescent with simple to T-shaped or stellate hairs, often densely hirsutulous. Leaves alternate. Heads often clustered or in syncephala with maturation nearly simultaneous, sometimes separate; involucral bracts in few to many series; receptacle without pales. Florets 1–60 in a head; corollas regular, mostly 5-lobed; anther bases rarely with tails, apical appendage glabrous, with thickened cell walls at least along margin; style base without node; branches with pointed hairs. Achenes terete to prismatic, with 8–10 veins, rarely dimorphic, with idioblasts, sometimes with glands or setulae; raphids subquadrate; pappus of capillary bristles or twisted straps, subpersistent to deciduous, with or without short outer series. Pollen grains type A, 40–55 µm in diameter. Chromosome numbers $n=15$, 17, 18. Characteristic sesquiterpene lactones being furoheliangolides.

INCLUDED GENERA.—*Lychnophora* (including *Haplostephium* Mart. ex DC.) (34 sp.), *Lychnophoriopsis* Sch. Bip. (4 sp.), *Eremanthus* Less. (including *Vanillosmopsis* Bentham & Hooker f.) (27 sp.), *Prestelia* Sch. Bip. (1 sp.), *Anteremanthus* H. Rob. (1 sp.), *Minasia* H. Rob. (5 sp.), *Piptolepis* Sch. Bip. (7 sp.), *Chromopappus* DC. (1 sp.), *Proteopsis* Mart. & Zucc. (1 sp.).

DISCUSSION.—The traditional definition of the Lychnophorinae based strictly on compound heads is now completely abandoned. The original inclusion of the compound headed *Elephantopus* and *Rolandra* Røttb. in the Lychnophorinae by Bentham and Hooker f. (1873) was mostly ignored after the work of Hoffmann (1890–1894). The unity of tribal members with compound heads was formally ended when the earlier described Elephantopinae and newly described Rolandrinae were recognized by Robinson et al. (1980). *Vanillosmopsis,* placed in the Ethulieae by Bentham and Hooker f. (1873), was synonymized with *Eremanthus* by MacLeish (1987). Robinson et al. (1980) also first placed genera with separate heads, namely *Proteopsis* and *Piptolepis,* in the Lychnophorinae. Additional genera with solitary heads, *Anteremanthus* and *Minasia* (Figure 18), have been added to the subtribe by Robinson (1992c), with the inclusion of species that have previously been placed in *Vernonia.* Three compound-headed genera (*Chresta, Soaresia,* and *Pithecoseris*) have been removed from this subtribe and have been placed in the new subtribe, Chrestinae, described above. The presently recognized genera of the subtribe Lychnophorinae are *Chronopappus, Eremanthus* (*Sphaerophora, Paralychnophora* MacLeish, *Vanillosmopsis*), *Lychnophora* (*Haplostephium* Mart. ex DC.), *Lychnophoropsis* (*Episcothamnus* H. Rob.) (Figure 17), and *Prestelia,* all with clustered or compound heads, and *Anteremanthus, Minasia, Piptolepis,* and *Proteopsis* with separate heads. The only dimorphic achenes in the subtribe are reported in the type species of *Lychnophoropsis.* The differences are in setulosity and the pappus.

The subtribe Lychnophorinae is almost completely restricted in distribution to Brazil. *Eremanthus jelskii* Hieron. and *Vanillosmopsis weberbaueri* Hieron. of Peru belong respectively to *Cuatrecasanthus* and *Critoniopsis* of the Piptocarphinae.

The presence of furoheliangolides in the Lychnophorinae has been noted by Robinson, Bohlmann, and King (1980) and Bohlmann and Jakupovic (1990). *Lychnophora* of the subtribe also contains unique caryophyllene derivatives and α-humulene derivatives (Bohlmann and Jakupovic, 1990). The subtribe also notably lacks glaucolides that are common elsewhere in the tribe.

SIPOLISIINAE subtribus nov.—Type: *Sipolisia* Glaziou ex D. Oliver

FIGURE 1E; TABLE 11

Plantae perennes herbaceae vel suffrutescentes rosulatae vel caulescentes plerumque ubique albo-tomentosae vel appresse stellate pilosae. Folia alterna base interdum amplexicaulia. Inflorescentiae axillares vel terminales interdum scaposae unicapitatae vel paucicapitatae et corymboso-cymosae, bracteis subcapitatis foliiformibus interdum trinervatis. Capitula sessilia vel longe pedunculata; bracteis involucri gradatim multiseriatis breviter vel anguste acutis; receptacula distincte aristata vel paleacea. Flores 20–60; corollae regulares 5-lobatae, tubis brevibus vel elongatis, faucibus brevibus, lobis longe pilosis vel spiculiferis; thecae antherarum base rotundatae vel breviter acuminatae, appendicibus nullis vel brevibus interdum scleroideis; appendices apicales glabrae in partibus scleroideae; basi stylorum non noduliferi. Achenia prismatica glabra circa 10-costata interne in parte carbonacea; setae pappi capillares vel lineares et barbellatae persistentes vel deciduae, seriebus exterioribus carentibus. Grana pollinis in diametro 40–55 µm tricolporata typis A.

The chromosome number is unknown. A furoheliangolide has been reported in *Xerxes* (as *Alcantara* hom. illeg.) (Bohlmann, Singh, Robinson, et al., 1982).

INCLUDED GENERA.—*Heterocoma* (1 sp.) (Toledo, 1941), *Bishopalea* (1 sp.), *Sipolisia* (1 sp.), *Xerxes* (1 sp.), *Hololepis* (1 sp.).

DISCUSSION.—All members of the subtribe have restricted distributions in southeastern Brazil.

Four genera of the subtribe, *Bishopalea, Heterocoma, Sipolisia,* and *Xerxes* J.R. Grant (1994), form an unquestionably related group with a partially carbonized layer in the achene wall. Such a layer has previously been seen only in the Eupatorieae, Heliantheae, and the *Blepharispermum* group that was once placed in the Inuleae (Eriksson, 1991). The Sipolisiinae is the only group with carbonization known in the family outside of the subfamily Asteroideae. As is the case of carbonized achenes elsewhere in the Asteraceae, raphids are not present in the achenes. The four genera fall in two groups. *Siplosia* and *Xerxes* have aristate receptacles and long basal corolla tubes, whereas *Bishopalea* and *Heterocoma* have paleaceous receptacles and short basal corolla tubes. The *Heterocoma* corolla lobes are spiculiferous, and they lack the long hairs seen in the other three genera.

The fifth genus included in the Siplosiinae, *Hololepis,* differs from the typical group by the petiolate leaves, the glabrous upper surfaces of the leaf blades, and the lack of carbonization in the achenes. Nevertheless, the genus has a similar general habit, glabrous prismatic achenes, and a receptacle with aristae. It is the aristae of the receptacle that seem to relate *Hololepis* to *Sipolisia* and *Xerxes,* and aristiferous or paleaceous receptacles are the most significant and consistent characteristic of the subtribe. Paleae have only a scattered occurrence among other American Vernonieae, such as *Bolanosa* and *Lepidonia* of Mexico and Guatemala. Keeley and Turner (1990) have called attention to the trinervate inflorescence bracts of *Hololepis.* It is the only American member of the Vernonieae with clear trinervation in a foliar structure, but its significance in a modified bract is unknown.

ELEPHANTOPODINAE Less., Linnaea 5:135. 1830.—Type: *Elephantopus* L.

FIGURE 7A–E; TABLE 12

Perennial herbs from stolons or rootstocks, rosulate to caulescent. Inflorescence corymbose to spicate or glomerulate. Head clusters sometimes subtended by secondary involucre of foliose bracts; true involucre usually with 4 pairs of bracts; receptacle unarmed. Florets mostly 2–4; corollas 4–10 mm long, usually unequally 5-cleft, lobes with either glandular dots or long hairs; bases of anther thecae shorter than collar, apical appendage glabrous, with thin-walled cells; style base without node or with very slight node. Achenes prismatic, with numerous setulae and idioblasts, often with glands, raphids elongate; pappus usually uniseriate, with few to many bristles or awns or with laciniate scales, awns sometimes strongly contorted. Pollen 35–37 µm in diameter, triporate, echinolophate or multicrested (subtype of type A). Chromosome numbers $n=11$, 13. Characteristic sesquiterpenes being germacranolides (dilactones) (Bohlmann and Jakupovic, 1990).

INCLUDED GENERA.—*Elephantopus* (16 American sp.), *Orthopappus* (1 sp.), *Pseudelephantopus* Rohr (2 sp.).

DISCUSSION.—The subtribe has been rather consistently recognized as distinct from the Vernoniinae on the basis of the clustered heads and the tendency for a reduced or modified pappus. The placement in the Lychnophorinae by Baker (1873) and Hoffmann (1890–1894) was both a nomenclatural and a systematic error because the name Elephantopodinae is older, and the relationship is distant. The distinction between the two latter groups is clear in both the triporate and lophate pollen and the presence of dilactone rather than furoheliangolide sesquiterpene lactones (Harborne and Williams, 1977; Robinson, Bohlmann, and King 1980; Bohlmann and Jakupovic, 1990).

Further features distinguishing the Elephantopodinae in the Western Hemisphere are the shortened basal spurs on the anther thecae and the often zygomorphic corollas.

The subtribe is pantropical but extends into temperate areas in the southeastern United States.

Both the pantropical distribution and the triporate pollen of the subtribe raise the question regarding the hemisphere in which the group originated. The lacunae in the polar region of the pollen grains are irregular in arrangement. This differs from the regular unilacunar or trilacunar polar organization seen in the lophate pollen types of the large, related foregoing American group that includes the Vernoniinae and Chrestinae. Still, the Elephantopodinae have endemic American elements, such as *Pseudelephantopus* with its contorted pappus awns, and it seems closely related to the American subtribe Rolandrinae.

Orthopappus ($n=11$) is frequently synonymized with *Elephantopus* ($n=11$) in recent taxonomic literature, even when the chromosomally distinct *Pseudelephantopus* ($n=13$) is held separate. The multisetose pappus alone cannot be used as a distinction in view of the variation in African members of *Elephantopus* shown by Philipson (1938b). As shown by Robinson (1992d), however, the pollen of *Orthopappus* is very unusual, with separate echinate crests filling the noncolpar regions. The pollen looks superficially like type A, but it is not a simple reversion to that type. The present study has not reviewed the African members of *Elephantopus* that resemble *Orthopappus* in the number of pappus bristles (Philipson, 1938a).

Telmatophila Mart. ex Baker has not been seen in this study, but the genus is retained near *Elephantopus* where it was placed by Baker (1873) because of the few subequal bracts of the involucre, the herbaceous habit, and the axillary clusters of heads. It is unusual in the group by having long hairs on the corolla lobes as shown by Baker (1873); the hairs are similar to those in many members of the *Lepidaploa* complex. The genus may be closely related to the new genus *Caatinganthus,* which is described in this treatment at the end of the section on American genera not placed in subtribes.

ROLANDRINAE Lessing, Linnaea 6:105. 1831.—Type: *Rolandra* Røttb.

FIGURES 7F, 8A,B; TABLE 12

Erect perennial herbs or shrubs. Inflorescence with clusters or glomerules of heads axillary or pedunculate. Heads with involucral bracts 2–6, subequal, apically spurred or aristate. Florets 1 in head; corollas ~2 mm long, regular, with 3–5 lobes, lobes sclerified outside distally; anther thecae with basal spurs longer than collar, without tails, apical appendages glabrous, with thin-walled cells; style base without node. Achenes with few spicules and many idioblasts, sometimes densely glandular-dotted, raphids minutely subquadrate to lacking; pappus of short squamellae. Pollen 35–40 µm in diameter, triporate, echinolophate. Chromosome number of *Spiracantha* H.B.K. reported as $n=8$ ($2n=16$, Semple, 1974). Characteristic sesquiterpene lactones glaucolides (Bohlmann and Jakupovic, 1990).

INCLUDED GENERA.—*Rolandra* (1 sp.), *Spiracantha* (1 sp.).

DISCUSSION.—The separate subtribal status is retained for the two genera *Rolandra* and *Spiracantha* from Central America, northern South America, and the West Indies. *Rolandra* has been introduced into Japan and Java (Pruski, 1992). The genera are evidently close to the Elephantopodinae, but they have single-flowered heads, small and regular corollas with sclerified lobe tips, and spurred anther bases of normal length for the Vernonieae.

The chromosome numbers of $n=8$, 11, and 13 in the Rolandrinae and Elephantopodinae are low for American members of the tribe, and they may be another indication of a separate Eastern Hemisphere origin of the combined group.

TRICHOSPIRINAE Less., Linnaea 6:690. 1831.—Type: *Trichospira* H.B.K.

Prostrate herbs with sessile leaves; leaves alternate on vegetative stems, subopposite on fertile stems. Heads axillary, with bracts intermixed in florets representing either palea or relicts of syncephaly; corollas ~2 mm long, deeply 4-lobed, with some glands outside; anther thecae not spurred; apical appendage ovate, glabrous, with thin-walled cells; style base without node, branches and upper shaft with pointed hairs. Achenes strongly compressed, densely spiculiferous and sparsely glanduliferous, without evident idioblasts or raphids; pappus of a pair of spreading apical awns, with cluster of smaller awns around corolla base. Pollen ~30–32 µm in diameter. Chromosome number not known. Chemistry unknown.

INCLUDED GENERA.—*Trichospira* (1 sp.).

DISCUSSION.—*Trichospira* was placed in the Heliantheae-Coreopsidinae in traditional systems (Bentham and Hooker f., 1873; Hoffmann, 1890–1894) because of the flattened and strongly biaristate achenes. The genus was returned to the Vernonieae by Robinson and Brettell (1973a). The considerable reduction in size of parts in the single, strictly American species, *T. verticillata* (L.) Blake, obscures any relationship. The distinctive achene shape, spiculiferous achene surface and the lack of any idioblasts suggest an isolated position of the subtribe in the Vernonieae. The subtribe seems to represent a particularly unrelated element among American Vernonieae, but a position outside of the tribe does not seem justified.

AMERICAN GENERA NOT PLACED IN SUBTRIBES

Unplaced American genera fall into five groups according to pollen.

1. *Bolanosa* of Mexico, *Gorceixia* of Brazil, and *Acanthodesmos* C.D. Adams & M.C. du Quesnay of Jamaica have type A pollen, and the three may relate closely to other American groups. *Bolanosa* and a few Mexican species placed in *Vernonia* may relate to the Leiboldiinae. The shrub, *Gorceixia,* has 5-flowered heads clustered as in the Elephantopodinae and Rolandrinae, and it may be related to that group. *Acanthodesmos* has a mixture of characters, large type A pollen (50 µm wide), a *Lepidaploa* habit, blunt sweeping hairs on the style, elongate raphids in the achene, pappus scales bearing glands, and sclerified anther appendages. The latter is the strongest candidate seen in the study for a intergeneric hybrid origin.

2. *Stokesia* of the southeastern United States, with tricolporate, echinolophate pollen (Figure 6D–F) could be accomodated in such subtribes as the Vernoniinae in spite of its mostly liguliform corollas and its reduced deciduous pappus. *Stokesia* belongs in the same phyletic line as the New World species of

Vernonia rather than in the African phyletic line according to Jeffrey (1988) and the chemical evidence of Harbourne and Williams (1977). It is held out at present because of the low chromosome number (n=7, Jones, 1974) that is unlike those in any of the Vernoniinae/Lychnophorinae series of subtribes given above. For subtribe Stokesiinae see Robinson (1999a).

3. The Cuban *Lachnorhiza* A. Rich. has triporate or shortly tricolporate, lophate pollen that is slightly echinate. It is the type referred to by Jones (1981a) as type F. Such pollen is not found in the Vernoniinae/Lychnophorinae subtribal series. The rosulate, scapose, monocephalic habit with multiflowered heads is thoroughly distinctive. A close Eastern Hemisphere relationship is possible. The genus was cited by Jeffrey (1988) in a possible related group with the African genera *Aedesia,* O. Hoffm., *Linzia* Sch. Bip. ex Walper., and *Kinghamia* C. Jeffrey. The same type of pollen seems to occur in American Vernoniinae only in the structurally very different *Caatinganthus* described below. Chemistry and chromosome number of *Lachnorhiza* are not known.

4. *Acilepidopsis, Mesanthophora,* and *Pacourina* have strictly triporate, lophate pollen with smooth crests lacking any perforated tectum (type E) (Figure 8C–F). Such pollen is found elsewhere in the Vernonieae only in African and Asian genera. Besides its neotropical distribution, *Pacourina* has the seriate-cymose habit that is primarily restricted to neotropical Vernonieae, but there is no other evidence that a type E pollen (Figure 8C,D) has evolved in any basically neotropical element of the tribe. *Acilepidopsis* and *Mesanthophora* (Figure 8E,F) have pollen similar to that of *Pacourina* and identical to each other. They have no characteristic that suggests closest relationship to other neotropical subtribes. Chromosome numbers have not been published, but guaianolides, bisabolene derivatives, and the only phenylpropanes (lignanes) in the tribe have been reported from *Acilepidopsis* (Bohlmann et al., 1981; Bohlmann and Jakupovic, 1990). *Acilepidopsis* also has sharp, sclerified tails on the anthers, reminiscent of, but obviously separately evolved from, the basal appendages in *Piptocarpha.* The best disposition of the three triporate psilolophate genera will not be known until more chemical and cytological data is available and until the African and Asian Vernonieae have been resolved to the level presently obtained in the neotropical members of the tribe. For subtribe Pacourininae see Robinson (1999a).

5. The following new genus, that is not placed as to subtribe, has been recognized in the late stages of the study, and is added here for the sake of completeness.

Caatinganthus H. Rob. gen. nov.

FIGURES 19, 20

Plantae herbaceae annuae vel breviter perennes erectae vel decumbentes 15–20 cm altae non vel pauce ramosae; caules teretes dense arachnoideo-tomentosi. Folia plerumque alterna raro base opposita sessilia anguste oblonga vel lineares 2–5 cm longa 2–4 mm lata margine integra vel minute argute denticulata apice breviter distincte pungentia supra plerumque dense hirtella subtus dense appresse arachnoideo-tomentosa uninervata, nervis secundariis obscuris vel nullis. Inflorescentiae axillares vel pseudaxillares spiciformes vel strobiliformes 1–3 cm longae, bracteis foliiformibus 1.0–1.5 cm longis; capitula sessilia secunda dorsaliter congesta biseriata; bracteae involucri triseriatae oblongae, bracteae exteriores 2 vel 3 base scariosae distaliter herbaceae foliiformes dense tomentosae, bracteae interiores 4 omnino scariosae extus dense sericeae intus glabrae; receptacula inter dissepimenta quadripartita. Flores 4 in capitulo; corollae 7–10 mm longae lavandulae vel purpureae, tubis angustis glabrous, faucibus brevibus, lobis 5 elongatis extus distaliter punctato-glanduliferis et interdum breviter pilosulis intus margine anguste vel distincte introrse alatis; filamenta antherarum in partibus inferioribus brevia; thecae antherarum base inornatae; appendices apicales antherarum tenues non glanduliferae ad medio plicatae; basi stylorum in annulis brevibus noduliferi. Achaenia turbinata circa 1.5 mm longa dense longe sericea, raphidis densis quadratis, carpopodiis obsoletis; pappus valde dimorphus persistens saepe ruber, seriebus exterioribus squamiformibus, squamis circa 10 late oblongis apice truncatis extus minute antrorse prorulosis, seriebus interiores setiformibus, setis circa 10 barbatis. Grana pollinis 55–60 µm in diametro lophata triporata vel minime tricolporata in marginis murorum minute denticulata sine tectis multo perforatis.

TYPE.—*Caatinganthus harleyi* H. Rob.

DISCUSSION.—Material of a second species of *Caatinganthus* was described initially as *Stilpnopappus rubropappus* by Soares Nunes (1981), and that species resembles *Stilpnopappus* in habit. Nevertheless, both Soares Nunes (1981) and the later monographer of *Stilpnopappus,* Esteves (1993), emphasized the anomalous nature of the material compared to other species in the genus. The present study confirms the anomalies, the clustered, 4-flowered rather than multiflowered heads, the dimorphic rather than uniformly lanceolate pappus segments, and the essentially triporate rather than distinctly tricolporate pollen.

Unusual features of *Caatinganthus* include the dorsoventrally modified branches of the inflorescence, bearing two congested rows of 4-flowered heads, the most strongly dimorphic pappus in the Vernonieae, and the type F pollen (Jones, 1981a), a type known primarily from the Eastern Hemisphere. The groups of 4-flowered heads might indicate relationship to the Elephantopinae; however, the corollas are not zygomorphic and the pubescence is a soft arachnoid tomentum not seen in that subtribe. A possible close relative *Telmatophila,* placed in the Elephantopinae, has actinomorphic corollas, but it has simple axillary clusters of heads and a simple uniseriate pappus. The highly dimorphic pappus of *Caatinganthus* is reminiscent of paleotropical Vernonieae, such as *Brachythrix* Wild & Pope, but the latter has separate heads with more numerous florets in the heads.

The triporate to slightly colporate type F pollen of *Caatinganthus* has a highly ordered lophate structure, single polar lacunae each surrounded by six temporal lacunae and then three blocks of 4 equatorial lacunae between the pores. The three intervening equatorial lacunae containing the pores have the crosswalls above and below the pores distinctly notched in their middle. The lacunae are much more regularly ordered than those in the Elephantopinae or unplaced genera, such as *Acilepidopsis* and *Mesanthophora.* The crests of the muri have a tectum with very few small perforations, not a total lack of perforated tectum.

The two species of *Caatinganthus* occur in the caatinga habitat along the São Francisco River in northeastern Brazil. The available collections show a separation between the two species of about 500 km and a strong difference in the habit of the plants. Further collecting might narrow the gap both geographically and structurally.

Key to the Species of *Caatinganthus*

Plants decumbent; inflorescence branches about 1 cm long, with 5–10 heads. (Bahia) . . . . *C. harleyi*

Plants erect; inflorescence branches to 3 cm long, with 20–30 heads. (Pernambuco) . . . . *C. rubropappus*

Caatinganthus harleyi H. Rob. sp. nov.

FIGURES 19, 20

Plantae decumbentes e radicibus centralibus; caules elongati arachnoideo-tomentosi. Folia alterna lineares 1.5–4.5 cm longa 1.5–2.0 mm lata supra leniter hirtella glabrescentia subtus appresse argente arachnoideo-tomentosa. Inflorescentiae in ramis axillaribus vel pseudaxillaribus subsessilibus congeste spiciformibus dorsoventraliter complanatis dispositae, bracteis primariis ramorum ventraliter dispositis lateraliter patentibus foliiformibus circa 1 cm longis. Capitula circa 5–10 in axilibus bractearum ramorum dorsaliter biseriate disposita; bracteis involucri circa triseriatis circa 7 mm longis oblongis distincte apiculatis, bracteis exterioribus 2 vel 3 base scariosis distaliter foliiformibus, bracteis interioribus 4 decussatis scariosis extus dense sericeis intus glabris. Flores 4 in capitulo; corollae pallide lavandulae vel purpureae circa 10 mm longae, tubis circa 4 mm longis, faucibus circa 1.5 mm longis, lobis circa 4 mm longis circa 0.8 mm latis distaliter pauce glandulo-punctatis non pilosulis; filamenta antherarum in partibus inferioribus brevia circa 0.6 mm longa, in partibus superioribus circa 0.35 mm longa; thecae anterarum circa 2 mm longae. Achaenia circa 1.5 mm longa dense sericeo-setulifera; squamae pappi circa 10 oblongae circa 1.5 mm longae late truncatae, setae pappi circa 10 circa 4 mm longae. Grana pollinis circa 60 µm in diametro.

TYPE.—Brazil: Bahia. Basin of the Upper São Francisco River, just beyond Calderao, ~32 km NE from Bom Jesus da Lapa, alt. ~500 m, 13°10'S, 43°13'W, 18 April 1980, Harley et al., 21507 (holotype, CEPEC; isotypes K, US).

DISCUSSION.—The label data indicates a decumbent herb from a central rootstock, stems brownish tinged, leaves rather bright yellow-green above, white tomentose beneath, corolla bright purple with dark lobes, paler within tube, anthers yellow. The species is presently known only from the type series.

Caatinganthus rubropappus (Soares Nunes) H. Rob., comb. nov. *Stilpnopappus rubropappus* Soares Nunes, Bradea 3(18):129. 1981.

