Chromosome Numbers in Compositae, XII: Heliantheae

Harold Robinson,
A. Michael Powell,
Robert M. King,
and James F. Weedin

ABSTRACT

Robinson, Harold, A. Michael Powell, Robert M. King, and James F. Weedin. Chromosome Numbers in Compositae, XII: Heliantheae. *Smithsonian Contributions to Botany*, number 52, 28 pages, 3 tables, 1981.—Chromosome reports are provided for 145 populations, including first reports for 33 species and three genera, *Garcilassa*, *Riencourtia*, and *Helianthopsis*. Chromosome numbers are arranged according to Robinson's recently broadened concept of the Heliantheae, with citations for 212 of the ca. 265 genera and 32 of the 35 subtribes. Diverse elements, including the Ambrosieae, typical Heliantheae, most Helenieae, the Tegeteae, and genera such as *Arnica* from the Senecioneae, are seen to share a specialized cytological history involving polyploid ancestry. The authors disagree with one another regarding the point at which such polyploidy occurred and on whether subtribes lacking higher numbers, such as the Galinsoginae, share the polyploid ancestry. Numerous examples of aneuploid decrease, secondary polyploidy, and some secondary aneuploid decreases are cited. The Marshalliinae are considered remote from other subtribes and close to the Inuleae. Evidence from related tribes favors an ultimate base of $X = 10$ for the Heliantheae and at least the subfamily Asteroideae.

Contents

Chromosome Numbers in Compositae, XII: Heliantheae

Harold Robinson,
A. Michael Powell,
Robert M. King,
and James F. Weedin

Introduction

The present paper continues a series dealing with chromosome numbers of Compositae (Raven et al., 1960; Raven and Kyhos, 1961; Ornduff et al., 1963, 1967; Payne et al., 1964; Solbrig et al., 1964, 1969, 1972; Anderson et al., 1974; Powell et al., 1974, 1975; King et al., 1976; Tomb et al., 1978) and is the first using a revised and broadened concept of the Heliantheae (Robinson, 1981). Reports are provided for 145 populations including first reports for 33 species and three genera, *Garcilassa, Riencourtia,* and *Helianthopsis* (marked by asterisks in Table 1), and the cytological history of the tribe is discussed.

The new reports in this paper are based on material collected by R. M. King and counted by A. M. Powell and J. F. Weedin. The chromosome counts have been made from acetocarmine or aceto-orceine squashes of microsporocytes in meiosis. Voucher specimens of the King collections are in the U.S. National Herbarium (US),

Harold Robinson and Robert M. King, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. A. Michael Powell and James F. Weedin, Department of Biology, Sul Ross State University, Alpine, Texas 79830.

with a nearly complete set at the Missouri Botanical Garden (MO).

The treatment of the tribe by Robinson (1981), used as the basis for comparison in this paper, recognizes 265 genera containing approximately 2970 species distributed in 35 subtribes. Included are elements that have been considered as separate tribes beginning with the Ambrosiinae followed by the typical Heliantheae in the paleaceous series. The system continues with *Dimeresia,* which is sometimes placed in the Inuleae, the Coreopsidinae and Pectidinae, which have recently been treated as tribes, and the epaleaceous series, which includes many genera from the traditional Senecioneae and most of the Helenieae. The isolated subtribe Marshalliinae is treated last. The tribe therefore is considerably altered from the traditional versions of Bentham and Hooker (1873) and Hoffmann (1890–1894) and from the recent revised treatment by Stuessy (1977), though the latter has proved to be a useful source of data. The tribe is considered somewhat specialized in the family by Robinson (1981), in contrast to the central phyletic position proposed by Cronquist (1955). The morphological, anatomical, and chemical characters that serve as a basis for Robinson's treatment are reviewed in that paper (1981).

TABLE 1.—Chromosome counts, localities, and vouchers for species of Heliantheae (asterisk
(*) = first report)

Species	n	Locality and collection number
Acanthospermum hispidum DC.	11	Bolivia: La Paz, 19 km from Chulumani, K7450
Alloispermum integrifolium (DC.) H. Robins.	16	Guatemala: Chimaltenango, 8 km WNW of Chimaltenango, K7196
* *Alloispermum scabrum* (Lag.) H. Robins.	17–18	Guatemala: Alta Verapaz, 6 km W of San Cristobal Verapaz, K7113
* *Alloisperum scabrum* (Lag.) H. Robins.	ca. 16	Guatemala: Quezaltenango, 20 km of Quezaltenango, K7256
Ambrosia artemisioides (Willd.) Meyen & Walp.	18	Ecuador: Pichincha, 20 km S of Quito, K6615
Baltimora recta L.	12–13+2–4[a]	Guatemala: Escuintla, Escuintla, K7017
Bidens andicola H.B.K.	24	Bolivia: La Paz, 24 km from La Paz, K7411
Bidens andicola H.B.K.	12	Bolivia: La Paz, 30 km from La Paz, K7413
Bidens andicola H.B.K.	12	Bolivia: La Paz, 67 km from Chulumani, K7473
Bidens andicola H.B.K.	12	Bolivia: La Paz, 32 km from La Paz, K7498
Bidens andicola H.B.K.	12	Bolivia: Oruro, 32 km from Oruro, K7518
Bidens andicola H.B.K.	ca. 12[b]	Ecuador: Azuay, 6 km SE of Cumbe, K6694
Bidens andicola H.B.K.	12	Ecuador: Chimborazo, 1 km W of San Juan, K6597
Bidens chiapensis Brandegee	23	Guatemala: Chimaltenango, 17 km N of Tecpan, K7075
Bidens ostruthioides (DC.) Sch.Bip.	12	Guatemala: Baja Verapaz, 3 km NE of Granados, K7086
Bidens pilosa L.	36	Ecuador: Azuay, 3 km E of Paute, K6651
Bidens squarrosa H.B.K.	24	Guatemala: Sacatepequez, 11 km N of Escuintla, K7176
Bidens squarrosa H.B.K.	24	Guatemala: Alta Verapaz, 15 km W of San Cristobal Verapaz, K7344
Bidens sp.	24	Bolivia: Cochabamba, near Parotani, K7572
Bidens sp.	34–36	Bolivia: Cochabamba, 26 km from Tolata, K7601
Clibadium anceps Greenm.	16	Costa Rica: Heredia, 2 km SW of Alto Gallito, K6805
Clibadium armanii Sch.Bip. ex Baker	16	Brasil: Bahia, 12 km from Ilhéus, K8008
Clibadium armanii Sch.Bip. ex Baker	16	Brasil: Distrito Federal, 32 km N of bridge at Asa Norte, K8205
Clibadium armanii Sch.Bip. ex Baker	16	Brasil: Goias, 21 km N of Alto Paraiso, K8286
Clibadium glomeratum Greenm.	16	Costa Rica: Cartago, El Muñeco, K6766
Clibadium glomeratum Greenm.	16	Costa Rica: San Jose, 2–3 km N of Nubes, K6778
* *Clibadium leiocarpum* Steetz in Seem.	16	Costa Rica: San Jose, 16 km W of Santa Ana, K6746
* *Clibadium leiocarpum* Steetz in Seem.	ca. 17	Costa Rica: Cartago, 3 km S of Pacayas, K6831
* *Clibadium microcephalum* Blake	16	Ecuador: Cañar, ca. 40 km E of bridge at Guayaquil, K7735
Clibadium surinamense L.	16	Bolivia: La Paz, 1 km from Chulumani, K7423
Clibadium surinamense L.	16	Bolivia: La Paz, 7 km from Chulumani, K7433
Clibadium surinamense L.	16	Bolivia: La Paz, 3 km from Chulumani, K7440
Clibadium surinamense L.	16	Bolivia: La Paz, 52 km from Chulumani, K7461
Clibadium surinamense L.	16	Bolivia: Cochabamba, 49 km from Colomi, K7701
Clibadium surinamense L.	16–17	Costa Rica: San Jose, 5 km NE of Santiago-Puriscal, K6750
Clibadium surinamense L.	16 + frag.[c]	Ecuador: Cañar, 77 km ESE of Guayaquil, K6871
Clibadium surinamense L.	17–20	Ecuador: Guayas, along road to Naranjal, K7005
Clibadium surinamense L.	16	Ecuador: Loja, 24 km S of Catamayo, K7951
Coreopsis lanceolata L.	13	United States: Maryland, Prince Georges Co., K7389
Coreopsis mutica DC.	28	Guatemala: Solola, 13 km SE of Panajachel, K7231
Coreopsis mutica DC.	28	Guatemala: Alta Verapaz, 5 km WNW of San Cristobal Verapaz, K7338
Cosmos caudatus H.B.K.	ca. 24	Bolivia: La Paz, 19 km from Chulumani, K7453
Cosmos caudatus H.B.K.	24	Ecuador: Guayas, along road to Vinces, K7009