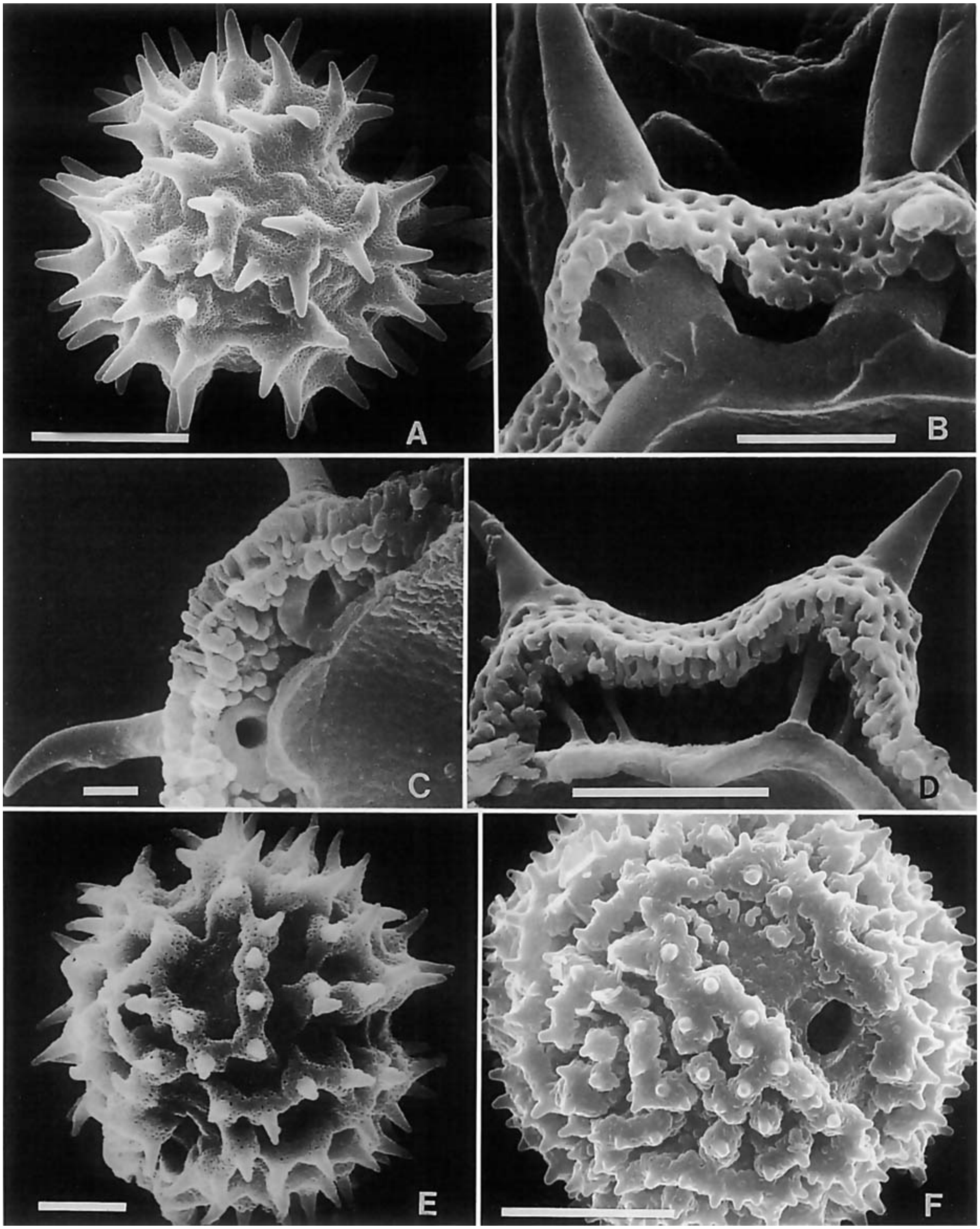


FIGURE 1.—Scanning electron photomicrographs (SEM) of pollen of Vernonieae and Liabeae, all specimens in the United States National Herbarium (US). A,B, *Critoniopsis uniflorus* (Sch. Bip.) H. Rob., Mexico, *Dunn 18698:* A, pollar view of grain; B, broken grain showing solid bases of columellae under spines. C, *Munnozia tenera* (Sch. Bip.) H. Rob. & Bretell, Colombia, *Killip 9775,* broken grain showing hollow columellae under spines. D, *Paranephelius uniflorus* Poepp., Peru, *Cerrate 1367,* broken grain showing group of columellae under spine. E, *Bishopalea erecta* H. Rob., Brazil, *King & Bishop 8729,* modified type A grain. F, *Orthopappus angustifolius* (Sw.) Gleason, Bolivia, *Buchtien 785,* modified type A grain. (Scale bars: A = 6.7 µm, B = 3 µm, C = 1 µm, D = 4 µm, E,F = 10 µm.)

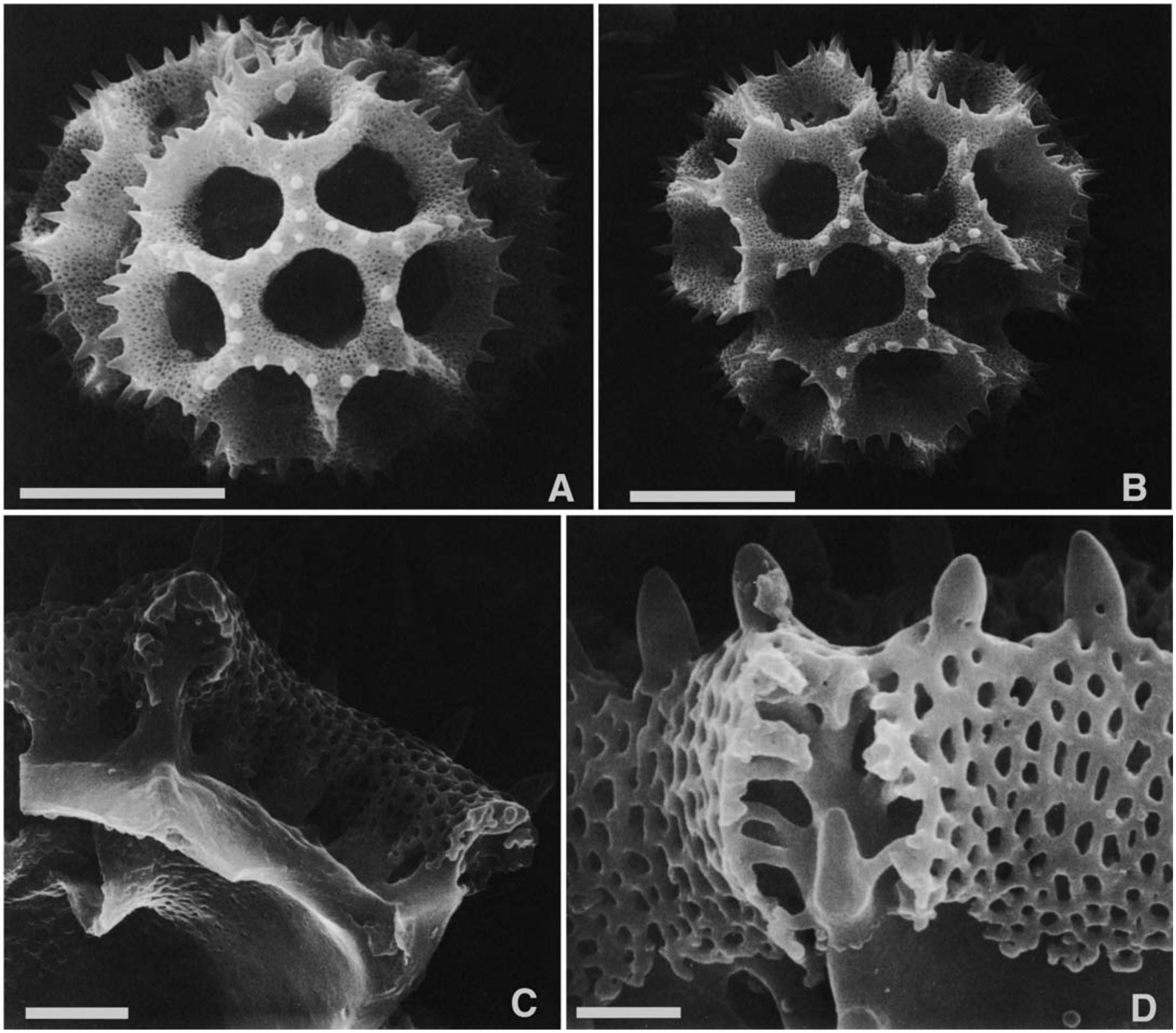


FIGURE 2.—SEM of pollen of *Lessingianthus argyrophyllus* (Less.) H. Rob., Brazil, *Heringer 16738* (US): A, intercolpar view showing 1:2:3:2:1 pattern; B, polar view showing three colpi meeting at pole; C, broken grain showing columellae; D, broken grain showing detail under perforated tectum. (Scale bars: A,B=10 μm, C=4 μm, D=2 μm.)

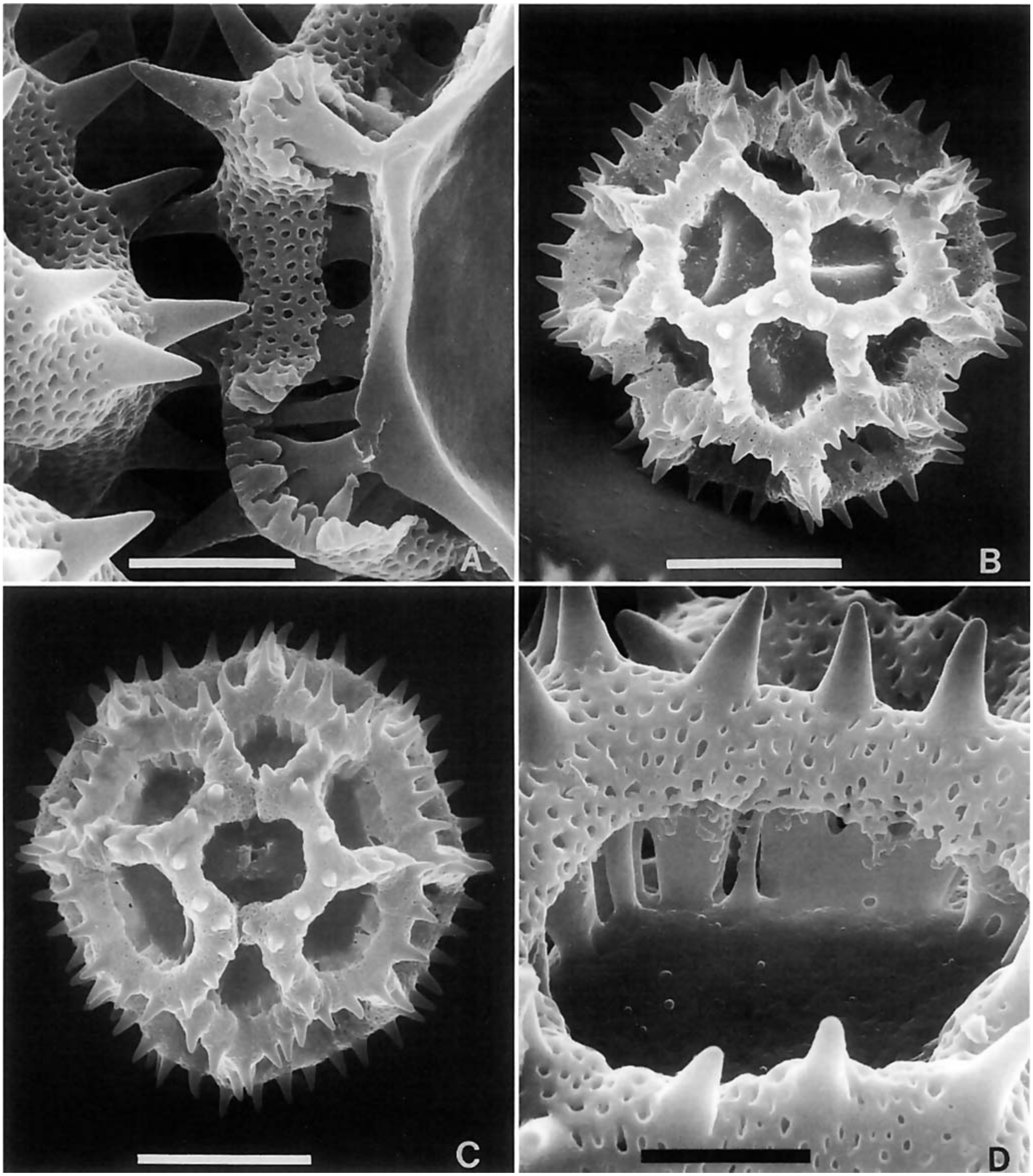


FIGURE 3.—SEM of pollen of Vernonieae (all US): A, *Lessingianthus laurifolius* (DC.) H. Rob., Bolivia, *Bang 1534,* broken grain showing columellae. B–D, *Aynia pseudascaricida* H. Rob., Peru, *Killip & Smith 22514:* B, polar view showing intercolpar lacunae meeting at pole; C, colpar view; D, lacuna showing columellae. (Scale bars: A=6 μm, B,C=20 μm, D=5 μm.)

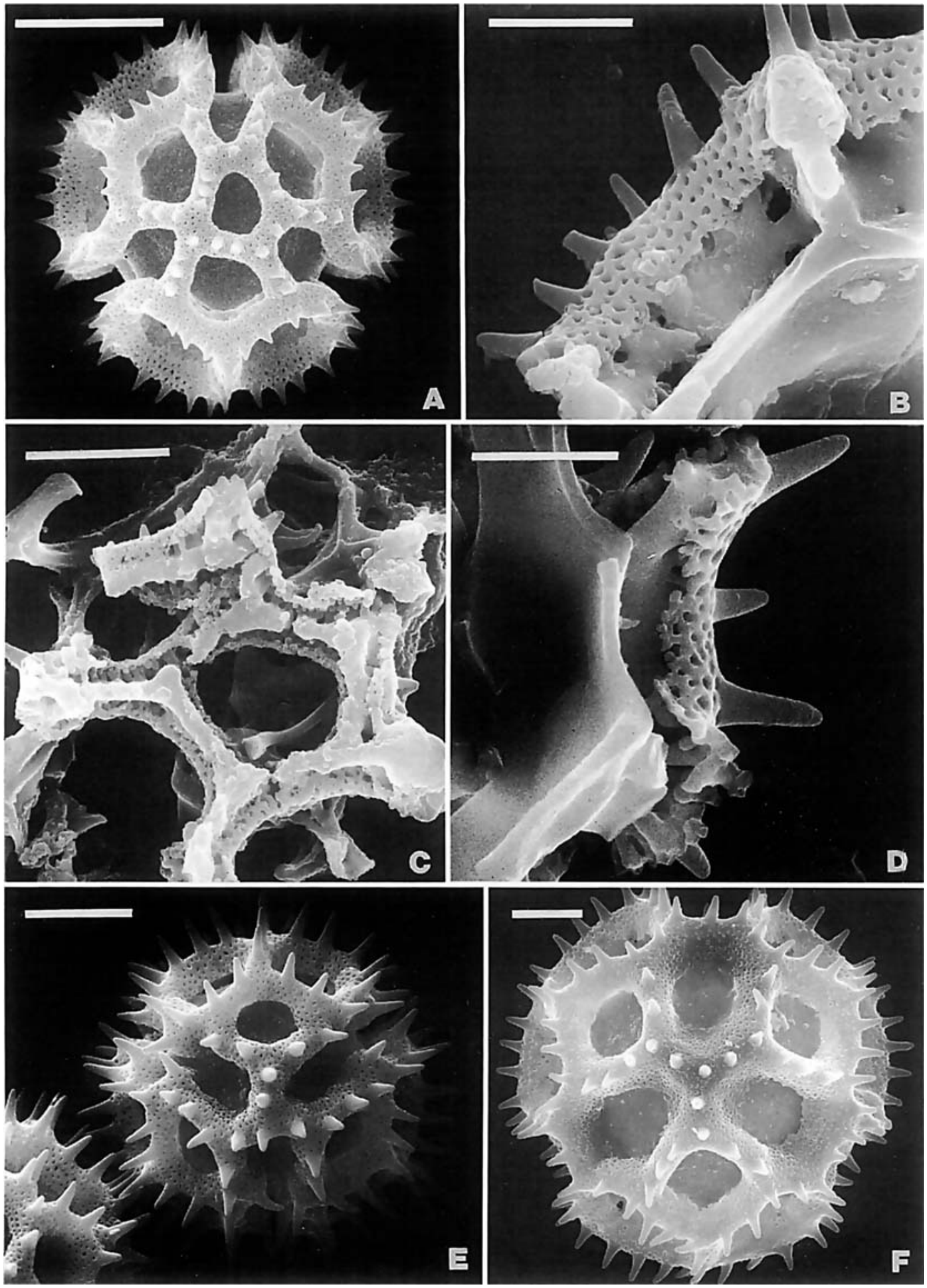


FIGURE 4.—SEM of pollen of Vernonieae, *Lepidaploa (*all US): A–C, *L. salzmannii* (DC.) H. Rob., Peru, *Ferreyra 9327:* A, type C, polar view showing polar lacuna; B, broken grain showing rhizomiform columellar structure loosely attached to footlayer; C, muri stripped from footlayer, view of underside. D,E, *L. subsquarrosa* (DC.) H. Rob., Brazil, *Rose 20194:* D, broken grain showing rhizomiform columellar structure weakly attached to footlayer; E, type G, polar view showing colpi meeting at pole. F, *L. chalybaea* (Mart. ex DC.) H. Rob., Brazil, *Mori & Benton 13094,* type D, polar view showing crosswalls in colpi near pores. (Scale bars: A=13.6 µm, B=4.3 µm, C=7.5 µm, D=3.8 µm, E=10 µm, F=6.8 µm.)

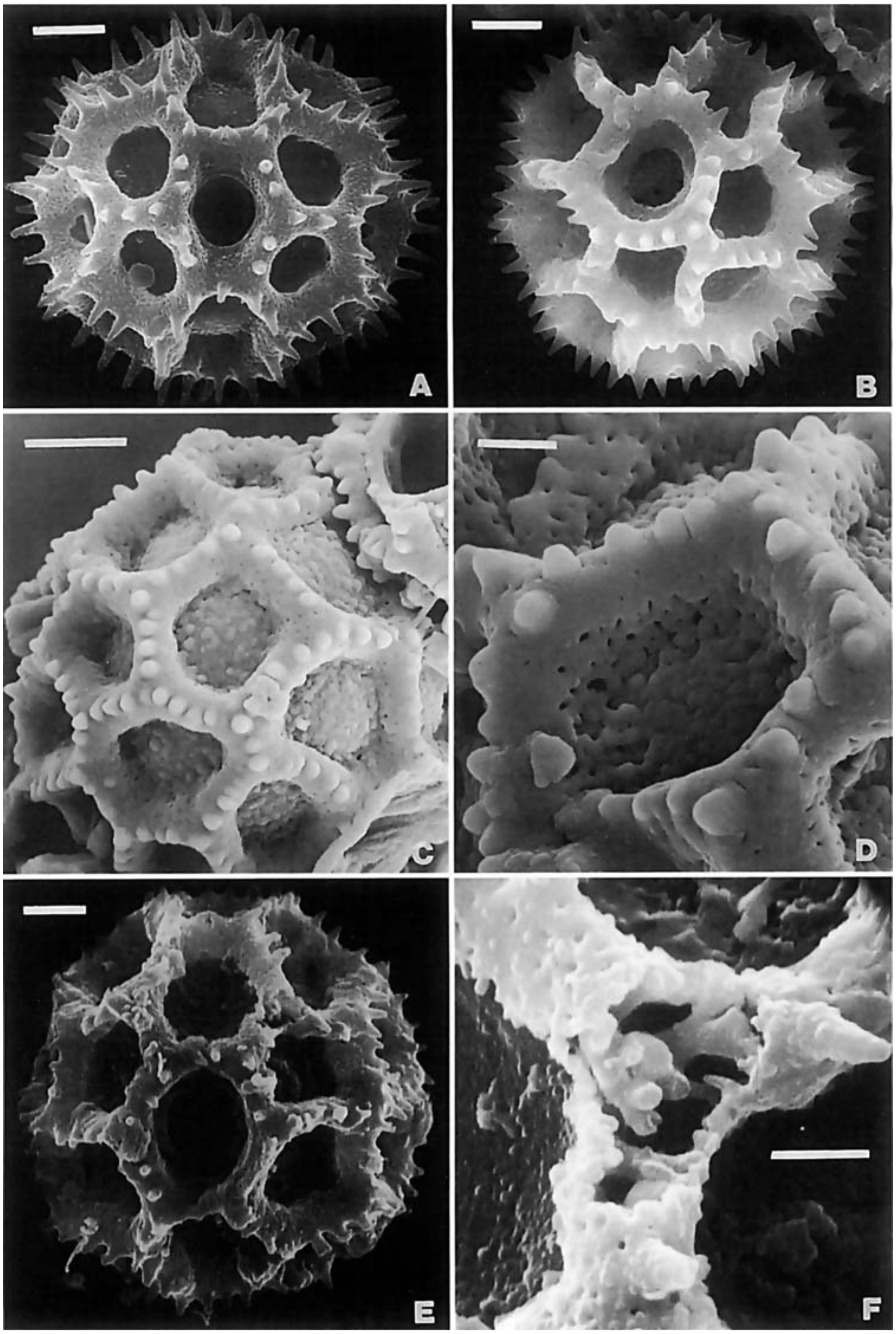


FIGURE 5.—SEM of pollen of Vernonieae (all US): A, *Lepidaploa chalybaea* (Mart. ex DC.) H. Rob., Brazil, *Mori & Benton 13094*, type D, colpar view showing crosswalls in colpi near pores. B, *Eirmocephala brachiata* (Benth. ex Örsted) H. Rob., Colombia, *Molina 19An007*, view showing crosswalls near pore and one of the polar lacunae, rhizomiform columellae visible in upper left. C,D, *Struchium sparganophorum* (L.) Kuntze, Venezuela, *Liesner 13370:* C, face of grain and part of broken grain; D, lacuna showing perforated tectum. E,F, *Heterocypsela andersonii* H. Rob., Brazil, *Anderson et al. 9223:* E, view showing pore, crosswalls near pore, and one of the polar lacunae; F, broken tectum showing branching columellae. (Scale bars: A,B=6.8 µm, C=5 µm, D=2 µm, E=10 µm, F=2 µm.)

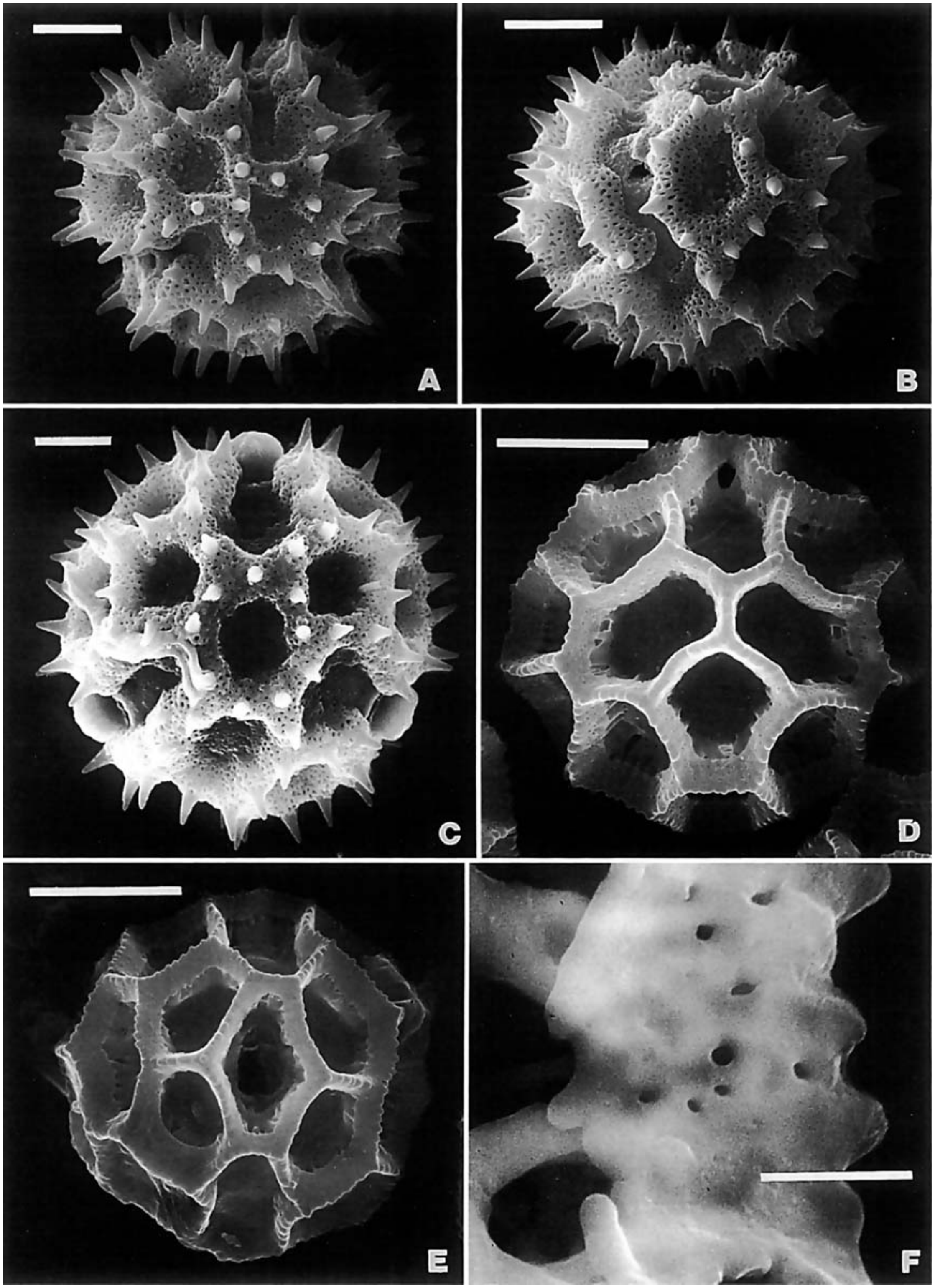


FIGURE 6.—SEM of pollen of Vernonieae (all US): A,B, *Chresta exsucca* DC., Brazil, *Heringer 7034:* A, type C, near polar view showing polar lacuna; B, near colpar view. C, *Pithecoseris pacourinoides* Mart. ex DC., Brazil, *Drouet 2392,* type C, polar view showing polar lacuna. D–F, *Stokesia laevis* (Hill) Greene, USA, *Knobloch 1426,* type D: D, polar view showing three lacunae meeting at pole; E, colpar view showing crosswalls above and below pore; F, enlargement of weakly developed perforated tectum. (Scale bars: A,B=10 µm, C=6.8 µm, D,E=20 µm, F=1.76 µm.)

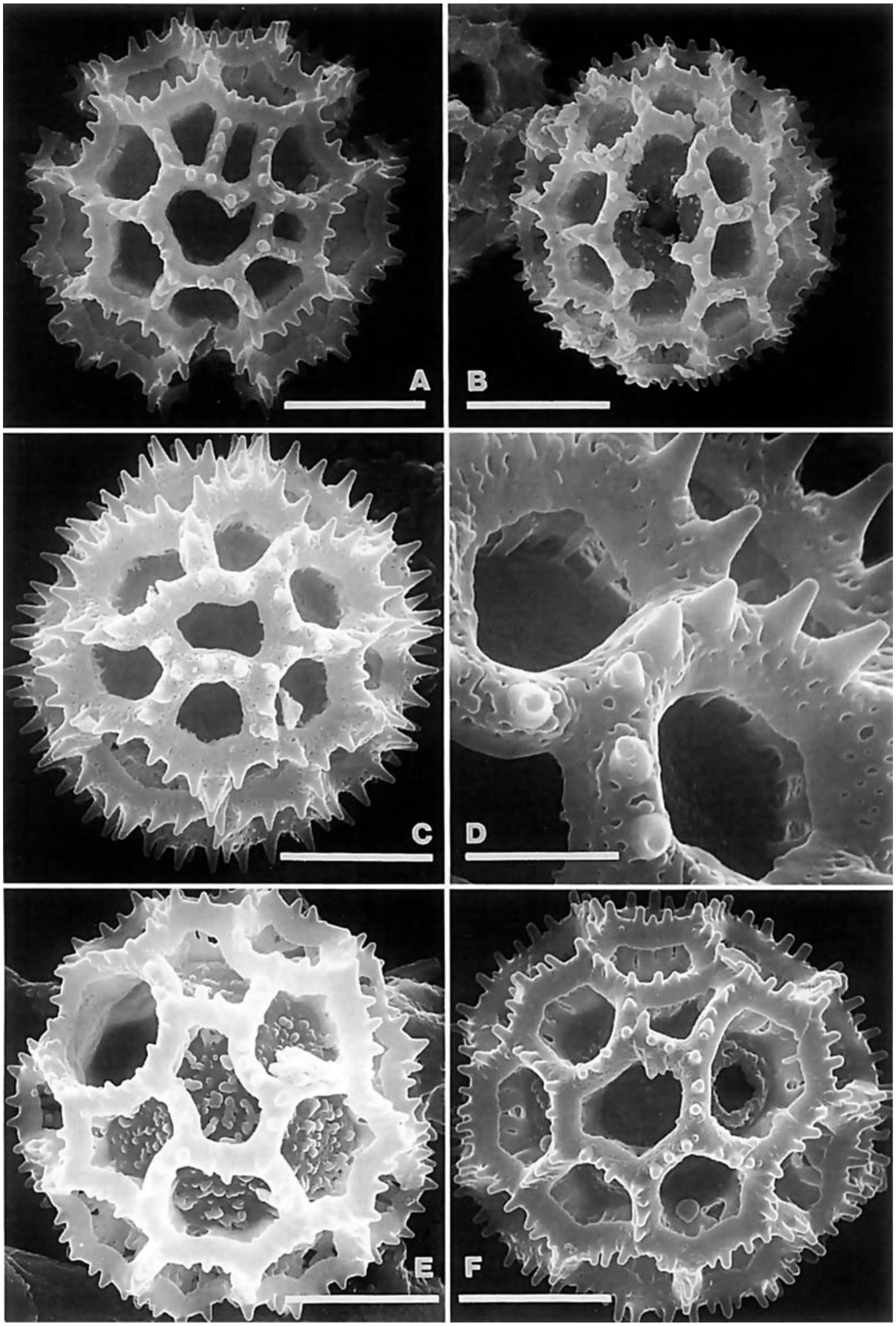


FIGURE 7.—SEM of pollen of Vernonieae (all US): A,B, *Elephantopus riparius* Gardn., Brazil, *Anderson 9941:* A, polar view showing irregular polar lacunae; B, colpar view showing short colpus. C,D, *Elephantopus mollis* H.B.K., Marianas Islands, *Fosberg 31849:* C, view with pore near center showing undifferentiated lacuna with pore; D, enlargement of lacunae showing columellae, pore in lower left corner. E, *Pseudelephantopus spicatus* (Juss. ex Aubl.) Rohr, Cuba, *Morton 4048,* view showing pore to left side. F, *Rolandra fruticosa* (L.) Kuntze, Brazil, *MacLeish 760,* view showing pore toward the right. (Scale bars: A=10.3 µm, B=12 µm, C=11.5 µm, D=4.3 µm, E=10 µm, F=12 µm.)

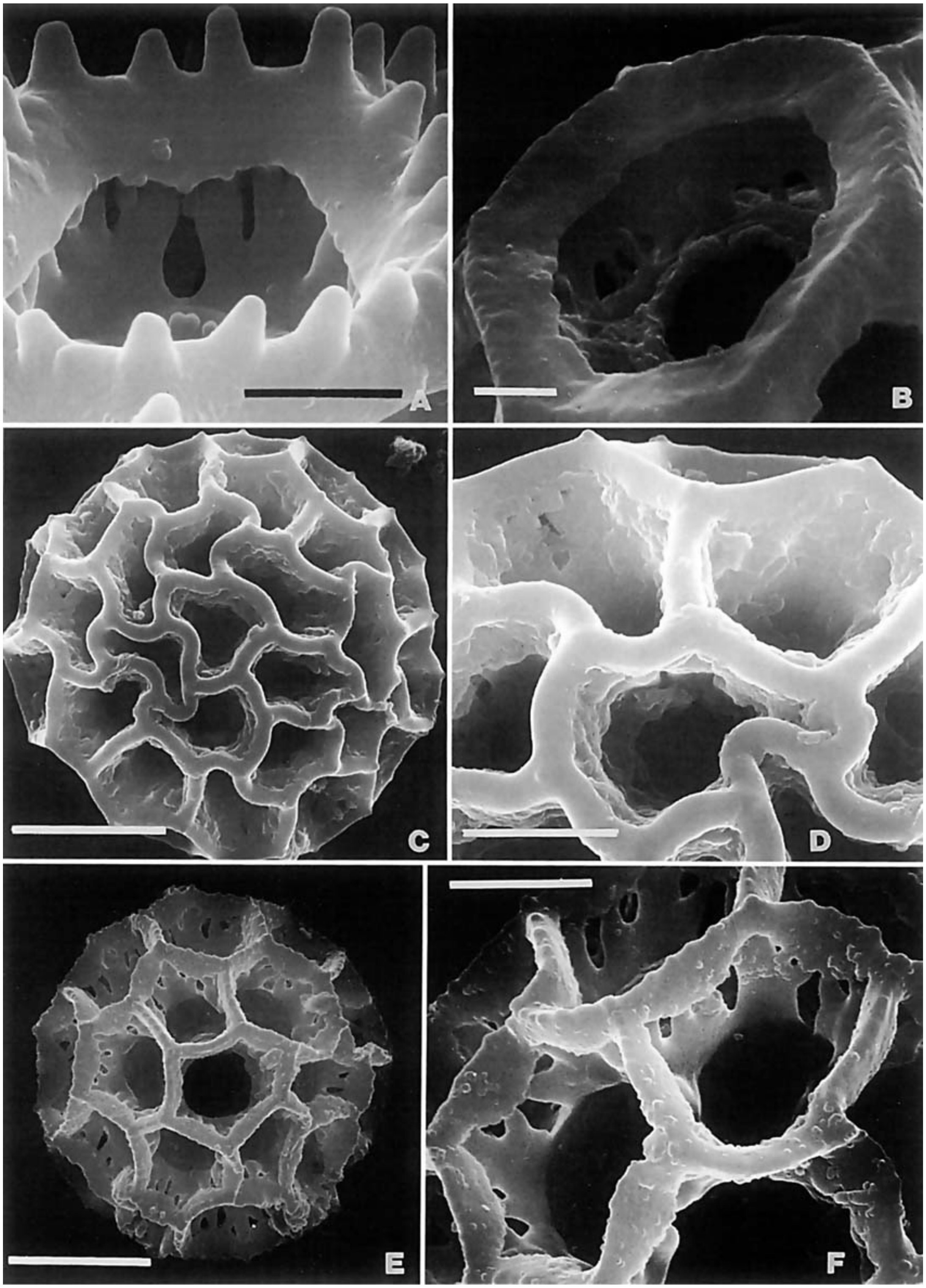


FIGURE 8.—SEM of pollen of Vernonieae (all US): A, *Rolandra fruticosa* (L.) Kuntze, Brazil, *MacLeish 760,* enlargement of lacuna, form showing lack of perforations in tectum. B, *Spiracantha cornifolia* H.B.K., Panama, *Bro. Paul s.n.,* enlargement of lacuna with pore. C,D, *Pacourina edulis* Aubl., Colombia, *Killip & Smith 14576:* C, grain showing lack of differentiated lacunae; D, enlargement showing poorly formed columellar structure. E,F, *Mesanthophora brunneri* H. Rob., Paraguay, *Brunner 1720:* E, view with pore in center; F, enlargement showing distinctive columellae centered at junctures of muri. (Scale bars: A=3 µm, B=2 µm, C=15 µm, D=6.7 µm, E=13.6 µm, F=6 µm.)

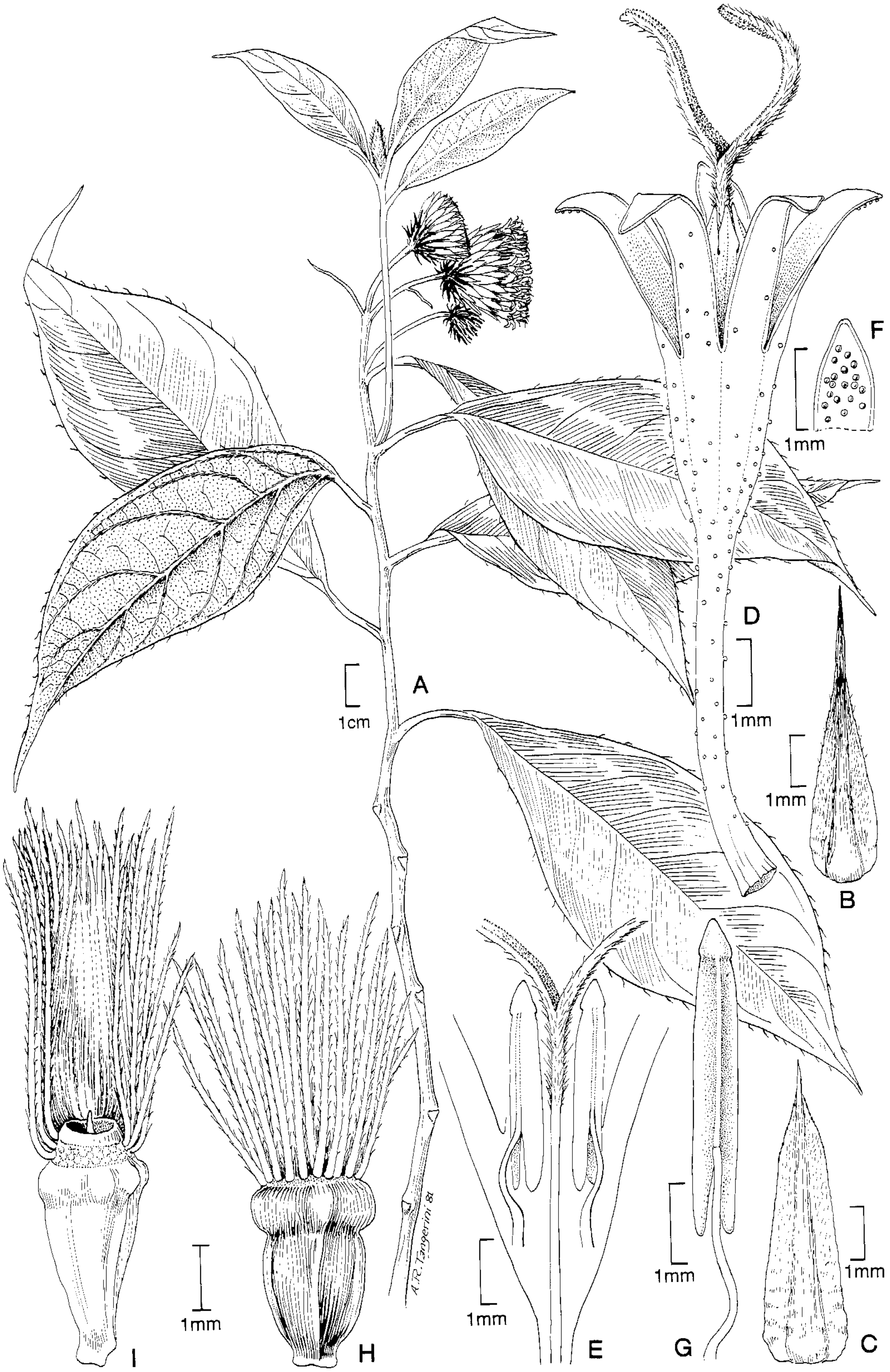


FIGURE 9.—*Stramentopappus pooleae* (B.L. Turner) H. Rob. & Funk, subtribe Leiboldiinae: A, habit; B,C, outer and inner involucral bracts; D, corolla showing tips of stamens and style; E, schematic section of corolla throat showing positions of stamens and style; F, tip of corolla lobe; G, stamen; H,I, achenes; I, with part of pappus removed, *Funk, Turner & Kerr 2729* (US). (From Robinson and Funk, 1987.)

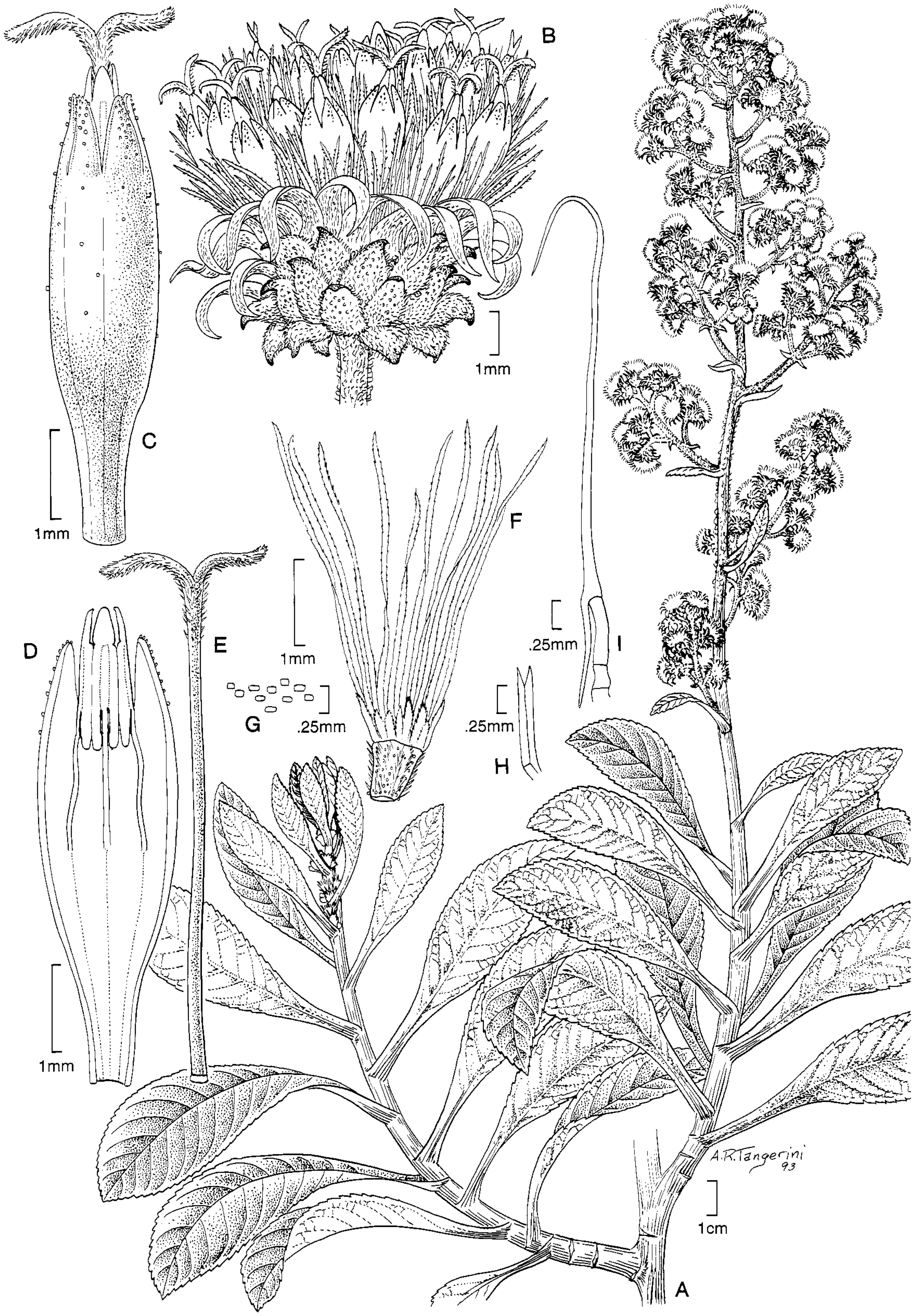


FIGURE 10.—*Cololobus* spp., subtribe Vernoniinae: A–H, *C. hatschbachii* H. Rob.: A, habit; B, head; C, corolla with anther and style tip; D, half of corolla with included stamens; E, style with small basal node; F, achene with pappus; G, raphids of achene wall; H, setula of achene. I, *C. rupestris*, T-shaped hair from achene, *Brade 19780* (US). (From Robinson, 1994c.)

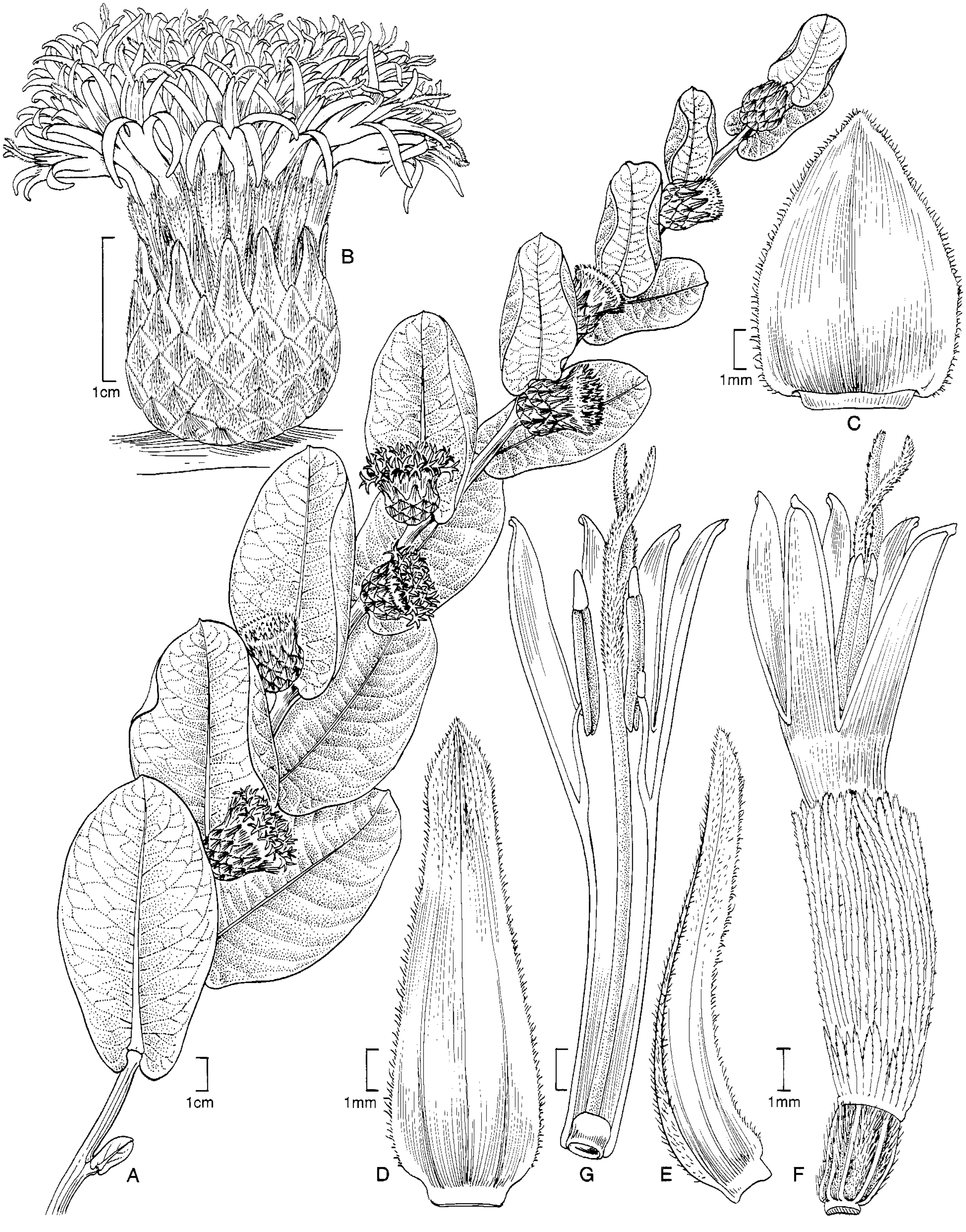


FIGURE 11.—*Lessingianthus fonsecae* (H. Rob.) H. Rob., subtribe Vernoniinae: A, branch; B, head; C–E involucral bracts; F, floret showing achene, pappus, upper corolla, and anther and style tips; G, corolla in long section showing anthers and style, style with nectary, without node. *Irwin et al. 24698,* isotype (US), habit. *Irwin et al. 24503* (US), head and floret.