TABLE 1.—Continued

Species	n	Locality and collection number
* Cosmos peucedanthifolius Wedd.	12–14	Bolivia: Cochabamba, 46 km from Challa, K7543
Echinacea tennessensis (Beadle) Small	11	United States: Maryland, Prince Georges Co., cult., K6849
Eclipta alba (L.) Hassk.	11	Costa Rica: Cartago, El Muñeco, K6765
Flaveria bidentis Kuntze	ca. 18	Ecuador: Loja, 16 km W of Catamayo, K6925
* Flourensia heterolepis Blake	ca. 18	Bolivia: Cochabamba, 11 km from Quillacolla, K7559
* Flourensia heterolepis Blake	ca. 18	Bolivia: Cochabamba, 19 km from Tolata, K7585
* Galinsoga mandonii Sch.Bip.	24	Bolivia: La Paz, 1 km from Chulumani, K7419
Galinsoga quadriradiata Ruiz & Pavon	16	Ecuador: Loja, 7 km S of Saraguro, K7830
* Garcilassa rivularis Poepp. & Endl.	17+1[d]	Ecuador: Chimborazo, 35 km NE of El Triunfo, K6954
Helenium mexicanum H.B.K.	12–13	Guatemala: Baja Verapaz, 32 km SE of Salama, K7094
* Helianthopsis hypargyreus (Blake) H. Robins.	17	Ecuador: Tungurahua, 25 km SE of Ambato, K6577
* Helianthopsis hypargyreus (Blake) H. Robins.	9	Ecuador: Azuay, 16 km N of Sigsig, K6646
* Helianthopsis pseudoverbesinoides (Hieron.) H. Robins.	17	Ecuador: Tungurahua, 1 km SE of Ambato, K6533
* Helianthopsis lehmannii (Hieron.) H. Robins.	ca. 17	Ecuador: Chimborazo, 25 km SW of Riobamba, K6970
Hymenoxys robusta (Rusby) K. Parker	15	Bolivia: Oruro, 32 km from Oruro, K7522
Kingianthus paniculatus (Turcz.) H. Robins.	ca. 30	Ecuador: Pichincha, 3 km SW of Chillogallo, K6509
Kingianthus paniculatus (Turcz.) H. Robins.	32–34	Ecuador: Tungurahua, 11 km S of Ambato, K6578
Lasianthaea fruticosa (L.) Becker	ca. 8	Costa Rica: Cartago, 8 km W of Tirro, K6843
Melampodium americanum L.	10	Guatemala: Baja Verapaz, 21 km SW of Granados, K7089
Melampodium paniculatum Gardn.	18	Guatemala: Escuintla, ca. 19 km NW of Escuintla, K7014
Melampodium perfoliatum (Cav.) H.B.K.	11	Costa Rica: San Jose, San Jose, K6745
* Monactis holwayae (Blake) H. Robins.	32 + ca. 6[e]	Ecuador: Azuay, 6 km SE of Cumbe, K6697
Monactis kingii H. Robins.	ca. 32[f]	Ecuador: Cañar, ca. 25 km N of Cañar, K7739
Neurolaena lobata (L.) R. Br.	11	Ecuador: Cañar, 23 km ESE of El Triunfo, K6998
Neurolaena lobata (L.) R. Br.	11	Guatemala: Sacatepequez, 7 km N of Escuintla, K7174
* Oyadaea boliviana Britton	14	Bolivia: La Paz, 23 km from Chulumani, K7455
* Oyadea boliviana Britton	14	Bolivia: La Paz, 52 km from Chulumani, K7464
Parthenium hysterophorus L.	ca. 18	Bolivia: Cochabamba, 11 km from Quillacolla, K7564
* Perymenium gymnolomoides (Less.) DC.	14 or 15	Guatemala: Solola, 16 km S of Chichicastenango, K7065
* Perymenium nicaraguense Blake	15–17	Guatemala: Jalapa, 8 km NE of Jalapa, K7137
Podachaenium eminens (Lag.) Sch.Bip.	18	Costa Rica: Cartago, 8 km W of Tirro, K6842
Podachaenium eminens (Lag.) Sch.Bip.	19	Guatemala: Alta Verapaz, 12 km W of San Cristobal Verapaz, K7119
Podachaenium eminens (Lag.) Sch.Bip.	ca. 19	Guatemala: Suchitepequez, 24 km N of Patubal, K7236
Podachaenium eminens (Lag.) Sch.Bip.	19	Mexico: Oaxaca, Cerro San Filipe, K6445
* Podachaenium skutchii (Blake) H. Robins.	19	Guatemala: Quezaltenango, 20 km S of Quezaltenango, K7257
* Podachaenium skutchii (Blake) H. Robins.	19	Guatemala: Totonicapan, 14 km NE of Totonicapan, K7279
Porophyllum ruderale (Jacq.) Cass.	34–36	Ecuador: Loja, 16 km W of Catamayo, K6927
Porophyllum ruderale (Jacq.) Cass.	22–24	Ecuador: El Oro, 13 km N of Machala, K7976
* Riencourtia tenuifolia Gardn.	ca. 16	Brazil: Goias, 20 km N of Alto Paraiso de Goias, K8808
Schistocarpha eupatorioides (Fenzl) Kuntze	8	Bolivia: La Paz, 8 km from Chulumani, K7436
Schistocarpha eupatorioides (Fenzl) Kuntze	8	Ecuador: Tungurahua, 11 km E of Baños, K6548