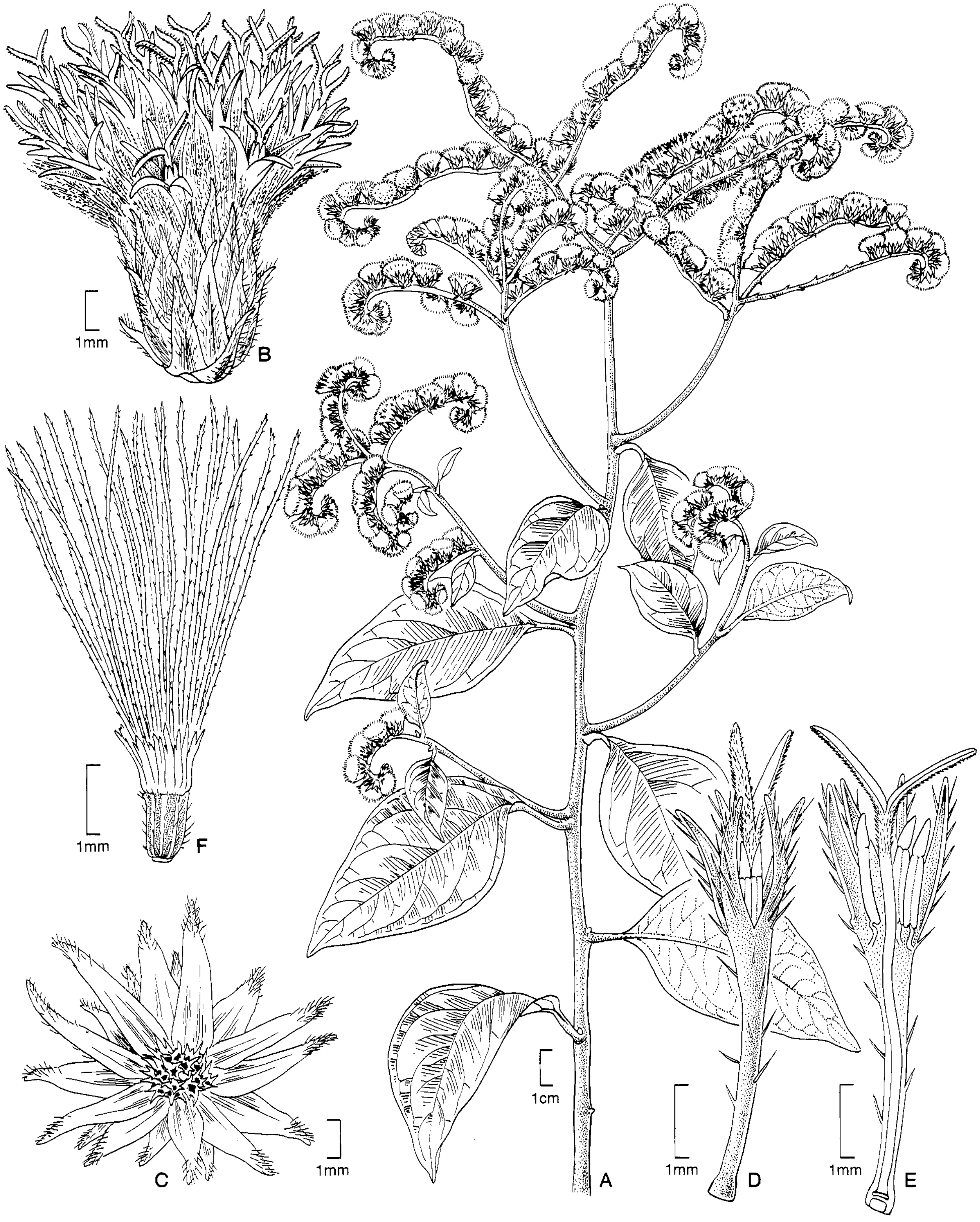


FIGURE 12.—*Cyrtocymura scorpioides* (Lam.) H. Rob., subtribe Vernoniinae: A, habit showing bracts at base of one branch after heads have fallen; B, head; C, spinulose receptacle surface and spreading involucral bracts, showing hairs on inner surface at tips of bracts; D, corolla with tips of anthers and style; E, corolla in long section showing anthers and style, base of style with nectary and basal node; F, achene. *Oscar Haught 2570* (US).

FIGURE 13.—*Dasyanthina* spp, subtribe Vernoniinae: A–H, *D. palustris* (Gardn.) H. Rob.: A. habit; B, head; C, corolla showing anthers and style; D, section of corolla showing tailed anthers, glands on connective, and short hairs on inner surface of corolla; E, short hairs from inner surface of corolla throat; F, style showing enlarged basal ring; G, achene; H, raphids from cells of achene wall. I, hairs from inner surface of corolla throat in *D. serrata* (Less.) H. Rob. (From Robinson, 1993b.)

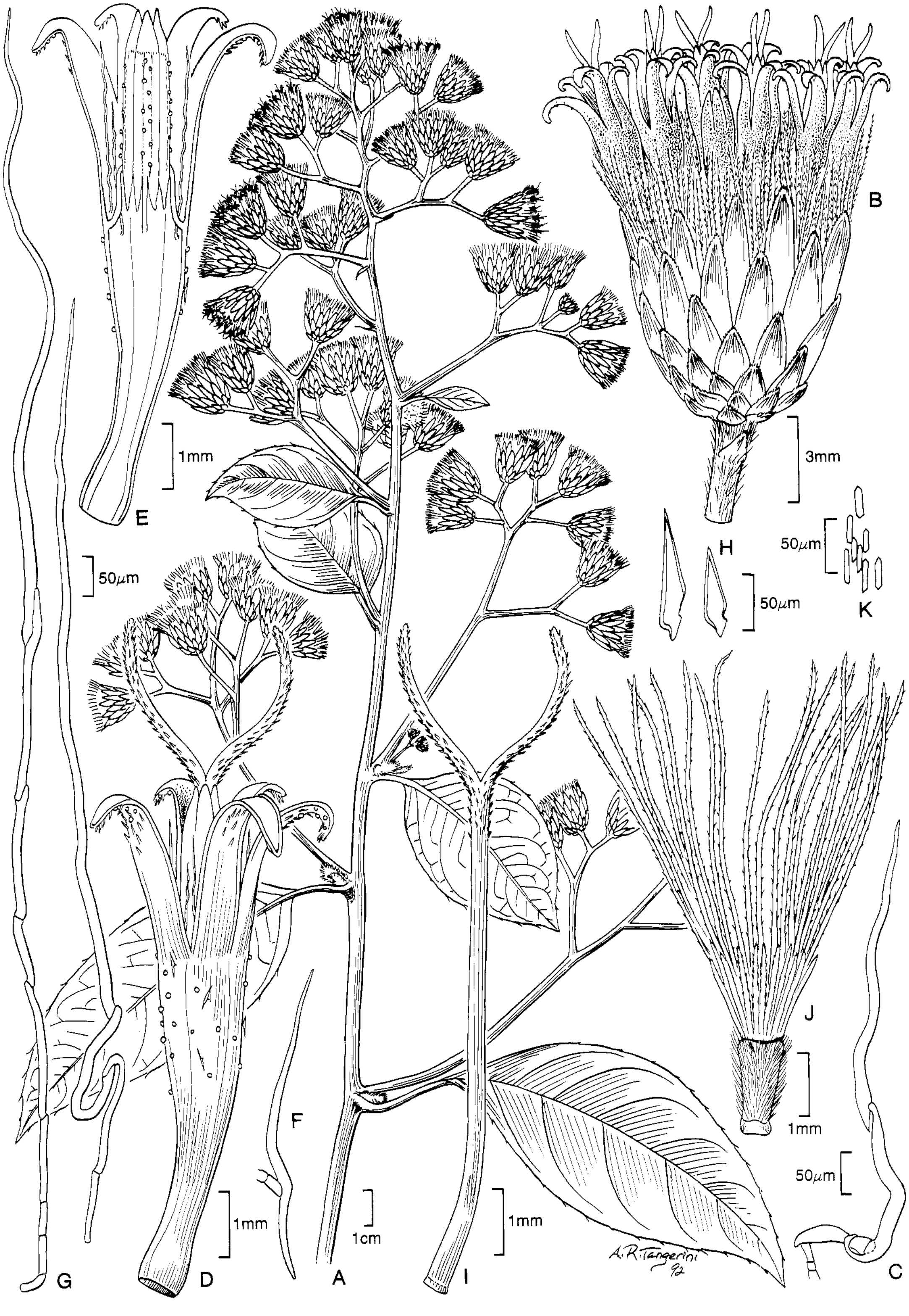


FIGURE 14.—*Quechualia fulta* (Griseb.) H. Rob., subtribe Vernoniinae: A, habit; B, head; C, hair from outer surface of involucral bract; D, corolla showing anther tips and style; E, section of floret showing tailed anthers, glands on connective, and long hairs on inner surface of corolla; F, T-shaped hair from outer surface of corolla; G, long hairs from inner surface of corolla; H, hairs from outer surface of corolla lobe; I, style; J, achene; K, raphids from cells of achene wall. (From Robinson, 1993b.)

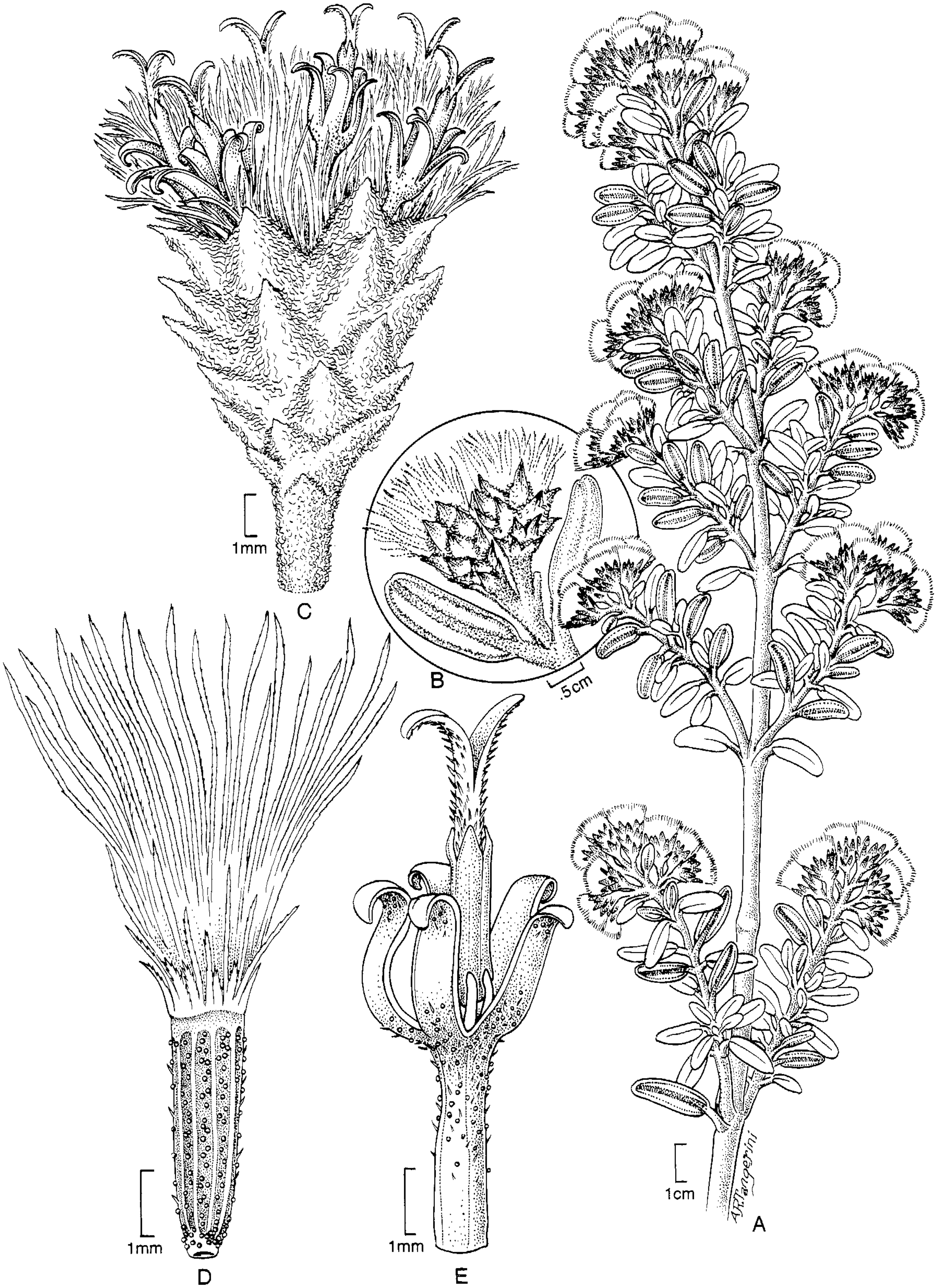


FIGURE 15.—*Joseanthus cuatrecasasii* H. Rob., subtribe Piptocarphinae: A, branch of postanthesis plant, *Camp E-3953* (US); B, enlargement of branch tip; C, enlargement of head, *Boeke 2410*, type (US); D, achene; E, corolla showing deeply cut lobes, stamens, and style branches. (From Robinson, 1989a.)

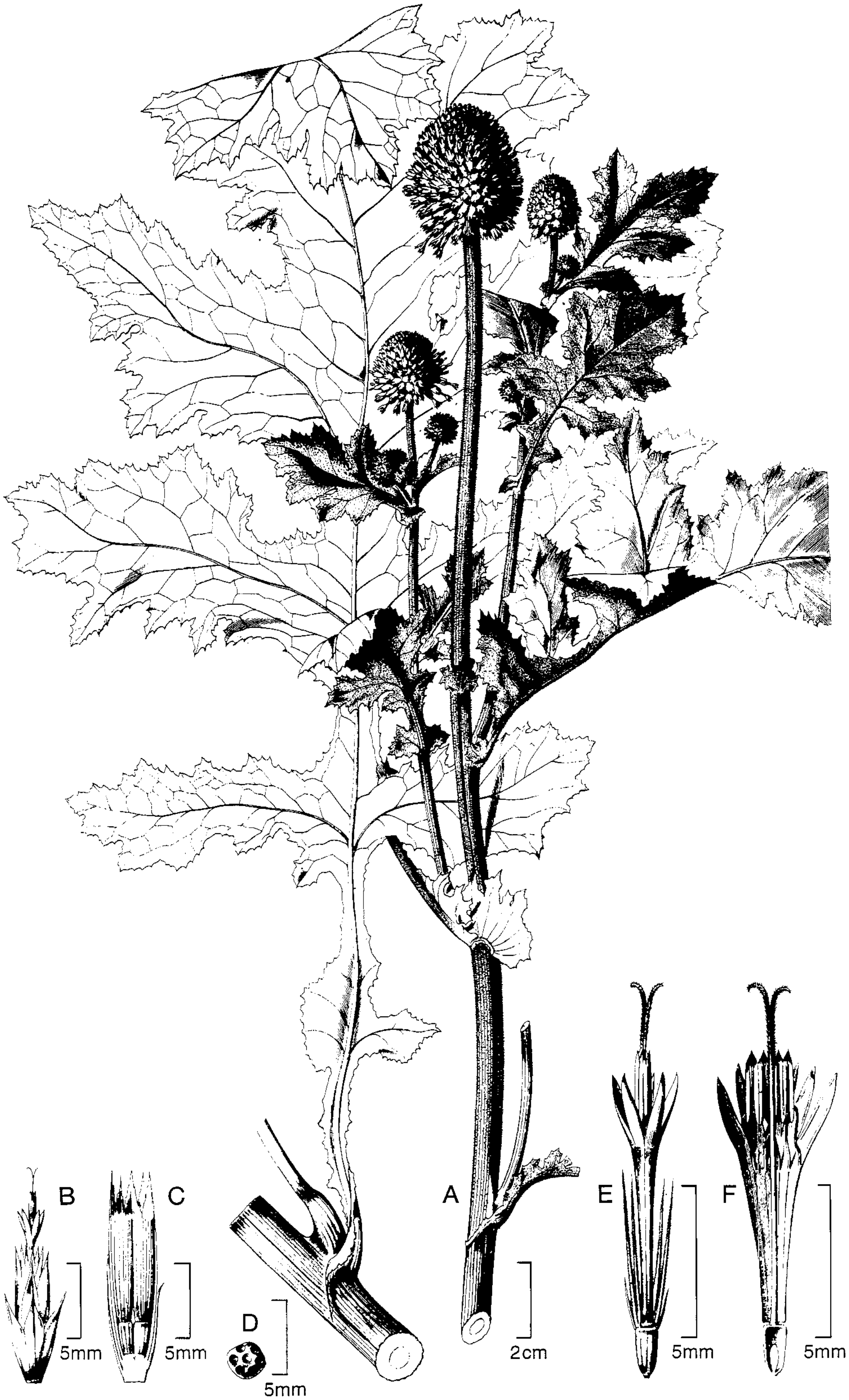


FIGURE 16.—*Pithecoseris pacourinoides* Mart. ex DC., subtribe Chrestinae: A, habit with inflorescences and lower leaf; B, single head at anthesis; C, head in long section with mature achene; D, surface of receptacle; E, floret with corolla and achene; F, floret in long section showing style and insertion of anthers. (From Baker, 1873.)

FIGURE 17.—*Lychnophoriopsis hatschbachii* H. Rob., subtribe Lychnophorinae: A, habit; B, underside of leaf base showing venation; C, head, moist; D, corolla with anthers and style; E, anthers; F, style with nectary at base; G, achene showing outer pappus segments; H, segments of deciduous inner pappus. *Hatschbach, Hatschbach, and Ribas 52026,* type (US). (From Robinson, 1992d.)

FIGURE 18.—*Minasia alpestris* (Gardn.) H. Rob., subtribe Lychnophorinae: A, habit; B, head; C, corolla with anthers and style; D, anthers; E, style and nectary; F, achene with complete pappus; G, achene without inner pappus; H, trichomes from corolla lobe.

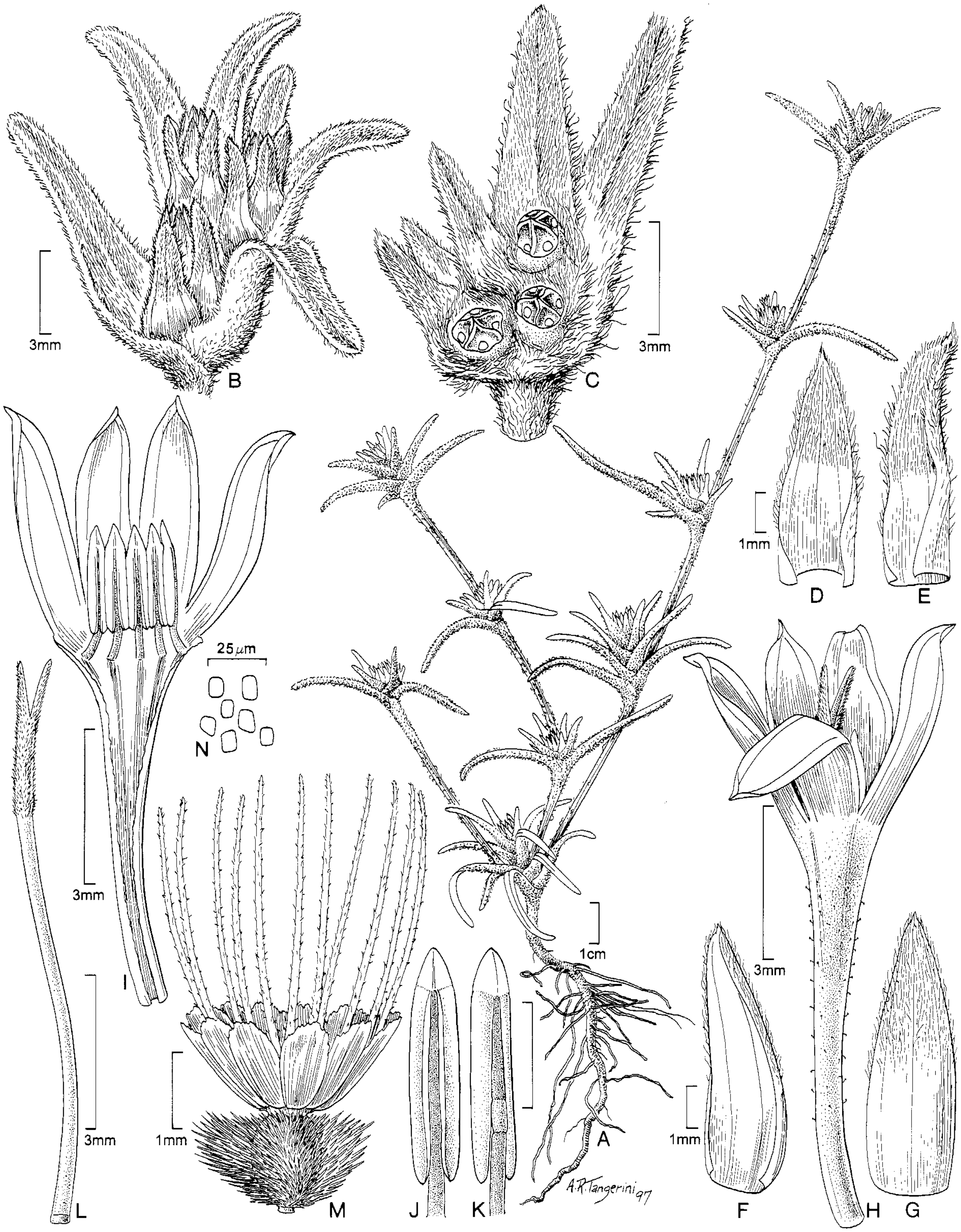


FIGURE 19.—*Caatinganthus harleyi* H. Rob.: A, habit; B, branch with 3 heads; C, branch dissected showing receptacles bearing thin partitions; D,E, outer involucral bracts with herbaceous tips; F,G, inner involucral bracts; H, corolla; I, corolla with nearest lobe removed to expose anthers; J,K, anther thecae, inner and outer views; L, style; M, achene with dimorphic persistent pappus; N, raphids from cells of achene wall.

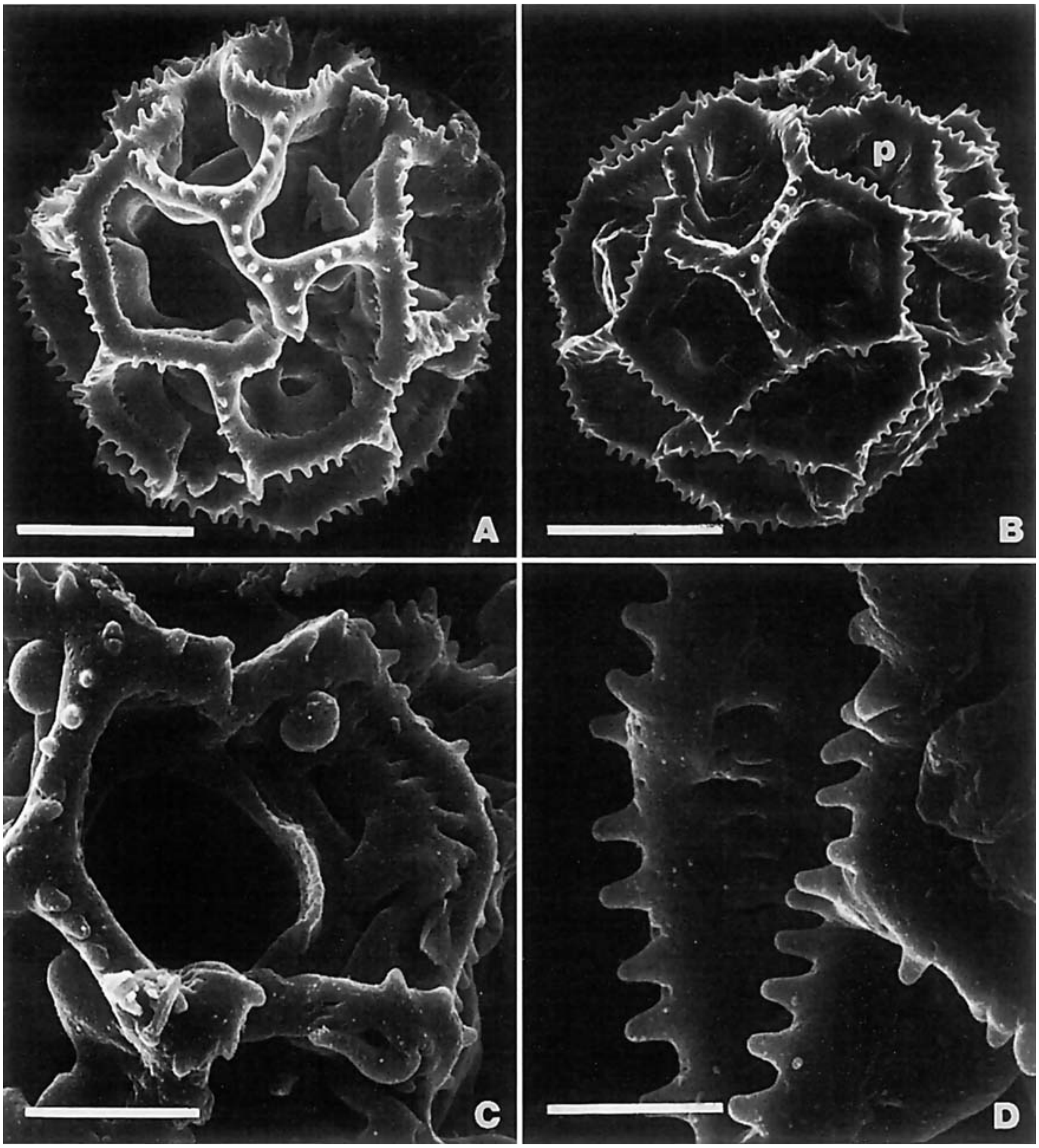


FIGURE 20.—SEM of pollen of *Caatinganthus harleyi* H. Rob. (US): A, grain showing lacuna with pore below middle, with notches in walls crossing colpus; B, unacetolized grain showing polar lacuna at upper right, and pores at left and lower right; C, lacuna with pore and notches in upper and lower crosswalls; D, crests of muri showing sparse minute perforations. (Scale bars: A=13.6 µm, B=14 µm, C=6.7 µm, D=3.8 µm.)

TABLE 1.—Leiboldiinae; stippled areas represent sclerified structures.

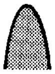
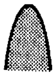
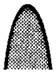
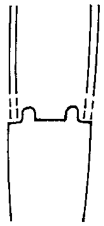
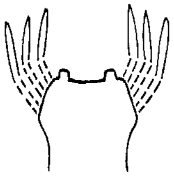
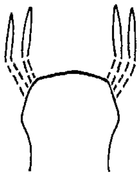
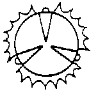
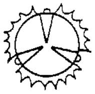
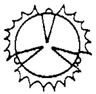
Leiboldiinae	Leiboldia	Stramentopappus	Lepidonia
	n=19	n=19	n=19
			pales in 1 sp. tips of inv. elab.
inv./fl.	c.100/100-120	c.100/c.110	c.100/c.100
anther base			
anther append			
style base			
achenes			
idioblasts			
raphids	▭	□	□ ⬡
pollen 50-60 um			
chemistry		eudesmanolide	glaucolides

TABLE 2.—Vernoniinae, typical group; lines in anther appendages represent weakly developed ducts.

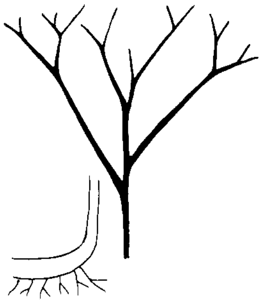
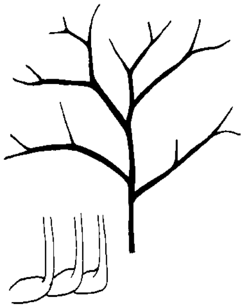
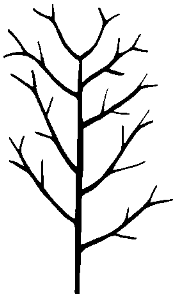
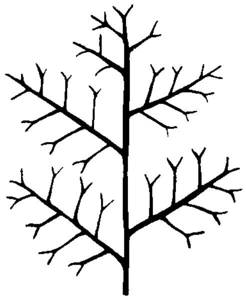
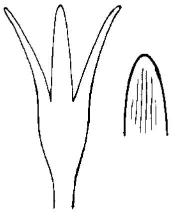
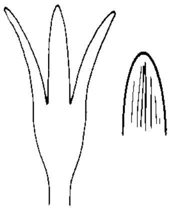
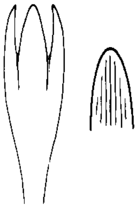
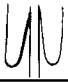
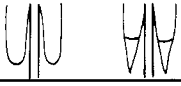
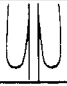
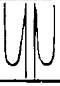
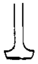
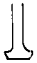
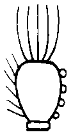
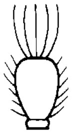
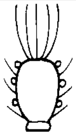
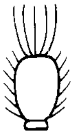
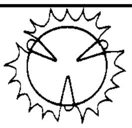
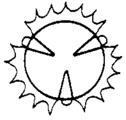
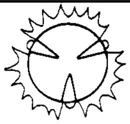
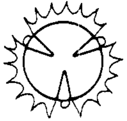
Vernoniinae	Vernonia	Vernonanthura	Cololobus	Trepadonia
n=17 inv. persistent habit base				
inv./fl	ca. 50/8-120	45-70/16-30(60)	35 22/20-30	25/8-10
corolla				
anther append.				
anther base				
style base				
achenes				
raphids	☐	☐	☐	⊏
pollen				
chemistry	glaucolides elemanolides some guaianolides	glaucolides eudesmanolides guaianolides nerolidol		
distribution	U.S. Mex. Bahamas	Trop. America	e. Brazil	Peru

TABLE 3.—Vernoniinae; group with lophate pollen and nonrhizomate muri.

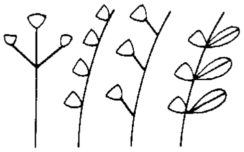
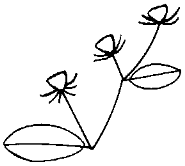
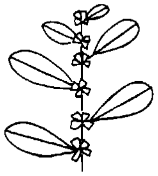
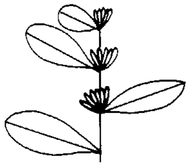
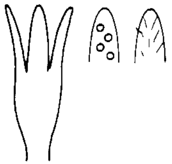
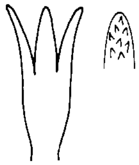
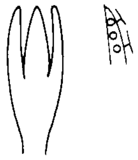
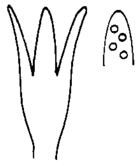
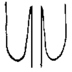
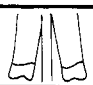
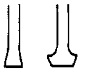
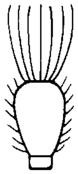
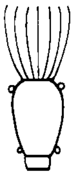
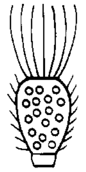
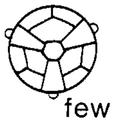
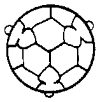
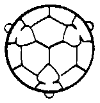
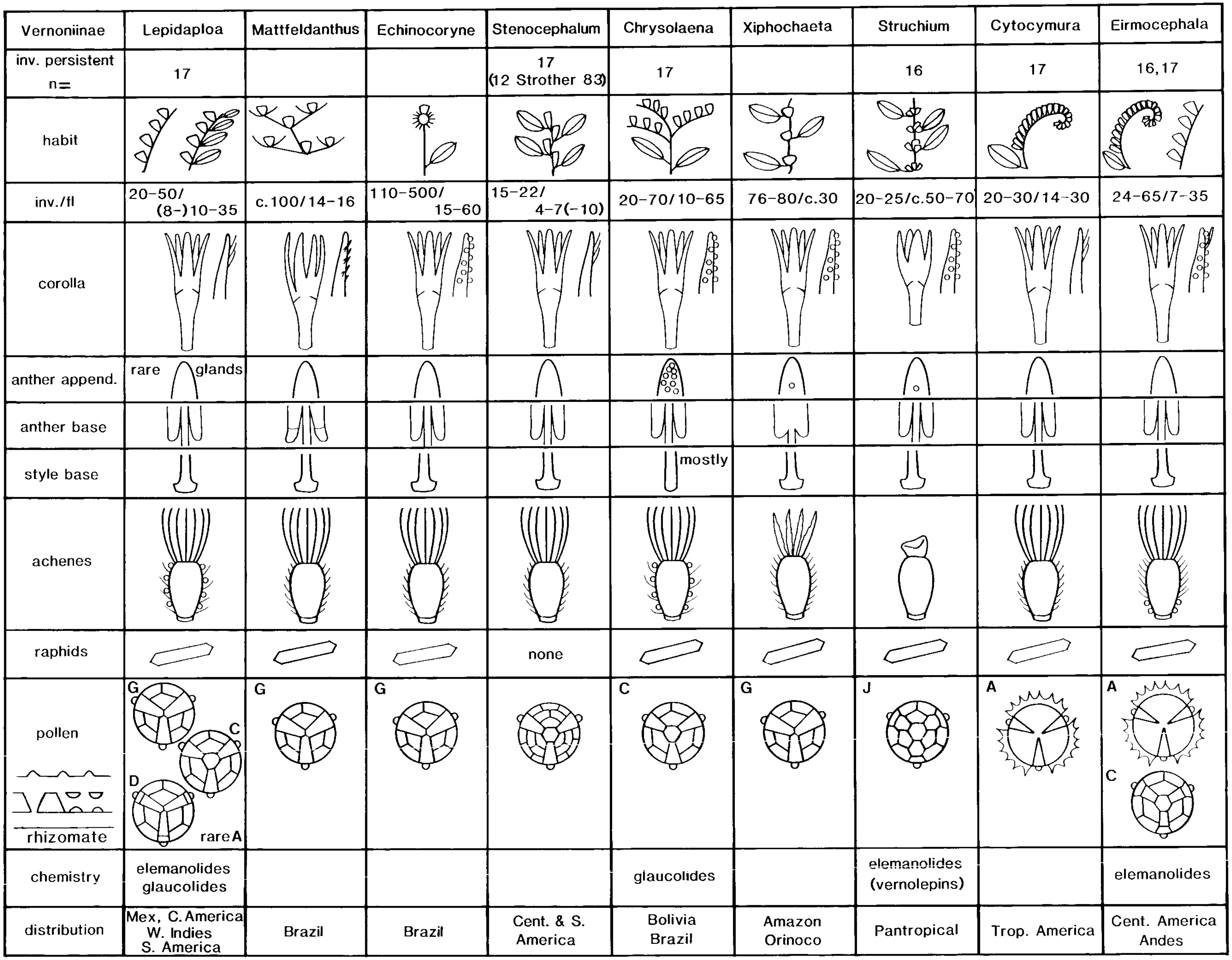
Vernoniinae	Lessingianthus	Aynia	Pseudopiptocarpha	Harleya
n=17 inv. persistent habit				
inv./fl	45-100/15-50	100/50	25-30/6-10	30-35/6-8
corolla				
anther append.				
anther base				
style base	 rare			
achenes	 often short no			
raphids	☐	☐	☐	☐
pollen 	 rare A  few			
chemistry	glaucolides elemanolides			
distribution	mostly Brazil	Peru	Colombia	Cent. America

TABLE 4.—Vernoniinae; group with usually lophate pollen and rhizomate muri.



Vernoniinae	Lepidaploa	Mattfeldanthus	Echinocoryne	Stenocephalum	Chrysolaena	Xiphochaeta	Struchium	Cytocymura	Eirmocephala
inv. persistent n=	17			17 (12 Strother 83)	17		16	17	16,17
habit									
inv./fl	20–50/ (8–)10–35	c.100/14–16	110–500/ 15–60	15–22/ 4–7(–10)	20–70/10–65	76–80/c.30	20–25/c.50–70	20–30/14–30	24–65/7–35
corolla									
anther append.	rare glands								
anther base									
style base					mostly				
achenes									
raphids				none					
pollen rhizomate	G C D rareA	G	G		C	G	J	A	A C
chemistry	elemanolides glaucolides				glaucolides		elemanolides (vernolepins)		elemanolides
distribution	Mex, C. America W. Indies S. America	Brazil	Brazil	Cent. & S. America	Bolivia Brazil	Amazon Orinoco	Pantropical	Trop. America	Cent. America Andes

TABLE 5.—Vernoniinae; groups (1) with hairs inside corollas, (2) obcompressed achenes, and (3) subulate pappus segment.

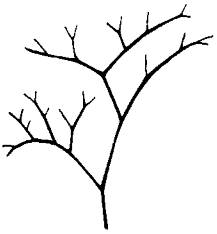
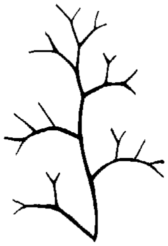
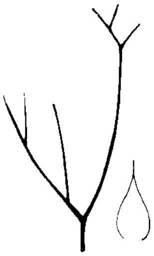
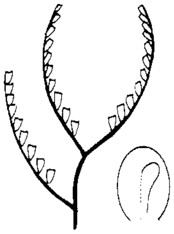
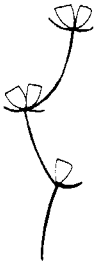
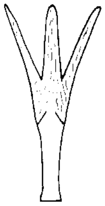
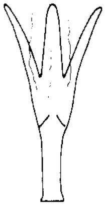
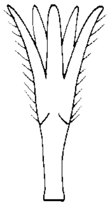
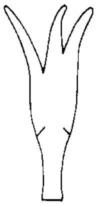
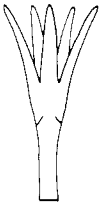
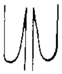
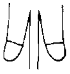
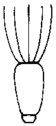
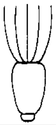
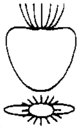
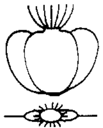
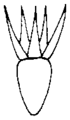
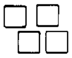
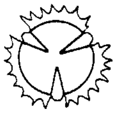
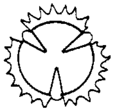
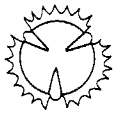
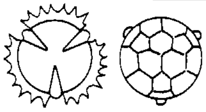
Vernoniinae	Dasyanthina	Quechualia	Heterocypsela	Dipterocypsela	Stilpnopappus
inv. persistent habit		n=17 			
inv./fl	c.60/c.25	60-90/30-55	70/60-70	10-12/c.26	20-50/6-50
corolla					
anther append.					
anther base					
style base					
achenes					
raphids					
pollen					
chemistry					glaucolides hirsutanolides
distribution	e. Brazil	c. Andes	e. Brazil	Colombia	Venez-Brazil

TABLE 6.—Vernoniinae; *Blanchetia* and *Albertinia* groups.

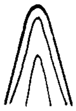
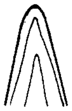
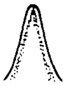
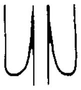
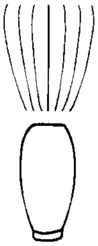
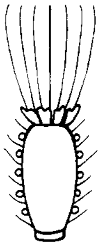
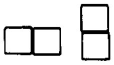
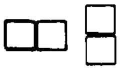
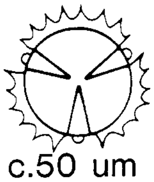
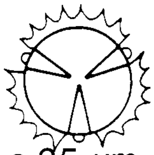
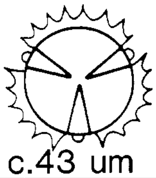
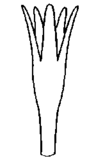
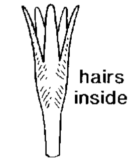
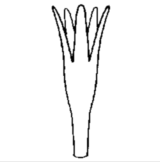
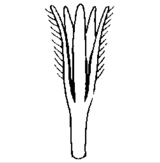
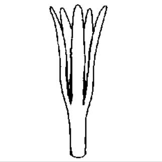
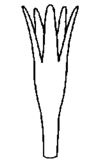
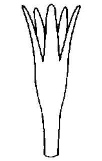
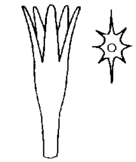
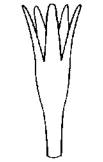
Vernoniinae	Blanchetia	Irwinia	Albertinia
pubescence heterotrichous	pilose & stellate	pilose & stellate	puberulous & lepidulous
receptacle	with thin partitions		 deeply pitted
corolla lobes glabrous veins thickened			
anther append.			
anther base			
style base			
achenes			
raphids			
pollen	 c.50 um	 c.35 um	 c.43 um
distribution	e. Brazil	e. Brazil	e. Brazil

TABLE 7.—Piptocarphinae; the South American *Pollalesta* proves to belong in the synonymy of the West Indian *Piptocoma* (Pruski, 1996).

Piptocarphinae	Critoniopsis	Dasyandantha	Piptocarpha	Joseanthus	Cuatrecasanthus	Pollalesta	Piptocoma	Ekmania	Huberopappus
inner involucre deciduous n=	17		17						
leaves	alt/opp	alt	alt/opp	opp	alt	alt	alt	alt	alt
habit	trees/shrubs	trees	shrubs/vines	trees/shrubs	trees/shrubs	trees/shrubs	shrubs	shrubs	shrubs
inv/fl	20-40/ 2-11(-20)	30/12	18-30/3-20	20-30/9-12	15/1	5-18/1-5(-6)	15-25/4-12	c.30/12	14-17/19-22
corolla									
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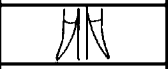
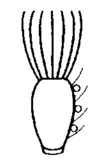
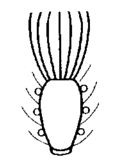
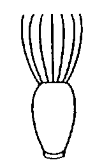
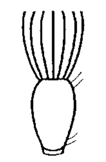
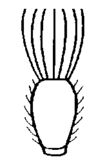
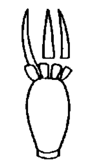
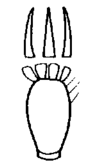
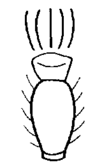
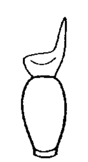
anther base									
style base									
achene									
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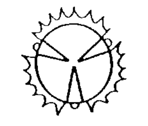
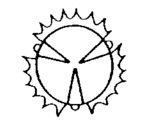
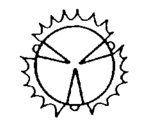
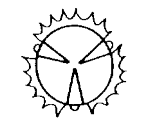
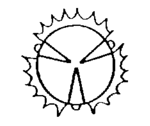
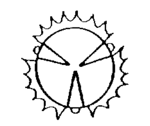
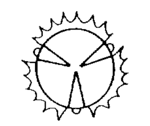
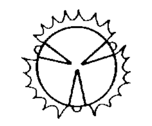
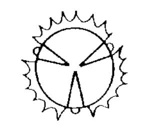
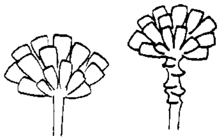
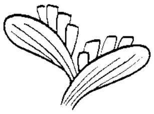
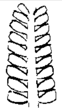
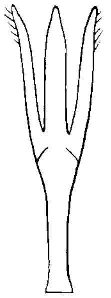
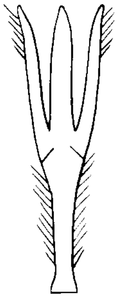
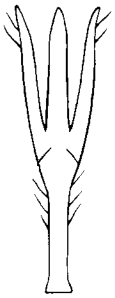
pollen									
chemistry	glaucolides guaianolides elemanolides		glaucolides						
distribution	Mex c.Amer S.Amer	Venez Andes	C.& S.Amer W.Ind	n.Andes	n.Andes	n.S.Amer	W.Ind	W.Ind	e.Venez

TABLE 8.—Chrestinae.

Chrestinae	Chresta	Soaresia	Pithecoseris
habit			 acropetal
corolla			
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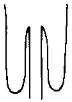
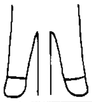
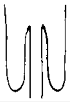
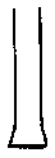
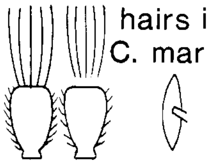
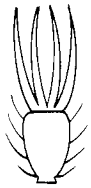
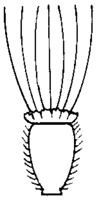
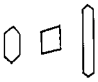
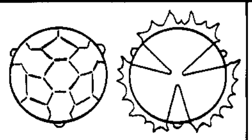
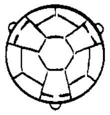
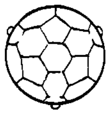
anther base			
style base no node			
achenes	T-shaped hairs in C. martii 		
raphids			
pollen			
pollen size	40–42 um	55–57 um	48–50 um
chemistry	glaucolides furoheliangolides (in roots)		
distribution	Brazil	Brazil	Brazil

TABLE 9.—Centrantherinae.

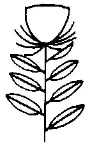
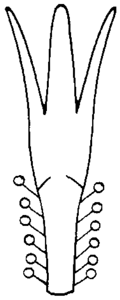
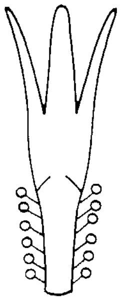
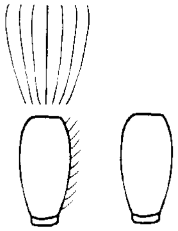
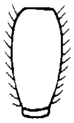
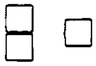
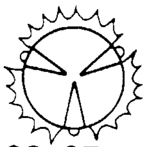
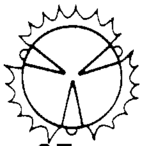
Centratherinae	Centratherum	Oispermum
inv. persistent n=	16,32	
habit		
inv./fl	80–100 /50	c.45/25
corolla		
anther append.		
style base		
achenes		
raphids		
pollen	 30–37 um	 c.37 um
chemistry	furoheliango-lides glaucolides guaianolides	
distribution	Trop. America, Austral, Philippines	n.e. Brazil

TABLE 10.—Lychnophorinae.

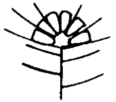
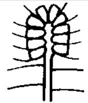
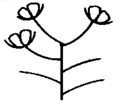
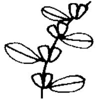
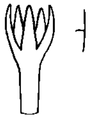
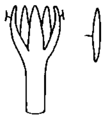
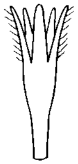
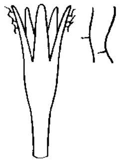
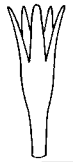
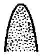
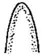
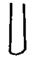
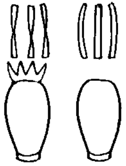
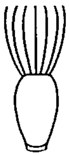
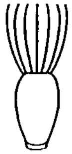
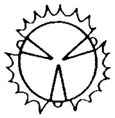
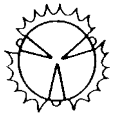
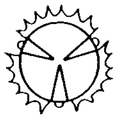
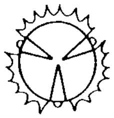
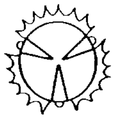
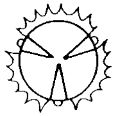
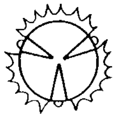
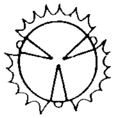
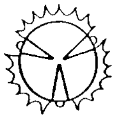
Lychnophorinae	Lychnophora (Haplostephium)	Lychnophoriopsis	Eremanthus (Vanillosmopsis)	Prestelia	Anteremanthus	Minasia	Piptolepis	Chromopappus	Proteopsis
n=	17	17	15, 18						
habit									
inv./fl	1-12	9-23	1-5	5-6	c.60	20-30	9-18(-25)	8-10	c.60
corolla									
anther append									
anther base									
style base									
achene									
raphides	☐	☐	☐	☐	☐	☐	☐	☐	☐
pollen	 c.42um	 50-60um	 40-42um	 40-42um	 c.45um	 c.55um	 45-50um	 c.42um	 c.50um
chemistry	furoheliangolides guaianolides bisabolane nerolidol	furoheliangolides	furoheliangolides				furoheliangolides		furoheliangolides
distribution	Brazil	Brazil	Brazil	Brazil	Brazil	Brazil	Brazil	Brazil	Brazil

TABLE 11.—Sipolisiinae.

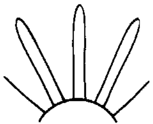
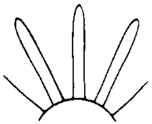
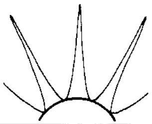
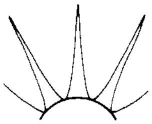
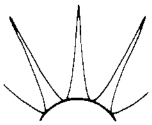
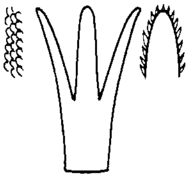
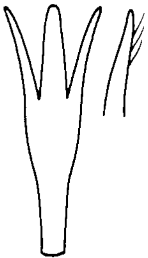
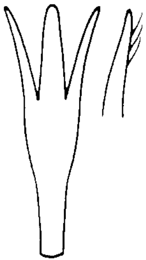
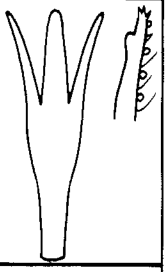
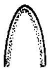
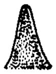
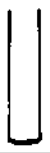
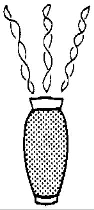
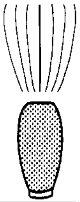
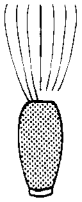
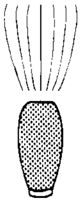
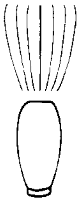
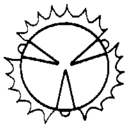
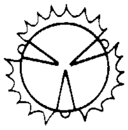
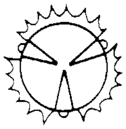
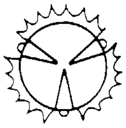
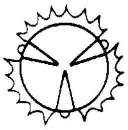
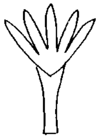
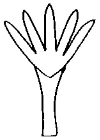
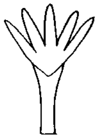
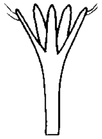
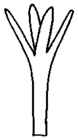
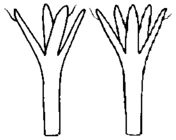
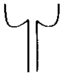
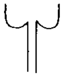
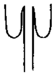
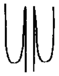
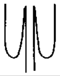
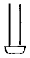
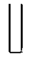
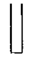
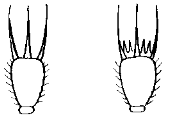
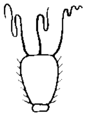
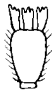
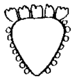
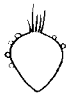
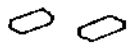
Sipolisiinae	Heterocoma	Bishopalea	Sipolisia	Xerxes (Alcantara)	Hololepis
pubescence	appressed tomentellous	tomentose	lanate	lanate	lepidote trinervate bract
receptacle (pales or bristles)					
inv./fl	c.100/c.50	30-35/c.20	55-100/25-50	100 /50	30-40/c.20
corolla lobes	 serial spicules papillae				
anther append.					
anther base					
style base					
achenes glabrous	carbonized 	carbonized 	carbonized 	carbonized 	
raphids	none	none	none	none	☐
pollen					
chemistry	guaianolides			furoheliangolides eudesmanolides	
distribution	Brazil	Brazil	Brazil	Brazil	Brazil

TABLE 12.—Elephantopinae and Rolandrinae.