TABLE 1.—Continued

Species	n	Locality and collection number
Schistocarpha eupatorioides (Fenzl) Kuntze	8	Ecuador: El Oro, 30 km NE of Machala, K6932
* *Schistocarpha longiligula* Rydberg	8	Guatemala: Alta Verapaz, 3 km ENE of Coban, K7326
* *Schistocarpha paniculata* Klatt	8	Costa Rica: Cartago, 6 km NE of San Rafael de Irazu, K6826
Schkurhia multiflora Hook. & Arn.	12	Bolivia: Cochabamba, 11 km from Quillacolla, K7566
Schkuhria multiflora Hook. & Arn.	12	Bolivia: Cochabamba, 19 km from Cochabamba, K7667
Schkuhria pinnata (Lam.) Kuntze	10	Ecuador: Loja, 16 km W of Catamayo, K6926
Sigesbeckia jorullensis H.B.K.	15	Ecuador: Azuay, 7 km SE of Cumbe, K6707
Simsia dombeyana DC.	17	Ecuador: Guayas, 17 km E of Palestina, K7008
Simsia holwayi Blake	17	Guatemala: Alta Verapaz, 5 km WNW of San Cristobal Verapaz, K7337
* *Smallanthus fruticosa* (Benth.) H. Robins.	29+1	Ecuador: Chimborazo, 25 km SW of Riobamba, K6971
Smallanthus maculatus (Cav.) H. Robins.	ca. 34	Costa Rica: Cartago, slopes of Volcán Irazú, K6810
Smallanthus maculatus (Cav.) H. Robins.	ca. 16	Costa Rica: San Jose, 5 km NE of Santiago-Puriscal, K6749
* *Smallanthus microcephala* (Hieron.) H. Robins	27–30	Ecuador: Azuay, 23 km SW of Girón, K6691
Smallanthus riparius (H.B.K.) H. Robins.	16	Bolivia: La Paz, 1 km from Chulumani, K7423
Spilanthus alba L'Her.	30–35	Guatemala: Jutiapa, N of Asuncion Mita, K7386
Spilanthes alba L'Her.	ca. 39	Ecuador: Cañar, 67 km W of Cañar, K7794
Spilanthes alba L'Her.	ca. 39	Ecuador: El Oro, 5 km W of Piñas, K7970
Spilanthes oppositifolia (Lam.) D'Arcy	ca. 26	Costa Rica: Cartago, El Muñeco, K6769
* *Steiractinia mollis* Blake	14	Ecuador: Chimborazo, 38 km SW of Riobamba, K6973
Tagetes ternifolia H.B.K.	ca. 24	Ecuador: Tungurahua, 39 km SSW of Baños, K6990
Tagetes zypaquirensis H.B.K.	12	Ecuador: Pichincha, 3 km SW of Chillogallo, K6507
Tagetes zypaquirensis H.B.K.	12	Ecuador: Pichincha, 1 km W of Aloag, K6522
Tagetes zypaquirensis H.B.K.	12	Ecuador: Chimborazo, 25 km SW of Riobamba, K6969
Tithonia diversifolia (Hemsl.) A. Gray	17	Costa Rica: Heredia, 2 km N of San Isidro, K6993
Tithonia rotundifolia (Miller) Blake	17	Guatemala: Suchitepequez, 10 km E of Mazatenango, K7243
Tithonia tubaeformis (Jacq.) Cass.	ca. 17	Guatemala: Guatemala, 8 km N of Villa Canales, K7084
Tithonia tubaeformis (Jacq.) Cass.	17	Guatemala: Huehuetenango, 16 km E of Chiantla, K7316
Verbesina apleura Blake	17	Guatemala: San Marcos, 20 km NE of San Marcos, K7039
* *Verbesina boliviana* Klatt	ca. 17	Bolivia: Cochabamba, 11 km from Quillacolla, K7558
* *Verbesina boliviana* Klatt	17	Bolivia: Cochabamba, 11 km from Quillacolla, K7563
* *Verbesina eggersii* Hieron.	17	Ecuador: Guayas, vicinity of Guayaquil Airport, K6944
Verbesina encelioides (Cav.) Benth. & Hook. f.	17	Bolivia: Santa Cruz, Comarapa, K7620
Verbesina gigantea Jacq.	17	Guatemala: Escuintla, 16 km SW of Amatitlan, K7168
Verbesina glabrata Hook. & Arn.	ca. 34	Bolivia: Santa Cruz, 2 km from Comarapa, K7636
* *Verbesina latisquamata* Blake	ca. 34	Ecuador: Cañar, 20 km NW of Azogues, K6884
Verbesina lindenii (Sch.Bip.) Blake	17	Mexico: Hidalgo, Jalapa, K6492
* *Verbesina minuticeps* Blake	17 + 1 frag.	Ecuador: Chimborazo, 12 km NE of Bucay, K6991
* *Verbesina oerstediana* Benth.	ca. 17	Costa Rica: San Jose, 8 km N of Nubes, K6779
* *Verbesina oerstediana* Benth.	15–17	Costa Rica: Cartago, 3 km NE of San Rafael de Irazú, K6819
* *Verbesina pentantha* Blake	34	Ecuador: Loja, 4 km W of Loja, K6923
* *Verbesina pentantha* Blake	34	Ecuador: Loja, 7 km W of Loja, K7882
* *Verbesina semidecurrens* Kuntze	17	Bolivia: Cochabamba, 11 km from Quillacolla, K7561
* *Verbesina semidecurrens* Kuntze	17	Bolivia: Cochabamba, 9 km from Parotani, K7575
* *Verbesina sodiroi* Hieron.	34	Ecuador: Pichincha, 20 km S of Quito, K6514
* *Verbesina sodiroi* Hieron.	34	Ecuador: Chimborazo, 1 km W of San Juan, K6594
Verbesina turbacensis H.B.K.	17	Costa Rica: San Jose, 22 km S of Cartago, K6753

TABLE 1.—Continued

Species	n	Locality and collection number
Verbesina turbacensis H.B.K.	ca. 17	Guatemala: Baja Verapaz, city limits of Purulha, K7100
Viguiera cordata (Hook. & Arn.) D'Arcy	ca. 40	Guatemala: Suchitepequez, 3 km W of Cocales, K7239
Viguiera cordata (Hook. & Arn.) D'Arcy	40	Guatemala: Suchitepequez, 30 km W of Mazatenango, K7248
* *Viguiera lanceolata* Britton	ca. 34	Bolivia: La Paz, 3 km from Chulumani, K7427
* *Viguiera pazensis* Rusby	ca. 34	Bolivia: La Paz, 69 km from Chulumani, K7477
* *Viguiera pazensis* Rusby	ca. 34	Bolivia: Cochabamba, 1 km from Quillacolla, K7552
* *Viguiera procumbens* (Pers.) Blake	ca. 34	Bolivia: Oruro, 20 km from Caracollo, K7526
* *Viguiera procumbens* (Pers.) Blake	ca. 34	Bolivia: Cochabamba, 46 km from Challa, K7542
* *Viguiera procumbens* (Pers.) Blake	17	Bolivia: Cochabamba, 26 km from Tolata, K7602
* *Viguiera rudbeckioides* (H.B.K.) H. Robins.	17 or 18[g]	Ecuador: Loja, 14 km S of Loja, K7862
* *Wedelia grandiflora* Benth.	12	Ecuador: Loja, 18 km N of Vilcabamba, K7870
Wedelia helianthoides H.B.K.	ca. 21	Ecuador: Azuay, 10 km SW of Azogues, K6613
Wedelia helianthoides H.B.K.	ca. 22	Ecuador: Cañar, 7 km SW of Azogues, K6880
Wedelia helianthoides H.B.K.	20–22	Ecuador: Guayas, vicinity of Guayaquil Airport, K6946
* *Wedelia holwayi* Blake	11	Bolivia: Cochabamba, 5 km from Parotani, K7573

[a] 12–13 + 2–4 univalents or supernumery chromosomes.
[b] ca. 12 (possibly $n=11$).
[c] 16 + 2(4)6 fragment.
[d] $17_{II}+1_I$ or $n=18$.
[e] 32 + ca. 6 ghost chromosome or $n+30_{II}+1_{IV}$.
[f] ca. 32 (30–34).
[g] 17 or 18 (probably 17).

It should be emphasized that the revised classification has been used as a basis for organizing the data in the present study, but it is of critical significance only in the discussions of various subtribes. The general conclusions are valid in comparison to any of the modern systems of classification, and one of the major conclusions, acceptance of higher base numbers for most of the subtribes of the Heliantheae, was anticipated by Smith (1975) on the basis of traditional subtribal concepts.

General Considerations

Many genera and subtribes of the Heliantheae show an extreme diversity of chromosome numbers (Tables 2 and 3; Strother, 1977; Stuessy, 1977; Turner and Powell, 1977b). Variation is particularly marked among groups having n less than 10. Stability, where it occurs, is usually found where $n=17–19$. Much diversity in numbers occurs within groups that are obviously closely related, and such diversity of chromosome number is not indicative of phyletic diversity. In contrast, diverse elements of the tribe tend to have uniformity of chromosome numbers at levels of $n=17–19$.

Examination of the Heliantheae seems to indicate that every possible process of karyotype evolution is involved in producing the chromo-

somal variation. As in other groups of plants, the chromosome numbers of the Heliantheae tend to correlate with the habit of the plant. The trend toward reduced DNA content in weedy, short-lived, herbaceous species (Bennett, 1972; King et al., 1976; Solbrig, 1977) is seen in the subtribes Galinsoginae, Dimeresiinae, Madiinae, and Chaenactidinae, among others. In some groups such as the Madiinae, the more herbaceous members of the subtribe in North America have lower chromosome numbers, whereas the more woody members in Hawaii show higher base numbers. The highest base numbers in the tribe are associated with more dendroid elements, such as the Espeletiinae, *Montanoa* of the Montanoinae, and *Podachaenium* of the Ecliptinae.

Polyploidy is apparently the most common evolutionary process in the tribe. Examples include series in the Galinsoginae on a base of $n=8$, *Chaenactis* on a base of $n=6$, many Coreopsidinae and *Pectis* of the Pectidinae on a base of $n=12$, *Spilanthes* (*Acmella*) on base of $n=13$, members of the Ambrosiinae on a base of $n=18$, and species of *Arnica* on a base of $n=19$. Polyploids of *Montanoa* having a base of $n=19$ reach $n=110-120$, the highest count known for the Asteraceae (Funk and Raven, 1980). It is clear that polyploid populations and individuals commonly are produced in the tribe and that they commonly survive.