	Elephantopinae				Rolandrinae	
	Elephantopus	Orthopappus	Pseudelephantopus	Telmatophila	Rolandra	Spiracantha
n=	11	11	13			8
habit	herb	herb	herb	herb	shrub	herb
inv./fl	8/2-4	8/4	8/4	4-6/4	2/1	c.6/1
corolla						
lobe	glabrous	glands & spicules	glands	hairs	glabrous	few long hairs
anther append.						
anther base						
style base						
achenes						
raphids				?	 minute or none	none
pollen	lophate triporate	odd type A	lophate triporate	?	lophate triporate	lophate triporate
chemistry	germacranolides (dilactones) bisabolane	germacranolides (dilactones)	glaucolides bisabolane		glaucolides	
distribution	Pan Tropical	Trop. America	Trop. America	Brazil	Trop. America	Cent. & S. America

Appendix I

Accepted Generic Names of the Vernonieae Native or Introduced in the New World

(includes synonyms)

Acanthodesmos C.D. Adams & M.C. du Quesnay, Phytologia 21:405. 1971.
Type: *A. distichus* C.D. Adams & M.C. du Quesnay
Achyrocoma (Cassini) Cass., Dict. Sci. Nat. 57:341. 1828, not *Achyrocome* Schrank 1824.
Vernonia subg. *Achyrocoma* Cass., Dict. Sci. Nat. 26:21. 1823. Herb with totally squamellate pappus, outer pappus multiseriate graduated. Palisot de Beauvois, Amérique Septentrionale ? (not likely). Type said to be in poor condition with heads separate.
Acilepidopsis H. Rob., Phytologia 67:289. 1989.
Type: *Vernonia echitifolia* Mart. ex DC.
Albertinia K.P.J. Spreng., Neue Entdeck. Pflanzenk. 2:133. 1820.
Type: *A. brasiliensis* K.P.J. Spreng.
Symblomeria Nutt., Trans. Amer. Philos. Soc. ser. 2. 7:284. 1840.
Type: *S. baldwiniana* Nutt.=*Albertinia brasiliensis* Spreng.
Anteremanthus H. Rob., Proc. Biol. Soc. Wash. 105:646. 1992.
Type: *A. hatschbachii* H. Rob.
Aynia H. Rob., Proc. Biol. Soc. Wash. 101:959. 1988.
Type: *A. pseudascaricida* H. Rob.
Baccharoides Moench, Methodus 528. 1794.
Type: *Conyza anthelmintica* L.
Ascaricida Cass., Dict. Sci. Nat. 3, suppl. 38. 1817, nom. superfl. for *Baccharoides* Moench
Candidea Tenora, Atti Reale Accad. Sci. Sez. Soc. Reale Borbon 4 (Cl. Botan.):104, t. 1, 2. 1839.
Type: *C. senegalensis* Tenora
Vernonia subsect. *Stengelia* Sch. Bip. ex Walp., Repert. Bot. Syst. 2:948. 1843.
Type: *Vernonia adoensis* Sch. Bip. ex Walp.
Stengelia Steetz in Peters, Naturw. Reise Mossamb., Bot. 360. 1864.
Type: *Vernonia schimperi* DC.
Vernonia sect. *Stengelia* (Sch. Bip. ex Walp.) Benth. in Benth. and Hook. f., Gen. Pl. 2:127. 1873.
Dolosanthus Klatt, Bull. Herb. Boiss. 4:473. 1886.
Type: *D. sylvaticus* Klatt=*B. anthelmintica* (L.) Moench
Bishopalea H. Rob., Phytologia 48:211. 1981.
Type: *B. erecta* H. Rob.
Blanchetia DC., Prodr. 5:75. 1836.
Type: *B. heterotricha* DC.
Bolanosa A. Gray, Smithson. Contr. Knowl. 3(5, Pl. Wright. 1): 82. 1852.
Type: *B. coulteri* A. Gray
Caatinganthus H. Rob., in text of present paper.
Type: *C. harleyi* H. Rob.
Centratherum Cass., Dict. Sci. Nat. 7:384. 1817.
Type: *C. punctatum* Cass.
Spixia Schrank., Pl. Rar. Hort. Monac. tab. 80. 1819.
Type: *S. violacea* Schrank
Ampherephis H.B.K., Nov. Gen. Sp., ed. fol. 4:24. 1818.
Type: *A. mutica* H.B.K.
Amphibecis Schrank, Syll. Ratisb. 1:86. 1824.
Type: *A. violacea* Schrank
Crantzia Vell., Fl. Flum. Ic. 8, tab. 153. 1827.
Type: *C. ovata* Vell.
Chresta Vell. ex DC., Prodr. 5:85. 1836.
Lectotype: *C. sphaerocephala* DC.
Vernonia sect. *Pycnocephalum* Less., Linnaea 6:630. 1831.
Lectotype: *P. plantaginifolium* (Less.) Baker (MacLeish, 1985b)
Pycnocephalum (Less.) DC., Prodr. 5:83. 1836.
Stachyanthus DC., Prodr. 5:84. 1836, nom. rej., not *Stachyanthus* Engl. nom. cons.
Type: *S. martii* DC.
Eremanthus sect. *Pycnocephalum* (Less.) Baker, Fl. Bras. 6(2):168. 1873.
Glaziovianthus G.M. Barroso, Revista Brasil. Biol. 7:114. 1947.
Type: *G. purpureus* G.M. Barroso
Argyrovernonia MacLeish, Taxon 33:106. 1984. nom. nov. for *Stachyanthus* DC.
Type: *S. martii* DC.
Chronopappus DC., Prodr. 5:84. 1836.
Type: *Serratula bifrons* Persoon
Chrysolaena H. Rob., Proc. Biol. Soc. Wash. 101:956. 1988.
Type: *Vernonia flexuosa* Sims
Vernonia subsect. *Flexuosae* Cabrera, Darwiniana 6:329. 1944.
Lectotype: *Vernonia cognata* Less. (Jones, 1979c)
Lectotype: *Vernonia flexuosa* Sims (Robinson, 1988c)
Vernonia series *Flexuousae* (Cabrera) Jones, Rhodora 81: 442. 1979.
Vernonia series *Verbascifoliae* Jones, Rhodora 81:438. 1979.
Type: *Vernonia verbascifolia* Less.
Cololobus H. Rob., Proc. Biol. Soc. Wash. 107(3):557. 1994.
Type: *C. hatschbachii* H. Rob.
Critoniopsis Sch. Bip., Jahresber. Pollichia 20/21:430. 1863.
Type: *C. lindenii* Sch. Bip.

Turpinia Lex. ex La Llave & Lex., Nov. Feg. Desc., fasc. 1:22. 1824; not *Turpinia* Humb. & Bonpl., 1807, nom. rej.; not *Turpinia* Ventenat, 1807, nom. cons.
Lectotype: *T. tomentosa* Lex.
Monosis sect. *Eremosis* DC., Prodr. 5:77. 1836.
Lectotype: *Monosis salicifolia* DC.
Tephrothamnus Sch. Bip., Jahresber. Pollichia 20/21:431. 1863.
Lectotype: *T. paradoxa* Sch. Bip.
Eremosis (DC.) Gleason, Bull. N.Y. Bot. Gard. 4:227. 1906.
Cuatrecasanthus H. Rob., Rev. Acad. Colomb. Cienc. Exact. 17(65):209. 1989.
Type: *Vernonia sandemanii* H. Rob. & B. Kahn
Cyanthillium Blume, Bidjr. 889. 1826.
Type: *C. villosum* Blume
Isonema Cass., Bull. Soc. Philom. Paris 1817:152. 1817, nom. illeg., not R. Br. (1810).
Type: *I. ovata* Cass.
Vernonia sect. *Tephrodes* DC., Prodr. 5:24. 1836.
Lectotype: *Conyza cinerea* Blume (Jones, 1981a).
Cyanopis Blume ex DC., Prodr., 5:69. 1836, nom. illeg. et superfl., not Cassini (1817).
Claotrachelus Zoll. & Mortiz ex Zoll., Natuur-Geneesk. Arch. Ned Indië 2:263, 565. 1845.
Type: *C. rupestris* Zoll. & Moritz ex Zoll.
Seneciodes L. ex Post & O. Kuntze, Lex. Gen. Phan. 2:515. 1903.
Type: *Conyza cinerea* L.
Triplotaxis Hutchins., Bull. Misc. Inform. 1914:355. 1914.
Lectotype: *Herderia stellulifera* Benth. in Hook. (Robinson, 1990a)
Vernonia subsect. *Tephrodes* (DC.) S.B. Jones, Rhodora 83:70. 1981.
Cyrtocymura H. Rob., Proc. Biol. Soc. Wash. 100:849. 1987.
Type: *Conyza scorpioides* Lam.
Dasyandantha H. Rob., Proc. Biol. Soc. Wash. 106:778. 1993.
Type: *Vernonia cuatrecasasiana* Aristeg.
Dasyanthina H. Rob., Proc. Biol. Soc. Wash. 106:778. 1993.
Type: *Vernonia serrata* Less.
Dipterocypsela S.F. Blake, J. Wash. Acad. Sci. 35:36. 1945.
Type: *D. succulenta* S.F. Blake
Echinocoryne H. Rob., Proc. Biol. Soc. Wash. 100:586. 1987.
Type: *Vernonia holosericea* Mart. ex DC.
Eirmocephala H. Rob., Proc. Biol. Soc. Wash. 100:853. 1987.
Type: *Vernonia brachiata* Benth. ex Örsted
Ekmania Gleason, Bull. Torrey Bot. Club 46:250. 1919.
Type: *Vernonia lepidota* Griseb.
Elephantopus L., Sp. Pl. 814. 1753.
Lectotype: *E. scaber* L. (Britton and Brown, 1913).
Elephantosis Less., Linnaea 4:322. 1829.
Lectotype: *E. biflora* Less. (Gleason, Bull. N.Y. Bot. Gard. 4:238. 1906).
Eremanthus Less., Linnaea 4:317. 1829.
Type: *E. glomerulatus* Less.
Vanillosmopsis Sch. Bip., Jahresber. Pollichia 18/19:166. 1861.
Type: *V. glomerata* Sch. Bip. = *Eremanthus erythropappus* (DC.) MacLeish
Sphaerophora Sch. Bip., Jahresber. Pollichia 20/21:403. 1863, not Blume.
Type: *Albertinia bicolor* DC.
Paralychnophora MacLeish, Taxon 33:106. 1984, nom. nov. for *Sphaerophora* Sch. Bip.
Ethulia L.f., Dec. Prima Pl. Rar. Horti Upsal. 1. 1762.
Type: *E. conyzoides* L.f.
Hoehnelia Schweinf. in L. Höhn., Zum Rudolf-See. Stephanie-See 861. 1892.
Type: *H. vernonioides* Schweinf.
Gorceixia Baker, J. Bot. 20:225. 1882.
Type: *G. decurrens* Baker
Gymnanthemum Cass., Bull. Soc. Philom. Paris 1817:10. 1817.
Type: *G. cupulare* Cass. = *Baccharis senegalensis* Pers.=*G. coloratum* (Willd.) H. Rob. & B. Kahn
Bracheilema R.Br. ex Salt, Abyss. Append. 65. 1814. nom. nud.
Decaneurum DC., Arch. Bot. (Paris) 2:516. 1833. nom. superfl.
Type: as in *Gymnanthemum* Cass.
Monosis DC. in Wight, Contrib. Bot. Ind. 5. 1834.
Type: *M. wightiana* DC. in Wight = *G. arboreum* (Buch.-Ham.) H. Rob.
Vernonia sect. *Strobocalyx* Blume ex DC., Prodr. 5:21. 1836.
Type: *Vernonia arborea* Buch.-Ham.
Plectreca Rafin., Fl. Tellur. 4:119. 1838 ["1836"].
Type: *Staehelina corymbosa* Thunb.
Keringa Rafin., Sylva Tellur. 144. 1838.
Type: *K. amygdalina* (Del.) Rafin.
Cheliusia Sch. Bip., Flora 24. I. Intell.: 26. 1841.
Type: *C. abyssinica* Sch. Bip. = *Gymnanthemum amygdalinum* (Del.) Sch. Bip. ex Walp.
Strobocalyx (Bl. ex DC.) Spach, Hist. Nat. Veg. Phan. 10: 39. 1841.
Punduana Steetz in Peters, Reise Mossamb. Bot. 345. 1864.
Type: *P. volkameriifolia* (DC.) Steetz
Vernonia subsect. *Urceolatae* S.B. Jones, Rhodora 83:67. 1981.
Type: V. *sphaerocalyx* O. Hoffm.
Harleya S.F. Blake, J. Wash. Acad. Sci. 22:379. 1932.
Type: *H. oxylepis* (Benth.) S.F. Blake, *Oliganthes oxylepis* Benth.
Heterocoma DC., Ann. Mus. Natl. Hist. Nat. 16:190, t. 7. 1810.
Type: *H. albida* (DC.) DC., *Serratula albida* DC.
Heterocypsela H. Rob., Phytologia 44:442. 1979.
Type: *H. andersonii* H. Rob.
Hololepis DC., Ann. Mus. Natl. Hist. Nat. 16:155, 189. 1810.
Type: *H. pedunculata* (DC.) DC., *Serratula pedunculata* DC. ex Pers.

Huberopappus Pruski, Novon 2:19. 1992.
Type: *H. maigualidae* Pruski

Irwinia G.M. Barroso, Rodriguésia 32(54):11. 1980.
Type: *I. coronata* G.M. Barroso

Joseanthus H. Rob., Rev. Acad. Colomb. Ci. Exact. 17(65): 210. 1989.
Type: *J. cuatrecasasii* H. Rob.

Lachnorhiza A. Richard in Sagra, Hist. Fis. Cuba 11:34. 1850.
Type: *L. piloselloides* A. Rich.

Leiboldia Schltdl. ex Gleason, Bull. N.Y. Bot. Gard. 4:161. 1906.
Type: *L. serrata* (D. Don) Gleason
Leiboldia Schltdl., Linnaea 19:742. 1847. nom. nud.
Vernonia sect. *Leiboldia* [Schltdl.] Benth. and Hook., f. Gen. Pl. 2:228. 1873.

Lepidaploa (Cass.) Cass. in Cuvier, Dict. Sci. Nat. 36:20. 1825; 60:586. 1830; H.G.L. Rchb., Consp. Regn. Veg. 1:99. 1829 [1828]; F.G. Bartl., Ord. Nat. Pl. 136. 1830; E. Spach, Hist. Nat. Vég. 10:39. 1841.
Vernonia subg. *Lepidaploa* Cass., Bull. Sci. Soc. Philom. 1817:66. 1817.
Lectotype: *Vernonia albicaulis* Pers. = *L. glabra* (Willd.) H. Rob. (Robinson, Bohlmann, and King, 1980).
Vernonia sect. *Lepidaploa* (Cass.) DC., Prodr. 5:26. 1836.
Flustula Rafin., Sylva Tell. 116. 1838 [1836].
Type: *F. tomentosa* Rafin., nom. illeg. = *Conyza arborescens* L.

Lepidonia S.F. Blake, J. Wash. Acad. Sci. 26:454. 1936.
Type: *L. paleata* S.F. Blake, *Vernonia salvinae* var. *canescens* J.M. Coulter

Lessingianthus H. Rob., Proc. Biol. Soc. Wash. 101:939. 1988.
Type: *Vernonia argyrophylla* Less.

Lychnophora Mart., Denkschr. Königl.-Baier. Bot. Ges. Regensburg 2:148. 1822.
Type: *L. salicifolia* Mart.
Haplostephium Mart. ex DC., Prodr. 5:78. 1836.
Type: *H. passerina* Mart. ex DC.
Lychnocephalus Mart. ex DC., Prodr. 5:83. 1836.
Type: *L. tomentosus* Mart. ex DC.

Lychnophoriopsis Sch. Bip., Jahresber. Pollichia 20/21:375. 1863.
Type: *L. heterotheca* Sch. Bip.
Episcothamnus H. Rob., Phytologia 48:209. 1981.
Type: *Lychnophora candelabrum* Sch. Bip.

Mattfeldanthus H. Rob. & R.M. King, Willdenowia 9:10. 1979.
Type: *M. mutisioides* H. Rob. & R.M. King

Mesanthophora H. Rob., Novon 2:172. 1992.
Type: *M. brunneri* H. Rob.

Minasia H. Rob., Proc. Biol. Soc. Wash. 105:648. 1992.
Type: *Chresta alpestris* Gardn.

Oiospermum Less., Linnaea 4:339. 1829.
Type: *Ethulia involucrata* Nees & Mart.

Orthopappus Gleason, Bull. N.Y. Bot. Gard. 4:237. 1906.
Type: *Elephantopus angustifolius* Sw.

Pacourina Aubl., Hist. Pl. Guiane 2:800, t. 316. 1775.
Type: *P. edulis* Aubl.
Haynea Willd., Sp. Pl. 3:1787. 1804 ["1800"].
Type: *Pacourina edulis* Aubl., nom. superfl.
Pacourinopsis Cass., Bull. Soc. Philom. 1817:151. 1817.
Lectotype: *P. dentata* Cass., nom. superfl., *Pacourina cirsiifolia* H.B.K.

Piptocarpha R. Br., Observ. Compos. 121. 1817 [1818].
Lectotype: *P. brasiliana* Cass. (Cassini, 1826).
Carphobolus Schott in Spreng., Syst. Veg. 4, Cur. Post. 469. 1827.
Lectotype: *C. sessiliflorus* Schott in Spreng. (Jones, 1980).
Vernonia sect. *Vanilosma* Less., Linnaea 6:630. 1831.
Lectotype: *Vernonia axillaris* Less.
Monanthemum Griseb., Fl. Brit. W. Indian Islands 354. 1861, not Steele 1843.
Type: *M. cruegeri* Griseb.

Piptocoma Cass., Bull. Philom. Paris 1817:10. 1817.
Type: *P. rufescens* Cass.
Odontoloma H.B.K., Nov. Gen. Sp., ed. fol. 4:34. 1818.
Type: *O. acuminata* H.B.K.
Dialesta H.B.K., Nov. Gen. Sp., ed. fol. 4:35. 1818.
Type: *D. discolor* H.B.K.
Pollalesta H.B.K., Nov. Gen. Sp., ed. fol. 4:36. 1818.
Type: *P. vernonioides* H.B.K.
Adenocyclus Less., Linnaea 4:337. 1829.
Type: *A. condensatus* Less.

Piptolepis Sch. Bip., Jahresber. Pollichia 20/21:380. 1863, nom. cons.
Type: *P. ericoides* Sch. Bip.

Pithecoseris Mart. ex DC., Prodr. 5:84. 1836.
Type: *P. pacourinoides* Mart. ex DC.

Prestelia Sch. Bip., Festschr. Naturf. Ges. Emden 73. 1864.
Type: *P. eriopus* Sch. Bip.

Proteopsis Mart. & Zucc. ex Sch. Bip., Jahresber. Pollichia 20/21:378. 1863.
Type: *P. argentea* Mart. & Zucc. ex Sch. Bip., *Vernonia proteopsis* DC.

Pseudelephantopus Rohr, Skr. Naturh.-Selsk. Kjøb. 2:213. 1793.
Type: *Elephantopus spicatus* Juss. ex Aubl.
Distreptus Cass., Bull. Soc. Philom. 1817:66. 1817; Dict. Sci. Nat. 13:366. 1819.
Type: *Elephantopus spicatus* Juss. ex Aub.
Matamoria La Llave & Lex., Nov. Veg. Descr. 1:8. 1824.
Type: *Elephantopus spicatus* Juss. ex Aubl.
Spirochaeta Turcz., Bull. Soc. Nat. Mosc. 24:166. 1851.
Type: *S. funckii* Turcz.

Pseudopiptocarpha H. Rob., Proc. Biol. Soc. Wash. 107:561. 1994.
Type: *Vernonia elaeagnoides* H.B.K.

Quechualia H. Rob., Proc. Biol. Soc. Wash. 106:780. 1993.
Type: *Vernonia fulta* Griseb.

Rolandra Røttb., Soc. Med. Havn. Collect. 2:256. 1775.
Type: *R. argentea* Røttb.
Sipolisia Glaz. ex Oliv., Hooker's Icon. Pl. 23. t. 2281. 1894.
Type: *S. lanuginosa* Glaz. ex Oliv.
Soaresia Sch. Bip. Jahresber. Pollichia 20/21:376. 1863. nom. cons., not F. Allemao (1857).
Type: *S. velutina* Sch. Bip.
Bipontia S.F. Blake, J. Wash. Acad. Sci. 27:374. 1937, nom. rej., nom. nov. for *Soaresia* Sch. Bip.
Spiracantha H.B.K., Nov. Gen. Sp. Pl., ed. fol. 4:22. 1818.
Type: *S. cornifolia* H.B.K.
Stenocephalum Sch. Bip., Jahresber. Pollichia 20/21:385. 1863.
Lectotype: *Vernonia monticola* DC. = *S. apiculata* (Mart. ex DC.) Sch. Bip.
Stilpnopappus Mart. ex DC., Prodr. 5:75. 1836.
Lectotype: *S. pratensis* Mart. ex DC.
Strophopappus DC., Prodr. 5:75. 1836.
Type: *S. bicolor* DC.
Stokesia L'Hér., Sertum Angl. 27. 1789.
Type: *S. cyanea* L'Her., nom. illeg., *Carthamus laevis* J. Hill, *S. laevis* (J. Hill) E.L.Greene
Cartesia Cass., Bull. Sci. Soc. Philom. Paris 1816:198. 1816.
Type: *C. centauroides* Cass.
Stramentopappus H. Rob. & Funk., Bot. Jahrb. Syst. 108:227. 1987.
Type: *S. pooleae* (B. Turner) H. Rob. & V. Funk, *Vernonia pooleae* B.Turner
Struchium P. Browne, Civ. Nat. Hist. Jamaica 312. 1756.
Type: *S. herbaceum* J. St. Hil., *Ethulia struchium* Sw. = *Struchium sparganophorum* (L.) O. Kuntze
Athenaea Adans., Fam. 2:121. 1763, not Sendtn. (Solanaceae), nom. conserv.
Sparganophorus Vaill. ex Crantz, Inst. 1:261. 1766.
Type: *S. vaillantii* Crantz
Telmatophila Mart. ex Baker, Fl. Bras. 6(2):170. 1873.
Type: *T. scolymastrum* Mart. ex Baker
Trepadonia H. Rob., Proc. Biol. Soc. Wash. 107:564. 1994.
Type: *Vernonia mexiae* H. Rob.
Trichospira H.B.K., Nov. Gen. Sp. Pl., ed. fol. 4:21. 1818.
Type: *T. menthoides* H.B.K.=*T. verticillata* (L.) S.F. Blake
Vernonanthura H. Rob., Phytologia 73:66. 1992.
Type: *Baccharis brasiliana* L.
Vernonia Schreb., Gen. 2:541. 1791. nom. cons.
Type: *Serratula noveboracensis* L. type cons.
Behen Hill, Veg. Syst. 4:41. 1762.
Type: *B. noveboracensis* (L.) Hill
Xerxes J.R. Grant, Nord. J. Bot. 14:287. 1994, nom. nov. for *Alcantara* Glaz. ex G.M. Barroso, Loefgrenia 36:1. 1969, not *Alcantarea* (Morren ex Mez) Harms (Bromeliaceae, 1929).
Type: *Alcantara petroana* Glaz. ex G.M. Barroso
Xiphochaeta Poepp., Nova Gen. Sp. 3:44, pl. 250, 8–11. 1842.
Type: *X. aquatica* Poepp.