Aneuploid increase, in contrast to polyploidy, seems to be rare in the Heliantheae. Examples undoubtedly exist, but numbers such as 11 or 12 are not assumed to represent simple increases from $n=9$ or 10 in this survey. Even the example of increase to $n=11$ and 12 from a base of $n=10$ in *Melampodium* (Stuessy, 1979) cannot of considered proven, since that study assumed primitiveness of lower numbers in the tribe (Stuessy, 1977; see also the discussion of Melampodiinae below). There is no detailed evidence on the cytological mechanisms involved, but aneuploid increase should not be any more difficult to produce than some forms of aneuploid decrease. The primary difference must be in the ability of the aneuploid increase to survive and stabilize. Any extra chromosome in an out-crossing plant would tend to

be unpaired and possibly eliminated in a subsequent generation. Most processes that increase chromosome number involve production of superfluous genetic material, and in the absence of other factors, elimination and simplification normally are favored.

Aneuploid decrease is common in the Heliantheae, and a number of unquestionably long series are evident. Either loss of superfluous chromosomes or reduction of centromeres through translocation could easily explain descending series from higher numbers such as $n=18$ exemplified by *Perityle*. Still, examples of reduction in other tribes, as in *Fleischmannia* in the Eupatorieae (Baker, 1967) and *Crepis* in the Lactuceae (Tobgy, 1943), indicate that extreme reductions correlated with annual habit are mostly by rearrangement of chromosome material on fewer centromeres rather than by loss. Such a mechanism seems to occur in the Heliantheae in *Lasthenia* (Ornduff, 1966) and *Pseudobahia* of the Baeriinae, *Sabazia* in the Galinsoginae (Solbrig et al., 1972), *Calycadenia* and *Holocarpha* in the Madiinae (Carlquist, 1959), and in two species of *Chaenactis* in the Chaenactidinae (Raven and Kyhos, 1961). Evidence from polyhaploidy might be an indication that rearrangement of chromosome material on fewer centromeres has occurred in members of the tribe with higher chromosome numbers.

Polyhaploidy may be a more common process than is generally realized. Its discovery depends on demonstrating that the ancestor was a polyploid, and this is usually not evident. When groups show more than one ploidy level, the higher levels ordinarily are considered derivatives of the lower ones. An apparent example in the Heliantheae seems to be the $n=9$ cited for *Flaveria campestris* Johnston (Anderson, 1973) in a subtribe of three genera, which otherwise show $X=18$ consistently. A related process seems to give the $X=8$ and $n=9$ of *Heliomeris* and the $n=9$ in *Helianthopsis hypargyrea* (Blake) H. Robins., both in the subtribe Helianthinae having a base of $X=17$. If our suppositions on the chromosomal history of the tribe are correct, many other lower numbers in the tribe may represent products of polyhaploidy.

Apomixis seems to be comparatively rare in the Heliantheae. The most obvious examples are the generic pair *Monactis-Kingianthus*, with $n =$ ca. 30–34. *Monactis dubia* H.B.K. has been erroneously considered dioicous and has been placed in a separate genus, *Astemma* Less., because of the defective anthers of the type specimen (Robinson, 1976).

Allopolyploidy is sometimes cited as the basis for chromosome variability or the basis for groups having obscure origins in the Heliantheae. In a recent example, Gardner (1977) cites a hybrid between elements of the genus *Lipochaeta* with $X=15$ and $X=26$ and suggests derivation of typical *Lipochaeta* with $X=26$ from a hybrid between elements having $X=11$ and $X=15$ (see also Rabakonandriana and Caro, 1981). Such a mechanism could explain many of the otherwise unexplained chromosome numbers in the tribe. Gardner's suggestion presumes that barriers to hybridization were not complete between plants that had achieved various karyotype differences. In this way, variation in a group, once present, could generate more variation. The process would be accentuated by any general reduction in the effectiveness of isolating mechanisms in the tribe.

Intergeneric hybridization is evident in the tribe. The sterile or nearly sterile natural hybrid cited by Gardner (1977) in his study of *Lipochaeta* was between elements not considered to be congeneric in this paper. Numerous experimental crosses have been attempted by one of the authors (Powell, 1972), and some sterile intergeneric hybrids have been produced. Rare but significant instances of fertile intergeneric hybrids are suspected on the basis of erratically distributed structural features in the Heliantheae (Robinson, 1981). Similar evidence is found in other tribes that have been examined critically, such as the Eupatorieae (Robinson and King, 1977) and the Senecioneae (Robinson and Brettell, 1974).

Chromosome History of the Tribe

The treatment of the Heliantheae in the recent Symposium on the Biology and Chemistry of the Compositae (Steussy, 1977), along with an earlier paper on the subtribe Melampodiinae by the same author (Steussy, 1973), are particularly notable because they most strongly represent the recent trend to give the chromosome number primacy in resolving relationships. This is most evident in the suggested overall phylogeny of the tribe in which Stuessy (1977) says, "The first and largest line is that centering around the Verbesininae with chromosome numbers based on $X=15$, 16, and 17 (and presumptive aneuploid derivatives). The second line is that centering around the Galinsoginae with chromosomal bases of $X=8$ and 9. The third and smallest line is that represented by the Coreopsidinae and its offshoot, the Fitchiinae, with base numbers of $X=12$ and 16." The schematic diagram provided by Stuessy places the Helianthinae in his first group, while the Galinsoginae, which have proved to be closely related, on the basis of anatomy and chemistry (Robinson, 1981), are in the second group. The Verbesininae and Ecliptinae are in Stuessy's first group, but the intimately related Engelmanninae are in the second. The Melampodiinae are placed in the first group although $n=11$ and adjacent numbers are common in the subtribe and although $n=9$, 10, 11, 12, 18, 20, and 23 occur in *Melampodium* itself. The Bahiinae from the Helenieae are included in the second group, although the base numbers are mostly $X=11$ and 12 or higher. As such, Stuessy's proposed phylogeny is internally inconsistent and seems to imply considerable chromosome number stability in a tribe where extreme variability is a most undeniable fact.

In a study of the chromosome numbers of *Coreopsis*, which has implications for the whole tribe, Smith (1975) suggests a generic ancestor with $X=14$ and separate aneuploid reductions to various groups with $n=12$ and 13. Smith further suggests derivation of *Coreopsis* from plants with chromosome numbers one to several aneuploid steps higher than *Coreopsis*. A high base number of $X=17–19$ is suggested for the tribe on the basis of the observations on the Coreopsidinae and the high numbers of other genera such as *Helianthus*,

Verbesina, and *Rudbeckia*. The Smith proposal furnishes a remarkable contrast to the chromosomal history proposed by Stuessy (1977) and runs counter to all previous suggestions of simple derivations of higher numbers in the tribe from lower base numbers.

In spite of the great variability in the chromosome numbers of the Heliantheae, a pattern can be seen when the evidence is fully reviewed. A few groups in the tribe, such as Galinsoginae, Baeriinae, and the *Engelmannia* group of the Ecliptinae, show a conventional pattern of polyploidy, with potential lower base numbers well represented and with higher numbers that can be interpreted directly as polyploids of those numbers. For instance, when $n=18$ occurs, it clearly is derived from a doubling of $X=9$ or a tripling of $X=6$ (in *Chaenactis* of the Chaenactidinae). In most subtribes distributed throughout most of the tribe, however, there are few or no lower chromosome numbers, and what stability there is in the tribe seems to be concentrated at the higher chromosome numbers. Numbers above $X=10$ often form patterns easily interpreted as decreasing aneuploid series. The pattern usually is confirmed when actual relationships of species are known, and such decreasing patterns in the Coreopsidinae led Smith (1975) to postulate a higher base number for the subtribe and tribe. The subtribes with high base numbers predominate throughout the paleaceous and epaleaceous groups of the Heliantheae, with only the isolated Marsallinae unquestionably excluded. Various groups with lower base numbers are few and mostly isolated in the tribe and are subject to conflicting interpretations by the authors of the present paper (see below).

A more complete picture of the nature of higher base numbers can be seen by using the example of other tribes that seem to show similar chromosome number patterns at earlier developmental stages. In the Senecioneae, the senecionoid series retains mostly $X=10$ and $X=20$, with one small group having $n=23$. A decreasing aneuploid series with $n=9$ and 7 is seen in the divergent Blennospermatinae, however, and the cacalioid series with a base of $X=30$ has a decreasing aneuploid series reaching $n=25$ (Robins and Brettell, 1973c, 1974; Nordenstam, 1977). In the Vernonieae, paleotropical species placed in *Vernonia* have bases of $X=10$ and 20 with some reductions to $n=9$, but the Western Hemisphere species have $n=16$, 17, and 18 as a base (Jones, 1977). In the Eupatorieae, the base of $X=10$ is widespread with one apparent increasing series to $n=11$ and 12 and two separate decreasing series to $n=9$. How-

TABLE 2.—Frequency of chromosome numbers in the Heliantheae by genus (chromosome number on horizontal axis, number of genera on vertical axis)
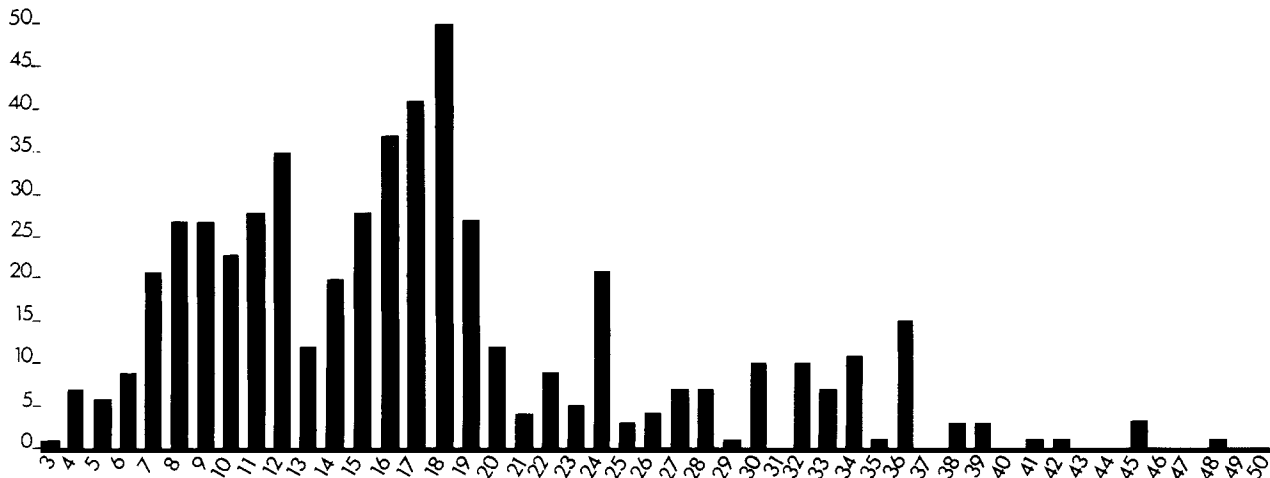
ever, a large element in the tribe seems to have base numbers of 19, 18, or 17 with some reductions to 16 (King et al., 1976). All three of these tribes show that the predominant form of increase is polyploidy and that aneuploid series are mostly decreasing. The latter two tribes show further that elements of the tribes with stabilized higher numbers often have bases less than twice the amount of the original base number. It is not difficult to see the majority of the Heliantheae as elements like those in the Eupatorieae and Vernonieae, which have attained higher numbers through polyploidy and show subsequent aneuploid decrease.

The case for higher base numbers in most subtribes of the Heliantheae seems clear, but the extent to which they share their polyploid ancestry is less obvious. Predominance of subtribes with higher base numbers leads Robinson and King, of the present authors, to consider that all the extant Heliantheae except the Marshalliinae are derived from a single ancestral stock with higher chromosome numbers and that there is a subsequent progression from stable higher numbers to increasingly unstable lower numbers, ending finally in either scattered recurrence of polyploidy or extreme reduction associated with the annual habit. There are a few examples where secondary polyploidy seems to be followed by a secondary aneuploid decrease. In contrast, Powell considers the higher numbers to be derived from a number of separate occurrences of polyploidy, with such subtribes as the Galinsoginae and Baeriinae having lacked polyploid ancestory. The authors agree that, considered in isolation, the internal evidence from the latter two subtribes favors an original base number for them of $X=10$.

Ultimate Base Number of the Tribe

Even with a general acceptance of the higher base number of $X=17-19$ suggested by Smith (1975) for the Heliantheae, there is still the question of the ultimate base number from which the higher number is derived. In a previous paper of this series (Solbrig et al., 1972), a base of $X=8-12$

was suggested for the Heliantheae, and in the review of the tribe by Stuessy (1977) an original $X=8$ or 9 was suggested. Such proposals did not take into account possible higher base numbers for most subtribes of the Heliantheae, and these suggested lower base numbers are given less credence here. Still, these suggestions to some extent were an attempt to bring the Heliantheae into conformity with other tribes of the Asteraceae, and this does seem to be the only profitable approach for a group in which the original base number has been so completely obscured by polyploidy.

A review of the entire family indicates a base number of $X=9$ or $X=10$. It is notable that $n=9$ is the most common number in the family (Solbrig, 1977), and it has been proposed as the base number for the family by Raven (1975). However, other evidence for an $n=9$ base for the family is weak. Examples of the number in older tribes such as the Eupatorieae are easily recognized as reductions from $n=10$, and tribes such as the Astereae and Anthemideae without evidence of a higher base number are highly advanced tribes with extensive evidence of aneuploid decrease. We find that the wide occurrence of $n=18$ offers little support for $X=9$ in view of the already mentioned tendency of higher numbers to stabilize at levels less than double the original base number.

The evidence for $X=10$ is very different. That base in the Vernonieae has been mentioned above, but it is more common in the subfamily Asteroideae, to which the Heliantheae belong. The tribes marked with the greatest stability in chromosome number, the Eupatorieae and Senecioneae, have nearly certain base numbers of $X=10$. The Calenduleae have a probable $X=10$ (Norlindh, 1977), and the Inuleae, which seem closest to the Heliantheae, are partly based on $X=10$. There seems to be no evidence that is convincing for any alternative number. Further supporting evidence from within the Heliantheae is the frequent occurrence of the number $X=19$, which would be more difficult to explain from an original base of X less than 10.

There remains perhaps the most divergent view on tribal and family base numbers to consider, the proposal that genera in various groups with low chromosome numbers evolved at a very early time, essentially to the morphological level as expressed in the genera now, at the basic level of $X=5$ and/or 4 (Turner et al., 1961; Johnston and Turner, 1962; Turner, 1977). The concept derives from the frequent absence of the $n=6$, 7, or 8 in groups having both $n=9$ and numbers of $n=5$ or below. In those examples where the phylogeny is well known, however, the direction of the change seems to be from the higher to the lower numbers. The present evidence does not preclude that there are only four or five basically different chromosomal elements in the ancestral complement of the Heliantheae and the family Asteraceae, which would facilitate reduction to lower numbers, but it does not seem that the ancestral stock of the Asteraceae actually had so few chromosomes.

Review of the Subtribes

The following 32 subtribes are treated in the order given by Robinson (1981). Three subtribes are omitted for lack of chromosome data, the Pinillosinae and Heptanthinae of the Greater Antilles and the Lycapsinae known only from San Felix and San Ambrosio islands off the coast of Chile. Chromosome reports are known for 212 of the approximately 265 recognized genera of the tribe (Table 3), but no attempt is made in the table to indicate the number of species of each genus that have been counted. This information is given in the text for some genera.

AMBROSIINAE.—In the previous paper on the Ambrosiinae (Payne et al., 1964), $X=18$ was regarded as the primitive chromosome number. Since that time, two genera have been transferred into the subtribe by Stuessy (1973). Seven of the eight genera in the subtribe have been reported. All have some counts of $n=18$, and both *Iva* and *Ambrosia* have multiples of that number. Reports of $n=27$ in *Iva* and *Parthenium* might indicate some traces of an original $X=9$, but the latter number apparently is not extant in any of the genera. A

more likely origin for $n=27$ in the subtribe would be hybridization between different ploidy levels of $n=18$. Lower numbers, including the $n=12$ found in two genera, also seem secondarily derived from $X=18$.