Genus Excluded

Pseudostifftia H. Rob., Phytologia 44:444. 1979.—Type: *P. kingii* H. Rob.
Tribe *Moquinieae* H. Rob. (Robinson, 1994a).

Appendix II

List of Species Names of Western Hemisphere Vernonieae

The following is a list of known species names of the Vernonieae of the Western Hemisphere with present dispositions and geography. Cases are marked with a question mark where the generic or specific disposition is uncertain.

Included in the list are names and combinations validated in this paper, the genus *Caatinganthus* and combinations of its two species provided in the text, and the following new combinations provided below: *Critoniopsis nonoensis*, *C. solorzanoana*, *C. villaregalis*, *Lepidaploa boquerona*, *L. diazlunana*, *L. koelzii*, *L. polypleura*, *L. sprengeliana*, *L. vauthieriana*, *Lessingianthus parvifolia*, *L. ramellae*, *Mesanthophora rojasii*, *Piptocarpha verticillata*, and *Vernonanthura hintoniorum*.

Acanthodesmos distichus C.D. Adams & M.C. du Quesnay, Phytologia 21:405. 1971. Jamaica.

Achyrocoma tomentosa Cass., Dict. Sci. Nat. 26:21. 1828, nom. inval., described before recognition of *Achyrocoma* at generic level.
= *Vernonia achyrocoma* Less.

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= *Piptocoma acuminata* (H.B.K.) Pruski

Albertinia arborea Gardn., Lond. J. Bot. 5:236. 1846.
= *Eremanthus arboreus* (Gardn.) MacLeish

Albertinia bardanoides Mart. ex Baker, Fl. Bras. 6(2):25. 1873, nom. nud. in synon.
= *Eremanthus crotonoides* (DC.) Sch. Bip.

Albertinia bicolor DC., Prodr. 5:81. 1836, not Gardn.
= *Eremanthus bicolor* (DC.) Baker

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= *Eremanthus incanus* (Less.) Less.

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= *Eremanthus erythropappus* (DC.) MacLeish

Albertinia capitata (Spreng.) DC., Prodr. 5:82. 1836.
= *Eremanthus capitatus* (Spreng.) MacLeish

Albertinia claussenii Sch. Bip. ex Baker, Fl. Bras. 6(2):15. 1873, nom. nud. in synon.
= *Eremanthus erythropappus* (DC.) MacLeish

Albertinia elaeagnus Mart. ex DC., Prodr. 5:81. 1836.
= *Eremanthus elaeagnus* (Mart. ex DC.) Sch. Bip.

Albertinia erythropappa DC., Prodr. 5:82. 1836.
= *Eremanthus erythropappus* (DC.) MacLeish

Albertinia glomerulata (Less.) DC., Prodr. 5:82. 1836.
= *Eremanthus glomerulatus* Less.

Albertinia gonoclados Mart. ex Baker, Fl. Bras. 6(2):144. 1873, nom. nud. in synon.
= *Piptolepis martiana* (Gardn.) Sch. Bip.

Albertinia goyazensis Gardn., Lond. J. Bot. 6:425. 1847.
= *Eremanthus goyazensis* (Gardn.) Sch. Bip.

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= *Eremanthus incanus* (Less.) Less.

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= *Eremanthus erythropappus* (DC.) MacLeish

Albertinia mollis Sch. Bip. ex Baker, Fl. Bras. 6(2):164. 1873, nom. nud. in synon.
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= *Piptolepis pseudo-myrtus* sensu Sch. Bip. & Baker, not *Piptolepis pseudo-mytus* (St. Hil.) Sch. Bip.

Albertinia multiflora Mart. ex Baker, Fl. Bras. 6(2):14. 1873, nom. nud. in synon.
= *Eremanthus polycephalus* (DC.) MacLeish

Albertinia obtusata Mart. ex DC., Prodr. 5:81. 1836, nom. nud. in synon.
= *Eremanthus glomerulatus* Less.

Albertinia oleaster Mart. ex DC., Prodr. 5:17. 1836, nom. nud. in synon.
= *Piptolepis oleaster* (DC.) Sch. Bip.

Albertinia pallidiseta DC., Prodr. 5:81. 1836.
= *Eremanthus glomerulatus* Less.

Albertinia polycephalus DC., Prodr. 5:82. 1836.
= *Eremanthus polycephalus* (DC.) MacLeish

Albertinia rufiseta DC., Prodr. 5:81. 1836.
= *Eremanthus glomerulatus* Less.

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= *Eremanthus polycephalus* (DC.) MacLeish

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  = *Centratherum punctatum* Cass.
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  = *Centratherum punctatum* Cass.
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  = *Centratherum punctatum* Cass.
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  = *Oiospermum involucratum* (Spreng.) Less.
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  = *Centratherum punctatum* Cass.
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  = *Lessingianthus venosissimus* (Sch. Bip. ex Baker) H. Rob.
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  = *Soaresia velutina* Sch. Bip.
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  = *Baccharoides anthelmintica* (L.) Moench
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  = *Centratherum punctatum* Cass.
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Baccharoides muticum (H.B.K.) Kuntze, Revis. Gen. Pl. 1:320. 1891.
  = *Centratherum punctatum* Cass.
Baccharoides punctatum (Cass.) Kuntze, Revis. Gen. Pl. 1: 320. 1891.
  = *Centratherum punctatum* Cass.
Baccharoides violaceum (Schrank) Kuntze, Revis. Gen. Pl. 1: 320. 1891.
  = *Centratherum punctatum* Cass.
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  = *Vernonia noveboracensis* (L.) Michx.
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  = *Vernonia praealta* (L.) Michx.
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  = *Vernonia acaulis* (Walter) Gleason
Cacalia acuminata (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
  = *Lepidaploa acuminata* (Less.) H. Rob.
Cacalia acutangula (Gardn.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
  = *Lepidaploa acutangula* (Gardn.) H. Rob.
Cacalia adamantia (Gardn.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
  = *Lepidaploa lilacina* (Mart. ex DC.) H. Rob.
Cacalia affinis (H.B.K.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
  = *Critoniopsis floribunda* (H.B.K.) H. Rob.
Cacalia alamanii (DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
  = *Vernonanthura* ?
Cacalia ammophila (Gardn.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
  = *Lessingianthus ammophilus* (Gardn.) H. Rob.
Cacalia angustifolia (Michx.) Kuntze, Revis. Gen. Pl. 1:323. 1891.
  = *Vernonia angustifolia* Michx.
Cacalia angustifolia var. *texana* (A. Gray) Kuntze, Revis. Gen. Pl. 1:323. 1891.
  = *Vernonia texana* (A. Gray) Small
Cacalia apiculata (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
  = *Stenocephalum apiculatum* (Mart. ex DC.) Sch. Bip.
Cacalia araneosa (Baker) Kuntze, Revis. Gen. Pl. 2:969. 1891.
  = *Lessingianthus durus* (Mart. ex DC.) H. Rob.

Cacalia araripensis (Gardn.) Kuntze, Revis. Gen. Pl. 2:968, 969. 1891.
= *Lepidaploa araripensis* (Gardn.) H. Rob.
Cacalia arborescens (L.) Kuntze, Revis. Gen. Pl. 1:323. 1891.
= *Lepidaploa arborescens* (L.) H. Rob.
Cacalia arenaria (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa arenaria* (Mart. ex DC.) H. Rob.
Cacalia argentea (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus argenteus* (Less.) H. Rob.
Cacalia argyropappa (Boek) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa salzmannii* (DC.) H. Rob.
Cacalia argyrophylla (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus argyrophyllus* (Less.) H. Rob.
Cacalia argyrotrichia (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa argyrotrichia* (Sch. Bip. ex Baker) H. Rob.
Cacalia arkansana (DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonia arkansana* DC.
Cacalia asteriflora (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 969. 1891.
= *Lessingianthus asteriflorus* (Mart. ex DC.) H. Rob.
Cacalia aurea (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa aurea* (Mart. ex DC.) H. Rob.
Cacalia auriculata (Griseb.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonanthura auriculata* (Griseb.) H. Rob.
Cacalia baccharoides (H.B.K.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonanthura patens* (H.B.K.) H. Rob.
Cacalia bahamensis (Griseb.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa arbuscula* (Less.) H. Rob.
Cacalia baldwinii (Torr.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonia baldwinii* Torr.
Cacalia baptizanda Kuntze, Revis. Gen. Pl. 2:968. 1891.
= *Critoniopsis uniflora* (Sch. Bip.) H. Rob.
Cacalia barbata (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa barbata* (Less.) H. Rob.
Cacalia barbinervis (Sch. Bip.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Critoniopsis barbinervis* (Sch. Bip.) H. Rob.
Cacalia bardanoides (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus bardanoides* (Less.) H. Rob.
Cacalia beyrichii (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonanthura beyrichii* (Less.) H. Rob.
Cacalia brachiata (Benth.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Eirmocephala brachiata* (Benth. ex Örsted) H. Rob.
Cacalia brevifolia (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus brevifolius* (Less.) H. Rob.
Cacalia brevipetiolata (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus brevipetiolatus* (Sch. Bip. ex Baker) H. Rob.
Cacalia buddleiaefolia (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus buddleiifolius* (Mart. ex DC.) H. Rob.
Cacalia bullata (Benth.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa canescens* (H.B.K.) H. Rob.
Cacalia canescens (H.B.K.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa canescens* (H.B.K.) H. Rob.
Cacalia carduoides (Baker) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus carduoides* (Baker) H. Rob.
Cacalia chalybaea (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 969. 1891.
= *Lepidaploa chalybaea* (Mart. ex DC.) H. Rob.
Cacalia chamaedrys (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonanthura chamaedrys* (Less.) H. Rob.
Cacalia chamaepeuces (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus chamaepeuces* (Sch. Bip. ex Baker) H. Rob.
Cacalia chamissonis (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa chamissonis* (Less.) H. Rob.
Cacalia chinensis (L.) Kuntze, Revis. Gen. Pl. 1:324. 1891, see *Conyza chinensis*.
= *Blumea chinensis* (L.) DC. [Plucheae]
Cacalia cincta (Griseb.) Kuntze, Revis. Gen. Pl. 3(2):138. 1898.
= *Cyrtocymura cincta* (Griseb.) H. Rob.
Cacalia cinerea (L.) Kuntze, Revis. Gen. Pl. 1:323. 1891.
= *Cyanthillium cinereum* (L.) H. Rob.
Cacalia clavata (Gardn.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa* ?
Cacalia cognata (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Chrysolaena platensis* (Spreng.) H. Rob.
Cacalia compacta (Gardn.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonanthura* ?
Cacalia compactiflora (Mart. ex Baker) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus compactiflorus* (Mart. ex Baker) H. Rob.
Cacalia cordata (H.B.K.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonanthura cordata* (H.B.K.) H. Rob.
Cacalia cordiaefolia (H.B.K.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa cordiaefolia* (H.B.K.) H. Rob.

Cacalia cordigera (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus cordiger* (Mart. ex DC.) H. Rob.
Cacalia coriacea (Less.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lessingianthus coriaceus* (Less.) H. Rob.
Cacalia corymbiformia (DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Vernonia karvinskiana* DC.
= *Vernonanthura* ?
Cacalia cotoneaster (Willd. ex Spreng.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa cotoneaster* (Willd. ex Spreng.) H. Rob.
Cacalia coulonii (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa sororia* (DC.) H. Rob.
Cacalia crotonoides (DC.) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Eremanthus crotonoides* (DC.) Sch. Bip.
Cacalia cuiabensis (Baker) Kuntze, Revis. Gen. Pl. 2:969. 1891.
= *Lepidaploa cuiabensis* (Baker) H. Rob.
Cacalia cuneifolia (Gardn.) Kuntze, Revis. Gen. Pl. 2:969–970. 1891.
= *Vernonanthura cuneifolia* (Gardn.) H. Rob.
Cacalia debilis (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa cotoneaster* (Willd. ex Spreng.) H. Rob.
Cacalia decumbens (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa decumbens* (Gardn.) H. Rob.
Cacalia densiflora (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura* ?
Cacalia deppeana (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura deppeana* (Less.) H. Rob.
Cacalia desertorum (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 290. 1891.
= *Lessingianthus desertorum* (Mart. ex DC.) H. Rob.
Cacalia dura (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:670. 1891.
= *Lessingianthus durus* (Mart. ex DC.) H. Rob.
Cacalia echitifolia (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 970. 1891.
= *Acilepidopsis echitifolia* (Mart. ex DC.) H. Rob.
Cacalia ehrenbergiana (Sch. Bip.) Kuntze, Revis. Gen. Pl. 2: 970. 1891.
= *Vernonanthura liatroides* (DC.) H. Rob.
Cacalia ehretiaefolia (Benth.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa ehretiifolia* (Benth.) H. Rob.
Cacalia elegans (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus elegans* (Gardn.) H. Rob.
Cacalia eremophila (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 970. 1891.
= *Lepidaploa rufogrisea* (St. Hil.) H. Rob.
Cacalia eriolepis (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa eriolepis* (Gardn.) H. Rob.
Cacalia erythrophila (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus erythrophilus* (DC.) H. Rob.
Cacalia eupatoriifolia (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Critoniopsis stellata* (Spreng.) H. Rob.
Cacalia fagifolia (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura fagifolia* (Gardn.) H. Rob.
Cacalia farinosa (Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus farinosus* (Baker) H. Rob.
Cacalia fasciculata (Michx.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonia fasciculata* Michx.
Cacalia flexuosa (Sims) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Chrysolaena flexuosa* (Sims) H. Rob.
Cacalia floccosa (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus floccosus* (Gardn.) H. Rob.
Cacalia frangulaefolia (H.B.K.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa frangulaefolia* (H.B.K.) H. Rob.
Cacalia fruticulosa (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa rufogrisea* (St. Hil.) H. Rob.
Cacalia fulta (Griseb.) Kuntze, Revis. Gen. Pl. 3(2):138. 1898.
= *Quechualia fulta* (Griseb.) H. Rob.
Cacalia geminata (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa canescens* (H.B.K.) H. Rob.
Cacalia gigantea (Walter) Kuntze, Revis. Gen. Pl. 1:324. 1891.
= *Vernonia gigantea* (Walter) Trelease ex Branner & Coville
Cacalia gigantea var. *baldwinii* (Torr.) Kuntze, Revis. Gen. Pl. 1:324. 1891.
= *Vernonia baldwinii* Torr.
Cacalia glabrata (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus glabratus* (Less.) H. Rob.
Cacalia glazioviana (Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus glaziovianus* (Baker) H. Rob.
Cacalia gnaphalioides (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa gnaphalioides* (Sch. Bip. ex Baker) H. Rob.
Cacalia gracilis (H.B.K.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa gracilis* (H.B.K.) H. Rob.
Cacalia graminifolia (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891, not *Cacalia graminifolia* (Walter) Kuntze
= *Lessingianthus psilophyllus* (DC.) H. Rob.
Cacalia graminifolia (Walter) Kuntze, Revis. Gen. Pl. 2:968. 1891.
= *Vernonia angustifolia* Michx.
Cacalia grisea (Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa grisea* (Baker) H. Rob.

Cacalia haenkeana (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura patens* (H.B.K.) H. Rob.

Cacalia havanensis (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura havanensis* (DC.) H. Rob.

Cacalia helophila (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 970. 1891.
= *Lepidaploa helophila* (Mart. ex DC.) H. Rob.

Cacalia hexantha (Sch. Bip.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Stenocephalum megapotamicum* (Spreng.) Sch. Bip.

Cacalia hieracioides (Griseb.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura hieracioides* (Griseb.) H. Rob.

Cacalia hirtiflora (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa remotiflora* (L.C. Rich.) H. Rob.

Cacalia holosericea (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Echinocoryne holosericea* (Mart. ex DC.) H. Rob.

Cacalia hoveaefolia (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus hoveaefolius* (Gardn.) H. Rob.

Cacalia hypochaeris (DC.) Kuntze, Revis. Gen. Pl. 2:270. 1891.
= *Lessingianthus hypochaeris* (DC.) H. Rob.

Cacalia ignobilis (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura ignobilis* (Less.) H. Rob.

Cacalia immunis (Griseb.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonia incana* Less.

Cacalia incana (Less.) Kuntze, Revis. Gen. Pl. 3(2):138. 1898.
= *Vernonia incana* Less.

Cacalia interjecta (Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Stenocephalum tragiaefolium* (DC.) Sch. Bip.?

Cacalia intermedia (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus rubricaulis* (Humb. & Bonpl.) H. Rob.

Cacalia inuloides (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonia karvinskiana* ssp. *inuloides* (DC.) S.B. Jones
= *Vernonanthura* ?

Cacalia karvinskiana (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura* ?

Cacalia karwinskii (Sch. Bip.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Critoniopsis tarchonanthifolia* (DC.) H. Rob.

Cacalia kuntzei (Hieron.) Kuntze, Revis. Gen. Pl. 3(2):138. 1898.
= *Lessingianthus asteriflorus* (Mart. ex DC.) H. Rob.

Cacalia lacunosa (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus lacunosus* (Mart. ex DC.) H. Rob.

Cacalia lanceolaris (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura patens* (H.B.K.) H. Rob.

Cacalia lappoides (Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus bardanoides* (Less.) H. Rob.

Cacalia laurifolia (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus laurifolius* (DC.) H. Rob.

Cacalia laxa (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura laxa* (Gardn.) H. Rob.

Cacalia lehmannii (Hieron.) Kuntze, Revis. Gen. Pl. 3(2):138. 1898.
= *Lepidaploa lehmannii* (Hieron.) H. Rob.

Cacalia leiboldiana (Schltdl.) Kuntze, Revis. Gen. Pl. 2:270. 1891.
= *Leiboldia serrata* (D. Don) Gleason

Cacalia leiocarpa (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Critoniopsis leiocarpa* (DC.) H. Rob.

Cacalia lessingiana (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 970. 1891.
= *Lepidaploa barbata* (Less.) H. Rob.

Cacalia lessingioides (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa barbata* (Less.) H. Rob.

Cacalia lettermannii (Engelm. ex A. Gray) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonia lettermannii* Engelm. ex A. Gray

Cacalia liatroides (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura liatroides* (DC.) H. Rob.

Cacalia ligulifolia (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 970. 1891.
= *Lessingianthus ligulifolius* (Mart. ex DC.) H. Rob.

Cacalia lilacina (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lepidaploa lilacina* (Mart. ex DC.) H. Rob.

Cacalia lindheimeri (A. Gray & Engelm.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonia lindheimeri* A. Gray & Engelm.

Cacalia linearifolia (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus linearifolius* (Less.) H. Rob.

Cacalia linearis (Spreng.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus linearis* (Spreng.) H. Rob.

Cacalia lithospermoides (Baker) Kuntze, Revis. Gen. Pl. 2: 970. 1891.
= *Lepidaploa remotiflora* (L.C. Rich.) H. Rob.

Cacalia lucida (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Vernonanthura lucida* (Less.) H. Rob.

Cacalia macrocephala (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus macrocephalus* (Less.) H. Rob.

Cacalia macrophylla (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus macrophyllus* (Less.) H. Rob.

Cacalia mansoana (Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.
= *Lessingianthus mansoanus* (Baker) H. Rob.

Cacalia marginata (Torr.) Kuntze, Revis. Gen. Pl. 2:968. 1891.

= *Vernonia marginata* (Torr.) Rafin.

Cacalia mariana (Mart. ex Baker) Kuntze, Revis. Gen. Pl. 2: 970. 1891.

= *Vernonanthura mariana* (Mart. ex Baker) H. Rob.

Cacalia mexicana (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidonia mexicana* (Less.) H. Rob. & Funk

Cacalia mollis (H.B.K.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa canescens* (H.B.K.) H. Rob.

Cacalia mollissima (D. Don ex Hook. & Arn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lessingianthus mollissimus* (D. Don ex Hook. & Arn.) H. Rob.

Cacalia monocephala (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lessingianthus monocephalus* (Gardn.) H. Rob.

Cacalia monosis (Sch. Bip.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Critoniopsis tomentosa* (La Llave & Lex.) H. Rob.

Cacalia montevidensis (Spreng.) Kuntze, Revis. Gen. Pl. 2:968. 1891.

= *Vernonanthura montevidensis* (Spreng.) H. Rob.

Cacalia moritziana (Sch. Bip.) Kuntze, Revis. Gen. Pl. 2:270. 1891.

= *Lepidaploa gracilis* (H.B.K.) H. Rob.

Cacalia mucronifolia (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa mucronifolia* (DC.) H. Rob.

Cacalia muricata (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa muricata* (DC.) H. Rob.

Cacalia myriocephala (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa myriocephala* (DC.) H. Rob.

Cacalia nitens (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa nitens* (Gardn.) H. Rob.

Cacalia noveboracensis (L.) Kuntze, Revis. Gen. Pl. 1:324. 1891.

= *Vernonia noveboracensis* (L.) Michx.

Cacalia nudiflora (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Vernonanthura nudiflora* (Less.) H. Rob.

Cacalia obovata (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Chrysolaena herbacea* (Vell.) H. Rob.

Cacalia obscura (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lessingianthus obscurus* (Less.) H. Rob.

Cacalia obtusata (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lessingianthus obtusatus* (Less.) H. Rob.

Cacalia obtusifolia (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa obtusifolia* (Less.) H. Rob.

Cacalia octanthus (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lessingianthus octanthus* (Sch. Bip. ex Baker) H. Rob.

Cacalia oligactoides (Less.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Vernonanthura oligactoides* (Less.) H. Rob.

Cacalia oligolepis (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Vernonanthura oligolepis* (Sch. Bip. ex Baker) H. Rob.

Cacalia oligophylla (Vell.) Kuntze, Revis. Gen. Pl. 2:968. 1891.

= *Chrysolaena oligophylla* (Vell.) H. Rob.

Cacalia onoporoides (Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lessingianthus onoporoides* (Baker) H. Rob.

Cacalia oxylepis (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa psilostachya* (DC.) H. Rob.

Cacalia paludosa (Gardn.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Vernonanthura paludosa* (Gardn.) H. Rob.

Cacalia paniculata (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Critoniopsis tomentosa* (La Llave & Lex.) H. Rob.

Cacalia patens (H.B.K.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Vernonanthura patens* (H.B.K.) H. Rob.

Cacalia patula (Aitch.) Kuntze, Rev. Gen. Pl. 1:324. 1891.

= *Cyanthillium patulum* (Aitch.) H. Rob.

Cacalia pellita (H.B.K.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lepidaploa pellita* (H.B.K.) H. Rob.

Cacalia pentacantha (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Lessingianthus pentacontus* (DC.) H. Rob.

Cacalia petiolaris (DC.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Vernonanthura petiolaris* (DC.) H. Rob.

Cacalia plantaginodes Kuntze, Revis. Gen. Pl. 2:969. 1891, not *Vernonia plantaginoides* Hieron.

= *Lessingianthus plantaginodes* (Kuntze) H. Rob.

Cacalia platensis (Spreng.) Kuntze, Revis. Gen. Pl. 2:970. 1891.

= *Chrysolaena platensis* (Spreng.) H. Rob.

Cacalia poeppigiana (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lepidaploa salzmannii* (DC.) H. Rob.

Cacalia polyanthes (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Vernonanthura phosphorica* (Vell.) H. Rob.

Cacalia praecox Kuntze, Revis. Gen. Pl. 3(2):139. 1898.

= *Vernonanthura squamulosa* (Hook. & Arn.) H. Rob.

Cacalia psilophylla (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus psilophyllus* (DC.) H. Rob.

Cacalia psilostachya (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lepidaploa psilostachya* (DC.) H. Rob.

Cacalia puberula (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Vernonanthura puberula* (Less.) H. Rob.

Cacalia pulverulenta (Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus pulverulentus* (Baker) H. Rob.

Cacalia pumilla (Vell.) Kuntze, Revis. Gen. Pl. 2:969. 1891.

= *Lessingianthus pumillus* (Vell.) H. Rob.

Cacalia punctata (Sw. ex Wikstr.) Kuntze, Revis. Gen. Pl. 2: 971. 1891.

= *Lepidaploa glabra* (Willd.) H. Rob.

Cacalia pungens (Gardn.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Echinocoryne pungens* (Gardn.) H. Rob.