Stuessy (1973) hypothesized an *Engelmannia*-like ancestor for the Ambrosiinae, having a base number of $X=9$. *Engelmannia*, which is placed in the Ecliptinae in this treatment, has achene complexes reminiscent of some Ambrosiinae. The Ambrosiinae, along with the Espeletiinae and the Clibadiinae, have an unstriated achene wall that may indicate relationship to the Ecliptinae, and all four subtribes have at least some species with male disk flowers. In determining the base number of the Ambrosiinae, it seems significant that the related subtribes Epeletiinae and Clibadiinae have bases of $X=19$ and $X=16$ respectively, and that more primitive elements of the Ecliptinae, such as *Podachaenium*, have $n=18-19$. The genus *Engelmannia* is regarded here as a more specialized element in the Ecliptinae.

ESPELETIINAE.—This distinctive group of the páramo and subpáramo of northern South America has recently been elevated to subtribal rank (Cuatrecasas, 1976). Seven genera presently are recognized, with chromosome reports for five of them (Powell and King, 1969; Powell and Cuatrecasas 1970, Powell and Powell, 1978). All reports are $n=19$, making the Espeletiinae one of the few subtribes of the Heliantheae without known variation. The recent proliferation of genera is based in part on striking differences in habits of the plants, but the consistent chromosome number and the comparatively recent origin of most páramo habitats would indicate that diversity within the subtribe is of rather recent origin.

Neither structure nor chromosome number seems to link the Espeletiinae with the Melampodiinae in which it has traditionally been placed. Two other genera with arborescent habits and chromosome numbers of $n=19$ are *Montanoa* of the Montanoinae and *Podachaenium* of the Ecliptinae, but other characters indicate that

TABLE 3.—General distribution, habit, and chromosome number of genera of the Heliantheae
(A = annual, B = biennial, P = perennial herb, sS = subshrub, S = shrub, L = liana, T = tree)

Subtribe and genus	General distribution	Habit	Approx. number of species	Chromosome numbers (mostly haploid)
Ambrosiinae Lessing				
Ambrosia	North America, Mexico, Central America, Andes, adventive	A, P	30	12, 17, 18, 36, 54, 62 or 63, 72
Dicoria	sw US, n Mexico	A	4	18
Hymenoclea	sw US, n Mexico	S	3	18
Iva	North America	A, P, sS	19	16, 17, 18, 27, 36
Parthenice	sw US, n Mexico	A	1	18
Parthenium	North America, tropical America, adventive	A, P	16	12, 17, 18, 27, $2n=35_{II}+1_I$
Xanthium	North America, tropical America, adventive	A	2	18
Espeletiinae Cuatr.				
Carramboa	Venezuela	S, T	4	19
Espeletia	n Andes	S	51	19
Espeletiopsis	Colombia, Venezuela	S	24	19
Libanothamnus	Columbia, Venezuela	S, T	13	19
Ruilopezia	Venezuela	S	21	19
Melampodiinae Lessing				
Acanthospermum	tropical and subtropical America adventive	A	6	10, 11, 12, 20
Ichthyothere	Central and South America	P, S	25	16, ca. 33
Lecocarpus	Galapagos	S	3	11
Melampodium	tropical America	A, P	36	9, 10, 11, 12, 18, 20, 23, 25±1, 27, 30, 33
Smallanthus	e North America, Mexico, Central and South America	S, T	20	ca. 15, 16, 17, 18, 27–30, 30
Polymniinae H. Robinson				
Polymnia	e North America	S	2	15
Milleriinae Benth.& Hook				
Guizotia	tropical Africa, cultivated	A, P, S	6	15, ca. 30
Milleria	Mexico, Central and n South America	A, P	2	15
Rumfordia	Mexico, Central America	P, S	6	24
Sigesbeckia	tropical America, Africa, Asia	A	12	10, 12, 15, 30
Trigonospermum	Mexico, Guatemala	A, P	3	15
Desmanthodiinae H. Robinson				
Desmanthodium	Mexico, Central and n. South America	P, S	10	18
Clibadiinae H. Robinson				
Clibadium	tropical America	S	40	16, 17, 17–20, 24, 32
Riencourtia	South America	P	8	ca. 16
Guardiolinae H. Robinson				
Guardiola	Mexico	P	10	12
Enhydrinae H. Robinson				
Enhydra	pantropical	A?	10	11, 15
Montanoinae				
Montanoa	Mexico, Central and n South America	S, T	33	19, 19±1, 57, 76, 110–120

TABLE 3.—Continued

Subtribe and genus	General distribution	Habit	Approx. number of species	Chromosome numbers (mostly haploid)
Rudbeckiinae H. Robinson				
Dracopis	s US	A	1	16
Ratibida	US n Mexico	P	6	13, 14, 16, 17–19, 2n= 27
Rudbeckia	North America	P	15	15, 17, 18, 19, 20, 20–24, 27, ca. 28, 36, 38, 51+
Zaluzaniinae H. Robinson				
Hybridella	Mexico	P	2	16
Zaluzania	Mexico	P, S	12	17, 18
Ecliptinae Lessing				
Aspilia	tropical America, Africa	P, S	60	14, ca. 17, 34±2
Balsamorrhiza	North America	P	14	19, 19+1, 20, 100±2
Baltimora	tropical America	A	2	15
Berlandiera	sw US	P	4	15
Blainvillea	pantropical	A, P	5	8, 17, 39
Borrichia	Gulf of Mexico, West Indies, Peru	S	3	13, 14
Calyptocarpus	s US, Mexico, West Indies, Central and e South America	A	4	12, 35±1, 36
Chrysogonum	e US	P	1	16
Delilia	tropical America	A	2	12
Dugesia	Mexico	P	1	18
Echinacea	e US	P	9	11, 22
Eclipta	pantropical	A	4	9, 10, 11, 22
Eleutheranthera	tropical America, Madagascar	A	2	15–16
Encelia	w US, Mexico, w South America, Argentina	S	15	17, 18
Enceliopsis	w US	P	4	17, 18
Engelmannia	sw US	P	1	9
Flourensia	tropical America	S	30	18
Geraea	sw US, Mexico	A, P	2	18
Helianthella	w US, Mexico	P	8	15
Heliopsis	w US, Mexico, Central America, Andes	P	13	14, ca. 24
Kingianthus	Ecuador	S	2	ca. 30, 32–34, 16?
Lasianthaea	Mexico, Central America	S	4	ca. 8, 10, 11, 11–12
Lindheimera	sw US, Mexico	A	2	8
Lipochaeta	Hawaii	S	5	26
Melanthera	pantropical	P, S, L	20	15
Monactis	Ecuador, Peru	S	10	30±B, 32+c.6
Otopappus	Mexico, Central America, n South America	S, L	9	ca. 15, 16
Oyedaea	Mexico, Central America, Andes	P, S	12	14, 28
Perymenium	Mexico, Central America, n South America	P, S, L, T	26	14–15, 15, 15–17, 16, ca. 30, ca. 45, ca. 86
Philactis	s Mexico, Guatemala	S	4	14, 28, 42
Phoebanthus	s US	P	2	17, 34
Podachaenium	Mexico, Central America	S, T	2	18, 19
Podanthus	Chile, Argentina	S	2	11

TABLE 3.—Continued

Subtribe and genus	General distribution	Habit	Approx. number of species	Chromosome numbers (mostly haploid)
Salmea	Mexico, Central America, West Indies	S, L	7	18, 32–33
Sanvitalia	sw US, Mexico, Central America	A, P	7	8, 9, 11, 16
Silphium	e US	P	23	7
Spilanthes	pantropical	P	60	7?, 12, 13, 16, 26, 39, 41
Steiractinia	n Andes	S	6	14
Synedrella	pantropical	A	2	16, 18, 19, 20, 36
Verbesina	US, tropical America, Africa	P, S	150	16, 17, 18, ca. 30, 34, $2n =$ ca. 88
Wedelia	s US, tropical America, Africa	P, S	60	11, 12, 14, 20–22, ca. 21, 22, 23, 25, ca. 26, 28, 28+1, 29±1, 33, ca. 36
Wollastonia	central and w Pacific	A, P	ca. 20	15
Wulffia	Panama, West Indies, South America	L	4	25, 30, 30±1
Wyethia	w US	P	14	19
Zexmenia	sw US, tropical America	P, S	40	10, 11, 14, ca. 17
Zinnia	sw US, Mexico, Central America, Andes, cultivated	A, P, S	22	10, 11, 12, 20, 21, 22, ca. 24, 42+
Neurolaeninae (Rydb.) Steussy, Turner & Powell				
Brasilia	Brazil	S	1	19
Calea	tropical America	P, S	95	16, ca. 17, 18, 19, ca. 32
Neurolaena	Mexico, Central America, Andes	P, S	9	11
Tetrachyron	Mexico, Guatemala	S	1	16
Unxia	Panama, n South America	A, P, S	3	16
Helianthinae Dumort.				
Aldama	Mexico, Central America, Venezuela	A	1	17
Alvordia	Baja California	S	3	15, 30, 60
Garcilassa	Central America, w South America	A	1	17+1 or 18
Helianthopsis	Andes	S	20	9, 17
Helianthus	North America, cultivated, adventive	A, P	ca. 50	17, 34, 51
Heliomeris	w US, Mexico	A, P	4	8, 9, 16
Iostephane	Mexico	P	2	17, ca. 34
Lagascea	tropical America, adventive	A, P	9	17, 18
Pappobolus	Peru	P, S	4	17
Rhysolepis	Mexico	S	3	17
Scalesia	Galapagos	S	14	34
Sclerocarpus	Mexico, Central America, n South America, Africa	A, P	8	11, 12, 14, 18
Simsia	s US, tropical America	A, P	35	17
Stuessya	Mexico	A, P	3	17
Tithonia	Mexico, Central America, cultivated	A, P, S	10	16, 17

TABLE 3.—Continued

Subtribe and genus	General distribution	Habit	Approx. number of species	Chromosome numbers (mostly haploid)
Viguiera	US, tropical America	A, P, S	160	12, 16, 17, 18, 21, ca. 33, ca. 34, 40±2, 50±2
Galinsoginae Benth. & Hook				
Alloispermum	Mexico, Central and South America	P, S	9	9, 15, 16, 17, or 18, ca. 19, 24, ca. 27, 32
Aphanactis	Central and n South America	A, P	7	8
Bebbia	sw US, Mexico	S	2	9
Cuchumatanea	Guatemala	A	1	8
Cymophora	Mexico	A, P	3–4	8, 9
Galinsoga	tropical America, adventive	A	14	8, 9, 16, 18?, 24, 32
Jaegeria	tropical America	A	8	9, 18, 36
Sabazia	Mexico, Central America, n Andes	A, P	15	4, 8, 9, 16, 24, 36
Schistocarpha	Mexico, Central America, Andes	A, P	16	8
Tetragonotheca	s US, Mexico	P?	4	17
Tridax	Mexico, Central and South America, adventive	A, P	25	9, 10, 18, 27
Dimeresiinae H. Robinson				
Dimeresia	w US	A	1	7
Coreopsidinae Lessing				
Bidens	cosmopolitan	A, P, S	230	10, 11, 12, 17, 18, 23, 24, 34, 36, 38, 73±2
Chrysanthellum	tropical America, Africa	A	10	8
Coreocarpus	sw US, n Mexico	P	10	12
Coreopsis	North and tropical America, Africa, cultivated	A, P, S	114	6, 7, 9, 10, 12, 13, 14, 24, ca. 26, 28, 32, 39, ca. 56
Cosmos	tropical America, cultivated	A, P	26	11, 12, 13, 17, 22, 23, 24, 33, 36
Dahlia	Mexico, Central America, cultivated	A, P	27	16, 17, 18, 32, 36
Dicranocarpus	sw US, Mexico	A	1	10
Glossocardia	India	A	2	12
Glossogyne	se Asia, East Indies, Australia, w Pacific	A	8	12
Henricksonia	Mexico	A, P	1	18
Heterosperma	sw US, tropical America	A	5	9, 11, 13, 24, 25
Hidalgoa	Mexico, Central and n South America	P, L	5	15, 16
Narvalina	West Indies	S	1	60
Thelesperma	w US, Mexico, e South America	P	12	8, 9, 10, 11, 12, 20, 22, 24, 2n=44
Fitchiinae Carlquist				
Fitchia	s Pacific	S, T	6	45
Coulterellinae H. Robinson				
Coulterella	Baja California	S	1	18
Pectidinae Lessing				
Adenophyllum	sw US, Mexico, Central America	S, L	8	13
Chrysactinia	sw US, Mexico	S	4	15
Dyssodia	sw US, Mexico, Central America	A, P	8	7, 13
Hydropectis	Mexico	A	2	9

<div align="center">TABLE 3.—Continued</div>

Subtribe and genus	General distribution	Habit	Approx. number of species	Chromosome numbers (mostly haploid)
Hymenatherum	sw US, Mexico, Central America, West Indies	A, P, S	17	7, 8, 13, 16, 24, 26, 32, $2n=52$
Nicolletia	sw US, Mexico	A, P	3	10
Pectis	sw US, Mexico, West Indies, South America	A, P	ca. 100	12, $2n=36$, 48, 72
Porophyllum	sw US, tropical America	A, P, S	30	11, 12, 15, 22, 24, $2n=36$, 72
Strotheria	n Mexico	sS	1	8
Tagetes	sw US, Mexico, Central and South America	A, P, S	ca. 50	11, 12, 24, $2n=36$
Urbinella	central Mexico	A	1	8
Flaveriinae Lessing				
Flaveria	sw US, Mexico, Central and South America, Australia	A, P	18	18, 9
Haploesthes	sw US, n Mexico	P, S	3	18
Sartwellia	sw US, n Mexico	A, P	4	18
Varillinae Turner and Powell ex H. Robinson				
Varilla	s US, Mexico	S	2	18
Clappiinae H. Robinson				
Clappia	sw US, n Mexico	S	1	16
Pseudoclappia	sw US, n Mexico	S	2	18 ± 1, 18 or 19, 19
Jaumeinae Benth. & Hook.				
Jaumea	w US, s South America	P	2	19
Madiinae Benth. & Hook.				
Achyrachaena	w US	A	1	8
Argyroxiphium	Hawaii	P, S	4	13, 14
Blepharipappus	w US	A	1	8
Blepharizonia	California	A	1	14
Calycadenia	w US, w Mexico	A	11	4, 5, 6, 7, 9
Dubautia	Hawaii	S	26	13, 14
Hemizonia	w US, w Mexico	A, P	31	9, 10, 11, 12, 13, 14
Holocarpha	California	A	1	4, 5, 6
Holozonia	w US	A	1	14
Lagophylla	w US	A, P	5	7
Layia	California, w Mexico	A, P	15	7, 8, 16
Madia	w US, w Mexico, Chile	A, P	18	6, 7, 8, 9, 14, 16, 24
Raillardella	w US	P	5	8, 9, 18
Wilkesia	Hawaii	S	1	ca. 12
Hymenopappinae Rydb.				
Galeana	Mexico, Central America	A	3	9
Hymenopappus	US, Mexico	B, P	10	17, 34
Loxothysanus	Mexico	P, S	2	15, 17?
Villanova	Mexico, Andes	A, P	10	19
Peritylinae Rydb.				
Amauria	w Mexico	P	3	ca. 17, 18
Eutetras	central Mexico	P	1	18
Pericoma	sw US, Mexico	P	1	18
Perityle	w US, Mexico, Peru, Chile	A, P	54	11, 12, 13, 16, 17, 18, 19, ca. 54