Cacalia pycnostachya (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus pycnostachyus* (DC.) H. Rob.
Cacalia pyrifolia (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Piptocarpha pyrifolia* (DC.) Baker
Cacalia quinqueflora (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Critoniopsis quinqueflora* (Less.) H. Rob.
Cacalia radula (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus glabratus* (Less.) H. Rob.
Cacalia reflexa (Gardn.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa reflexa* (Gardn.) H. Rob.
Cacalia remotiflora (L.C. Rich.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa remotiflora* (L.C. Rich.) H. Rob.
Cacalia riedelii (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa eriolepis* (Gardn.) H. Rob.
Cacalia rigiophylla Kuntze, Revis. Gen. Pl. 2:971. 1891, based on *Vernonia rigiophylla* Sch. Bip. ex Baker, not *Vernonia rigiophylla* DC.
= *Vernonanthura rigiophylla* (Kuntze) H. Rob.
Cacalia rosea (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus roseus* (Mart. ex DC.) H. Rob.
Cacalia rosmarinifolia (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus rosmarinifolius* (Less.) H. Rob.
Cacalia rubricaulis (Humb. & Bonpl.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus rubricaulis* (Humb. & Bonpl.) H. Rob.
Cacalia rubricaulis var. *pseudo-incana* (Hieron.) Kuntze, Revis. Gen. Pl. 3(2):139. 1898.
= *Lessingianthus rubricaulis* (Humb. & Bonpl.) H. Rob.
Cacalia rubriramea (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Vernonanthura* ?
Cacalia ruficoma (Schltdl. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Vernonanthura membranacea* (Gardn.) H. Rob.
Cacalia rugulosa (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus rugulosus* (Sch. Bip. ex Baker) H. Rob.
Cacalia rupestris (Gardn.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Cololobus rupestris* (Gardn.) H. Rob.
Cacalia salicifolia (Mart.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lychnophora salicifolia* Mart.
Cacalia salvinae (Hemsl.) Gleason, Bull. N.Y. Bot. Gard. 4: 162. 1906.
= *Lepidonia salvinae* (Hemsl.) H. Rob. & Funk
Cacalia salzmannii (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa salzmannii* (DC.) H. Rob.
Cacalia saxicola (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa rufogrisea* (St. Hil.) H. Rob.
Cacalia scapigera (Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891, not *Vernonia scapigera* Less.
= *Minasia scapigera* H. Rob.
Cacalia schiedeana (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa tortuosa* (L.) H. Rob.
Cacalia schwenkiaefolia (Mart.) Kuntze, Revis. Gen. Pl. 2: 971. 1891.
= *Echinocoryne schwenkiaefolia* (Mart. ex DC.) H. Rob.
Cacalia scorpioides (Lam.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Cyrtocymura scorpioides* (Lam.) H. Rob.
Cacalia scorpioides var. *sororia* (DC.) Kuntze, Revis. Gen. Pl. 3(2):139. 1898.
= *Lepidaploa sororia* (DC.) H. Rob.
Cacalia secunda (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus secundus* (Sch. Bip. ex Baker) H. Rob.
Cacalia seemanniana (Steetz) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa tortuosa* (L.) H. Rob.
Cacalia sellowii (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus sellowii* (Less.) H. Rob.
Cacalia sericea (L.C. Rich.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa sericea* (L.C. Rich.) H. Rob.
Cacalia serrata (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Dasyanthina serrata* (Less.) H. Rob.
Cacalia serratuloides (H.B.K.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Vernonanthura serratuloides* (H.B.K.) H. Rob.
Cacalia sessiliflora (Willd. ex Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa remotiflora* (L.C. Rich.) H. Rob.
Cacalia sessilifolia (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus pumillus* (Vell.) H. Rob.
Cacalia simplex (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lessingianthus simplex* (Less.) H. Rob.
Cacalia sinclairii (Benth.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Vernonanthura sinclairii* (Benth.) H. Rob.
Cacalia sordidopapposa (Hieron.) Kuntze, Revis. Gen. Pl. 3(2):139. 1898.
= *Lepidaploa sordidopapposa* (Hieron.) H. Rob.
Cacalia sororia (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Lepidaploa sororia* (DC.) H. Rob.
Cacalia squamulosa (Hook. & Arn.) Kuntze, Revis. Gen. Pl. 2: 971. 1891.
= *Vernonanthura squamulosa* (Hook. & Arn.) H. Rob.
Cacalia steetzii (Sch. Bip.) Kuntze, Revis. Gen. Pl. 2:971. 1891.
= *Critoniopsis foliosa* (Benth.) H. Rob.

Cacalia stellaris (La Llave & Lex.) Kuntze, Revis. Gen. Pl. 2: 971. 1891.

= *Vernonanthura deppeana* (Less.) H. Rob.

Cacalia stoechas (Mart. ex Baker) Kuntze, Revis. Gen. Pl. 2: 971. 1891.

= *Lessingianthus stoechas* (Mart. ex Baker) H. Rob.

Cacalia stricta (Gardn.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Echinocoryne stricta* (Gardn.) H. Rob.

Cacalia suaveolens (H.B.K.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Critoniopsis suaveolens* (H.B.K.) H. Rob.

Cacalia subulata (Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Echinocoryne subulata* (Baker) H. Rob.

Cacalia subverticillata (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Vernonanthura subverticillata* (Sch. Bip. ex Baker) H. Rob.

Cacalia syncephala (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus syncephalus* (Sch. Bip. ex Baker) H. Rob.

Cacalia tarchonanthifolia (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Critoniopsis tarchonanthifolia* (DC.) H. Rob.

Cacalia tarijensis (Griseb.) Kuntze, Revis. Gen. Pl. 3(2):140. 1898.

= *Lepidaploa tarijensis* (Griseb.) H. Rob.

Cacalia thomae (Benth.) Kuntze, Revis. Gen. Pl. 1:324. 1891.

= *Lepidaploa glabra* (Willd.) H. Rob.

Cacalia tomentella (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 971. 1891.

= *Lessingianthus pycnostachyus* (DC.) H. Rob.

Cacalia tomentosa (La Llave & Lex.) Kuntze, Revis. Gen. Pl. 2:969. 1891.

= *Critoniopsis tomentosa* (La Llave & Lex.) H. Rob.

Cacalia tournefortioides (H.B.K.) Kuntze, Revis. Gen. Pl. 2: 971. 1891.

= *Cyrtocymura scorpioides* (Lam.) H. Rob.

Cacalia tragiaefolia (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Stenocephalum tragiaefolium* (DC.) Sch. Bip.

Cacalia triantha (Nees & Schauer) Kuntze, Revis. Gen. Pl. 2: 971. 1891.

= *Critoniopsis triflosculosa* (H.B.K.) H. Rob.

Cacalia tricephala (Gardn.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lepidaploa rufogrisea* (St. Hil.) H. Rob.

Cacalia triflosculosa (H.B.K.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Critoniopsis triflosculosa* (H.B.K.) H. Rob.

Cacalia uniflora (Mill.) Kuntze, Revis. Gen. Pl. 2:969. 1891.

= *Lepidaploa uniflora* (Mill.) H. Rob.

Cacalia varroniifolia (DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus varroniifolius* (DC.) H. Rob.

Cacalia venosissima (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus venosissimus* (Sch. Bip. ex Baker) H. Rob.

Cacalia vepretorum (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 971. 1891.

= *Lessingianthus vepretorum* (Mart. ex DC.) H. Rob.

Cacalia verbascifolia (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Chrysolaena verbascifolia* (Less.) H. Rob.

Cacalia vestita (Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus vestitus* (Baker) H. Rob.

Cacalia virens (Sch. Bip. ex Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lepidaploa salzmannii* (DC.) H. Rob.

Cacalia virgulata (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2: 971. 1891.

= *Lessingianthus virgulatus* (Mart. ex DC.) H. Rob.

Cacalia viscidula (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Vernonanthura viscidula* (Less.) H. Rob.

Cacalia warmingiana (Baker) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus warmingianus* (Baker) H. Rob.

Cacalia westiniana (Less.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Vernonanthura westiniana* (Less.) H. Rob.

Cacalia xanthophylla (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus xanthophyllus* (Mart. ex DC.) H. Rob.

Cacalia zuccariniana (Mart. ex DC.) Kuntze, Revis. Gen. Pl. 2:971. 1891.

= *Lessingianthus zuccarinianus* (Mart. ex DC.) H. Rob.

Calea sessiliflora Stokes, Bot. Mat. Med. 4:172. 1812, nom. nov. for and = *Pacourina edulis* Aubl.

Calydermos repens Spreng., Neue Entd. 1:278. 1820.

= *Oiospermum involucratum* (Spreng.) Less.

Carphobolus asterotrichius (Poepp.) Sch. Bip., Jahresber. Pollichia 20/21:426. 1863.

= *Piptocarpha asterotrichia* (Poepp.) Baker

Carphobolus axillaris (Less.) Sch. Bip., Jahresber. Pollichia 20/21:417. 1863.

= *Piptocarpha axillaris* (Less.) Baker

Carphobolus blanchetianus (DC.) Sch. Bip., Jahresber. Pollichia 20/21:423. 1863.

= *Piptocarpha lundiana* (Less.) Baker

Carphobolus cinereus Sch. Bip., Jahresber. Pollichia 20/21: 419. 1863.

= *Piptocarpha quadrangularis* (Vell.) Baker

Carphobolus cuneifolius Sch. Bip., Jahresber. Pollichia 20/21: 413. 1863.

= *Piptocarpha oblonga* (Gardn.) Baker

Carphobolus latifolius Sch. Bip., Jahresber. Pollichia 20/21: 426. 1863.

= *Piptocarpha opaca* (Benth.) Baker var. *latifolia* (Sch. Bip.) Baker

Carphobolus lechleri Sch. Bip., Jahresber. Pollichia 20/21:428. 1863.
= *Piptocarpha lechleri* (Sch. Bip.) Baker

Carphobolus lepidotus Sch. Bip., Jahresber. Pollichia 20/21: 414. 1863.
= *Piptocarpha oblonga* (Gardn.) Baker

Carphobolus leprosus (Less.) Sch. Bip., Jahresber. Pollichia 20/21:419. 1863.
= *Piptocarpha leprosa* (Less.) Baker

Carphobolus lucidus (Spreng.) Sch. Bip., Jahresber. Pollichia 20/21:413. 1863.
= *Piptocarpha lucida* (Spreng.) Benn. ex Baker

Carphobolus lundianus (Less.) Sch. Bip., Jahresber. Pollichia 20/21:421. 1863.
= *Piptocarpha lundiana* (Less.) Baker

Carphobolus macropodus (DC.) Sch. Bip., Jahresber. Pollichia 20/21:418. 1863.
= *Piptocarpha macropoda* (DC.) Baker

Carphobolus neurophyllus Sch. Bip., Jahresber. Pollichia 20/21:414. 1863.
= *Piptocarpha pyrifolia* (DC.) Baker

Carphobolus notatus (Less.) Sch. Bip., Jahresber. Pollichia 20/21:420. 1863.
= *Piptocarpha notata* (Less.) Baker

Carphobolus oblongus (Gardn.) Sch. Bip., Jahresber. Pollichia 20/21:416. 1863.
= *Piptocarpha oblonga* (Gardn.) Baker

Carpholobus opacus Sch. Bip., Jahresber. Pollichia 20/21:427. 1863, not *Piptocarpha opaca* (Benth.) Baker.
= *Piptocarpha polycephala* Baker

Carphobolus oxyphyllus (DC.) Sch. Bip., Jahresber. Pollichia 20/21:415. 1863.
= *Piptocarpha verticillata* (Vell.) G.L. Smith ex H. Rob.

Carphobolus pellucidus Sch. Bip., Jahresber. Pollichia 20/21: 420. 1863.
= *Piptocarpha leprosa* (Less.) Baker

Carphobolus poeppigianus (DC.) Sch. Bip., Jahresber. Pollichia 20/21:422. 1863.
= *Piptocarpha poeppigiana* (DC.) Baker

Carphobolus pyrifolius (DC.) Sch. Bip., Jahresber. Pollichia 20/21:415. 1863.
= *Piptocarpha pyrifolia* (DC.) Baker

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= *Piptocarpha ramiflora* (Spreng.) Baker

Carphobolus regnellii (Sch. Bip.) Sch. Bip., Jahresber. Pollichia 20/21:417. 1863.
= *Piptocarpha axillaris* (Less.) Baker

Carphobolus riedelii Sch. Bip., Jahresber. Pollichia 20/21:425. 1863.
= *Piptocarpha riedelii* (Sch. Bip.) Baker

Carphobolus rotundifolius (Less.) Sch. Bip., Jahresber. Pollichia 20/21:424. 1863.
= *Piptocarpha rotundifolia* (Less.) Baker

Carphobolus sellowii Sch. Bip., Jahresber. Pollichia 20/21:421. 1863.
= *Piptocarpha sellowii* (Sch. Bip.) Baker

Carphobolus semiserrulatus Sch. Bip., Jahresber. Pollichia 20/21:416. 1863.
= *Piptocarpha axillaris* (Less.) Baker

Carphobolus sessiliflorus Schott in Spreng., Syst. Veg. 4: Cur. Post. 409. 1827.
= *Piptocarpha lucida* (Spreng.) Benn. ex Baker

Carphobolus tereticaulis (DC.) Sch. Bip., Jahresber. Pollichia 20/21:422. 1863.
= *Piptocarpha poeppigiana* (DC.) Baker

Carphobolus umbellulatus Schott in Spreng., Syst. Veg. 4: Cur. Post. 409. 1827.
= *Piptocarpha brasiliana* Cass.

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= *Stokesia laevis* (Hill) Greene

Carthamus laevis Hill, Hort. Kew. 57. 1768.
= *Stokesia laevis* (Hill) Greene

Centratherum aristatum (H.B.K.) Cass. ex Jackson, Ind. Kew. 1:478. 1895.
= *Centratherum punctatum* Cass.

Centratherum brachylepis Sch. Bip. ex Baker, Fl. Bras. 6(2): 12. 1873.
= *Centratherum punctatum* Cass.

Centratherum brevispinum Cass., Dict. Sci. Nat. 57:346. 1829.
= *Centratherum punctatum* Cass.

Centratherum camporum (Hassl.) Malme, Ark. Bot. 24(6):15. 1931.
= *Centratherum punctatum* Cass.

Centratherum camporum (Hassl.) Malme var. *albicans* (Hassl.) Malme, Ark. Bot. 24A(6):15. 1931.
= *Centratherum confertum* Kirkman

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= *Centratherum punctatum* Cass.

Centratherum cardenasii H. Rob., Phytologia 46:444. 1980. Bolivia.

Centratherum chinense (L.) Less., Linnaea 6:105, 674. 1829, based on erroneous interpretation of Lamarck.
= *Blumea chinensis* (L.) DC. [Plucheae]

Centratherum confertum Kirkman, Rhodora 83:21. 1981, based on *Centratherum punctatum* ssp. *camporum* Hassl. var. *albicans* Hassl. Argentina, Paraguay.

Centratherum holtonii Baker, Fl. Bras. 6(2):12. 1873.
= *Centratherum punctatum* Cass.

Centratherum intermedium (Link) Less., Linnaea 4:320. 1829.
= *Centratherum punctatum* Cass.

Centratherum longispinum Cass., Dict. Sci. Nat. 57:346. 1828.
= *Centratherum punctatum* Cass.

Centratherum muticum (H.B.K.) Less., Linnaea 4:320. 1829.

= *Centratherum punctatum* Cass.

Centratherum parviflorum Moricand ex Baker, Fl. Bras. 6(2): 12. 1873, nom. nud. in synon.

= *Centratherum punctatum* Cass.

Centratherum pulchellum (Cass.) Steud., Nom. Bot. ed. 2, 324. 1840.

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= *Centratherum confertum* Kirkman

Centratherum punctatum ssp. *camporum* Hassl. var. *longipes* Hassl., Repert. Spec. Nov. Regni Veg. 12:369. 1913.

= *Centratherum punctatum* Cass.

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= *Pseudelephantopus spiralis* (Less.) Cronq.

Chresta alpestris Gardn. Lond. J. Bot. 1:239. 1842.

= *Minasia alpestris* (Gardn.) H. Rob.

Chresta angustifolia Gardn., Lond. J. Bot. 1:240, t. 8. 1842. Brazil.

Chresta cordata Vell., Fl. Flum. 8. pl. 150. 1835, nom. inval.

= *Chresta sphaerocephala* DC.

Chresta curumbensis (Philipson) H. Rob., Phytologia 45:91. 1980. Brazil.

Chresta eriopus (Sch. Bip.) H. Rob., Phytologia 45:91. 1980.

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Chresta exsucca DC., Prodr. 5:85. 1836. Bolivia, Brazil.

Chresta halimodendron Mart. ex Baker, Fl. Bras. 6(2):380. 1873, nom. nud.

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Chresta intermedia Gardn., Lond. J. Bot. 4:236. 1845.

= *Chresta sphaerocephala* DC.

Chresta lanceolata Vell., Fl. Flum. 8: pl. 151. 1831.

= *Eremanthus* ? Brazil.

Chresta martii (DC.) H. Rob., Phytologia 45:91. 1980. Brazil.

Chresta pinnatifida (Philipson) H. Rob., Phytologia 78:384. 1995. Brazil.

Chresta plantaginifolia (Less.) Gardn., Lond. J. Bot. 1:241. 1842. Brazil.

Chresta pycnocephala DC., Prodr. 5:85. 1836. Brazil.

Chresta pycnocephala var. *halimodendron* DC., Prodr. 5:85. 1836.

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Chresta spathulaefolia (DC.) Gardn., Lond. J. Bot. 1:241. 1842.

= *Chresta plantaginifolia* (Less.) Gardn.

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= *Vernonia acaulis* (Walter) Gleason

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= *Vernonanthura crassa* (Vell.) H. Rob.

Chrysocoma cymosa Vell., Fl. Flum. 327. 1825 [1829], not *Vernonia cymosa* Blume

= *Vernonanthura cymosa* (Vell.) H. Rob.

Chrysocoma gigantea (Walter) Kuntze, Revis. Gen. Pl. 1:324. 1891.

= *Vernonia gigantea* (Walter) Trelease ex Branner & Coville

Chrysocoma graminifolia Walter, Fl. Carol. 196. 1788.

= *Vernonia angustifolia* Michx.

Chrysocoma herbacea Vell., Fl. Flum. 330. 1825 [1829].

= *Chrysolaena herbacea* (Vell.) H. Rob.

Chrysocoma horizontalis Vell., Fl. Flum., Icones Atlas 8; pl. 28. 1827 [1831].

= *Lepidaploa* ?

Chrysocoma oligophylla Vell., Fl. Flum.. 324. 1825, Icones Atlas 8; pl. 2. 1827 [1831].

= *Chrysolaena oligophylla* (Vell.) H. Rob.

Chrysocoma paniculata Vell., Fl. Flum. 327. 1825 [1829], not *Chrysocoma paniculata* J.F. Gmel., 1792.

= *Lepidaploa* ?

Chrysocoma pedunculata Vell., Fl. Flum., Icones Atlas 8; pl. 37. 1827 [1831].

= *Lessingianthus* ?

Chrysocoma phosphorica Vell., Fl. Flum. 325. 1825 [1829].

= *Vernonanthura phosphorica* (Vell.) H. Rob.

Chrysocoma quadrangularis Vell., Fl. Flum., Icones Atlas 8; pl. 25. 1827 [1831].

= *Piptocarpha quadrangularis* (Vell.) Baker

Chrysocoma repanda Vell., Fl. Flum., Icones Atlas 8; pl. 13. 1827 [1831].

= *Cyrtocymura scorpioides* (Lam.) H. Rob.

Chrysocoma sessilis Vell., Fl. Flum., Icones Atlas 8; pl. 20. 1827 [1831].

= *Lessingianthus macrophyllus* (Less.) H. Rob. ?

Chrysocoma singularis Vell., Fl. Flum., Icones Atlas 8; pl. 7, 1827 [1831].

= *Vernonanthura montevidensis* (Spreng.) H. Rob. ?

Chrysocoma tomentosa Walter, Fl. Carol. 196. 1788.
= *Vernonia noveboracensis* (L.) Michx.

Chrysocoma verticillata Vell., Fl. Flum., Icones Atlas 8; pl. 26. 1827 [1831].
= *Piptocarpha verticillata* (Vell.) G.L. Smith ex H. Rob.

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Conyza anthelmintica L., Sp. Pl., ed. 2, 1207. 1763.
= *Baccharoides anthelmintica* (L.) Moench

Conyza arborescens L., Syst. Nat. ed. 10, 2:1213. 1759.
= *Lepidaploa arborescens* (L.) H. Rob.

Conyza capitata Spreng., Syst. Veg. 3:507. 1826.
= *Eremanthus capitatus* (Spreng.) MacLeish

Conyza chinensis Lam., Encycl. 2:83. 1786, apparently not intended as new species, based on *Conyza chinensis* L.
= *Blumea chinensis* (L.) DC. [Plucheae]

Conyza cinerea L., Sp. Pl. 862. 1753.
= *Cyanthillium cinereum* (L.) H. Rob.

Conyza clethraefolia Willd. ex Baker, Fl. Bras. 6(2):100. 1873, nom. nud. in synon.
= *Vernonanthura brasiliana* (L.) H. Rob.

Conyza cotoneaster Willd. ex Spreng., Syst. Veg. 3:509. 1826.
= *Lepidaploa cotoneaster* (Willd. ex Spreng.) H. Rob.

Conyza divaricata Spreng., Syst. Veg. 3:508. 1826.
= *Vernonanthura divaricata* (Spreng.) H. Rob.

Conyza fruticosa L., Sp. Pl. ed. 2, 1209. 1763.
= *Lepidaploa fruticosa* (L.) H. Rob.

Conyza glabra Willd., Sp. Pl. 3:1940. 1803, not *Vernonia glabra* Vatke, 1877.
= *Lepidaploa glabra* (Willd.) H. Rob.

Conyza lucida Spreng., Neue Entd. 2:142. 1821.
= *Piptocarpha lucida* (Spreng.) Benn. ex Baker

Conyza patula Aitch., Hortus Kew. 3:184. 1789.
= *Cyanthillium patulum* (Aitch.) H. Rob.

Conyza platensis Spreng., Syst. Veg. 3:509. 1826.
= *Chrysolaena platensis* (Spreng.) H. Rob.

Conyza portoricensis Bertero ex DC., Prodr. 5:52. 1836.
= *Lepidaploa sericea* (L.C. Rich.) H. Rob.

Conyza ramiflora Spreng., Syst. Veg. 3:509. 1829.
= *Piptocarpha ramiflora* (Spreng.) Baker

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= *Cyrtocymura scorpioides* (Lam.) H. Rob.

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= *Piptocarpha lucida* (Spreng.) Benn. ex Baker

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= *Critoniopsis stellata* (Spreng.) H. Rob.

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= *Lepidaploa tortuosa* (L.) H. Rob.

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= *Lepidaploa uniflora* (Mill.) H. Rob.

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= *Rolandra fruticosa* (L.) Kuntze

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= *Rolandra fruticosa* (L.) Kuntze

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= *Trichospira menthoides* H.B.K.

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= *Ichthyothere terminalis* (Spreng.) S.F. Blake [Heliantheae]

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= *Chronopappus bifrons* (DC. ex Pers.) DC.

Serratula caroliniana Mill., Gard. Dict., ed. 8, Serratula no. 7. 1768.
= *Vernonia noveboracensis* (L.) Michx.

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= *Vernonia noveboracensis* (L.) Michx.

Serratula pedunculata DC. ex Pers., Syn. 2:391. 1807.
= *Hololepis pedunculata* (DC. ex Pers.) DC.

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= *Eremanthus bicolor* (DC.) Baker

Spiracantha cornifolia H.B.K., Nov. Gen. Sp., ed. fol. 4:23. 1818. Belize to Venezuela.

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= *Pseudelephantopus spiralis* (Less.) Cronq.

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= *Centratherum punctatum* Cass.

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= *Chresta martii* (DC.) H. Rob.

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Stenocephalum apiculatum (Mart. ex DC.) Sch. Bip., Jahresber. Pollichia 20/21:387. 1863. Brazil, Venezuela.

Stenocephalum brevifolium (DC.) Sch. Bip., Jahresber. Pollichia 20/21:387. 1863.
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Stenocephalum megapotamicum (Spreng.) Sch. Bip., Jahresber. Pollichia 20/21:388. 1863. Argentina, Brazil, Paraguay.

Stenocephalum melanotrichium (DC.) Sch. Bip., Jahresber. Pollichia 20/21:388. 1863.
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Stenocephalum penicillatum Sch. Bip., Jahresber. Pollichia 20/21:389. 1863.
= *Stenocephalum megapotamicum* (Spreng.) Sch. Bip.

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= *Piptocarpha stifftioides* H. Rob.

Stilpnopappus agrestis Gardn. ex Baker, Fl. Bras. 6(2):136. 1873, nom. nud. in synon.
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