TABLE 3.—Continued

Subtribe and genus	General distribution	Habit	Approx. number of species	Chromosome numbers (mostly haploid)
Baeriinae Benth. & Hook.				
Amblyopappus	California, nw Mexico, Peru, Chile	A	1	8
Antheropeas	California	A	5	4, 5
Baeriopsis	Baja California	A	1	8
Eatonella	w US	A, B	1	19
Eriophyllum	w US, British Columbia	A, P	11	4, 5, 6, 7, 8, 15, 16, 24, 32–34
Lasthenia	California	A	16	4, 5, 6, 7, 8, 12, 16, 24
Lembertia	California	A, P	1	10
Monolopia	California	A	4	10
Oxypappus	w Mexico	A	2	10
Pseudobahia	California	A	3	3, 4, 6, 8
Chaenactidinae Rydb.				
Achyropappus	Mexico	A	1	10
Arnica	north temperate zone	P	30	19, ca. 28, ca. 36, ca. 38, 2n=54, 56, 57, 58, 60, ca. 67, 70, ca. 74, 76, 95, ca. 97
Bahia	sw US, Mexico, Guatemala, Chile	A, P	13	8, 10, 11, 12, 24, 36
Bartlettia	sw US, n Mexico	A	1	11
Chaenactis	sw US, nw Mexico	A, P	40	5, 6, 7, 8, 12, 18
Chamaechaenactis	w US	P	1	16
Florestina	Texas, Mexico, Central America	A	7	10, 12
Hulsea	w US, Baja California	A, P	8	19
Hymenothrix	sw US, Mexico	A, B	5	12, 24
Hypericophyllum	tropical Africa	P	7	9
Mallotopus	e Asia	P	1	9
Orochaenactis	California	A	1	9
Palofoxia	s and sw US, n Mexico	A, P	12	10, 11, 12
Peucephyllum	sw US, nw Mexico	S	1	10, 20
Platyschkuhria	w US	P	3	12, 24, 36
Psathyrotopsis	Texas, n Mexico	P	2	19
Schkuhria	sw US, Mexico, Central and w South America, Argentina	A, P	10	10, 11, 12, 20, 21±1
Syntrichopappus	sw US	A	2	6, 7
Venegesia	California, Baja California	P	1	19
Whitneya	California	P	1	19
Gaillardiinae Lessing				
Actinospermum	s US	A, B	3	18
Amblyolepsis	Texas, n Mexico	A	1	18, 19
Baileya	sw US, Mexico	P	4	16, 17
Balduina	s US	B, P	3	18, 36
Dugaldia	sw US, Mexico, Guatemala	P	3	15
Gaillardia	s and w US, Mexico, s South America, cultivated	A, P	29	17, 18, 19, 34
Helenium	US, tropical America	A, P	40	13, 14, 15, 16, 17, 18
Hymenoxys	c and w US, n Mexico, s South America	A, P	25	11, 15
Psathyrotes	w US, nw Mexico	A, B	4	17

TABLE 3.—Continued

Subtribe and genus	General distribution	Habit	Approx. number of species	Chromosome numbers (mostly haploid)
Psilostrophe	sw US, Mexico	P	6	16, 17, 18, 32
Tetraneuris	c and w US, n Mexico	A, P	26	14, 15, 28, 35, ca. 45, 56
Trichoptilium	sw US, w Mexico	A	1	13
Marshalliinae H. Robinson				
Marshallia	e and s US	P	10	9

these are not particularly closely related to the Espeletiinae or to each other.

MELAMPODIINAE.—The subtribe traditionally has contained most of the Heliantheae having functionally male disk flowers. Stuessy (1973, 1977) has successively removed various genera from the group, but the present view reduces the subtribe further to include only five genera. Differences between the remaining genera leave some question about the naturalness of the group, but the genera themselves seem entirely natural. In spite of some variation in chromosome number, a case can be made for a base number of $X=11$ in the three herbaceous genera of the subtribe, with the more woody *Smallanthus* being a remotely related element having $X=16$–17.

The chromosome number in *Melampodium* shows considerable instability. The variation has been discussed by Turner and King (1962) and is reviewed by Stuessy (1971, 1972, 1979). The annual and perennial section *Melampodium* has $X=10$ on the basis of 14 species, the annual section *Zarabellia* has $X=9$ on the basis of four species, the annual section *Serratura* has $X=12$ on the basis of three species, the rhizomatous perennials of section *Rhizomeria* have $X=11$ on the basis of two species, and the annuals of section *Aloina* have $X=11$ on the basis of three species with a few reports of $n=12$. Stuessy (1971, 1979) suggests that section *Melampodium* with $X=10$ is an ancestral type in the genus.

Because *Melampodium* represents the most citable example of presumable aneuploid increase in the tribe, it is worthy of special reconsideration (see page 6). Stuessy's conclusions in his 1971 paper were restated in cladistic form in 1979. On the basis of his earlier treatments of the genus, the characters used include chromosome number, habit, distribution, number of outer involucral bracts, form of bract margin, and presence or lack of a unique type of ovary in the disk flowers. Primitive states are determined in part by comparison with the apparently related genera *Acanthospermum* and *Lecocarpus*. The chromosome numbers are evaluated on a simple distance basis, apparently without considering that aneuploid decrease might be much more likely than increase. Careful study of Stuessy's (1971, 1979) concept shows that it requires three parallel aneuploid increases from 10 to 11 or 12, two in *Melampodium* and one in the *Acanthospermum-Lecocarpus* line, and it requires two parallel origins of the unique undifferentiated ovary of the disk flowers. In our own view, a monophyletic origin of the unique type of ovary is more likely, even at the cost of considering the type of ovary in section *Melampodium* as a limited reversion. Such reversion or de-differentiation is not difficult when it represents a return to a form present in the ray florets of all the species. Our concept would eliminate the need for parallel aneuploid increase at the $n=11$ level. The $n=12$ of section *Serratura* possibly did occur by aneuploid increase.

An anomaly in *Melampodium* not yet explained is the annual habit of most of the species with higher base numbers. The perennial subshrubs seem restricted mostly to two groups apparently specialized into less tropical habitats; section *Rhizomaria* of higher elevations in central and southern Mexico is among those with $X=11$, and section *Melampodium* series *Leucantha* of the southwestern United States and northern Mexico is among those with $X=10$.

Ichthyothere is usually placed adjacent to the genus *Clibadium*, and the two are considered closely related by Stuessy (1977). Robinson (1981) separates the two and places *Ichthyothere* in the Melampodiinae nearer *Smallanthus* on the basis of achene wall structure. The reports of $n=16$ (Turner et al., 1979) and $n =$ ca. 33 in *Ichthyothere* (Coleman, 1970) could correlate with either suggested relative.

POLYMNIINAE.—The one genus of the subtribe has been placed in the Melampodiinae in previous systems, and *Polymnia* has included *Smallanthus* in its synonymy. Achene structure combined with nonpapillose limbs of the rays distinguish *Polymnia* from all members of the Melampodiinae. The $X=15$ of *Polymnia* furnishes a slight but apparently consistent additional difference from *Smallanthus* with $X=16-17$. The similarity between *Polymnia* and the Melampodiinae does not necessarily indicate close relationship. *Unxia*, which has similar characters, and which has species until recently placed in *Melampodium* and *Polymnia*, proves to be a relative of *Calea* in the Neurolaeninae (Robinson, 1980).

MILLERIINAE.—The present concept retains only *Milleria* of the genera traditionally placed in the subtribe. The other genera included here have previously been placed in the Melampodiinae or the Ecliptinae (Verbesininae), depending on the extent to which the disk flowers are bisexual.

One genus, *Guizotia*, has been placed traditionally in the Coreopsidinae, a position first questioned by Robinson and Brettell (1973a) and later by Baagøe (1974). More recently, Stuessy (1977) has returned the genus to the Coreopsidinae, and Baagøe (1977) has concurred. *Guizotia* is one of the two members of the Compositae in which the cytochrome *c* sequence has been studied. The eight amino acid differences between *Guizotia* and *Helianthus* are at least a partial basis for the recent elevation of the Coreopsidinae to tribal rank (Turner and Powell, 1977b). In both anatomy and cytology, however, *Guizotia* is out of place in the Coreopsidinae. There is much better correlation with members of the Milleriinae, but

the genus falls outside of the closely related group formed by the other members of the subtribe.

The variation of chromosome number in *Sigesbeckia* is discussed briefly by Keil and Stuessy (1975), and the predominance of $n=15$ and 30 is emphasized. There are reports of $n=12$ (Subramanyan and Kamble, 1967) and $2n=20$ (Hsu, 1967) for *S. orientalis* L. A base of $X=12$ has also been suggested for the related genus *Rumfordia* (Sanders, 1977).

DESMANTHODIINAE.—One chromosome report is available for one species, *Desmanthodium fruticosum* Greenm. The $n=18$ conforms with the general pattern of high base numbers in the tribe.

CLIBADIINAE.—Chromosome counts are known from about 10 species of *Clibadium*, including three new reports for *C. armanii* Sch. Bip. ex Baker of Brasil, and $X=16$ seems to be the base number of the genus. A previous count of $n=24$ from *C. armanii* (Coleman, 1968) suggests a more basic 8 chromosome complement, but such a count could also result from hybridization between plants with $n=16$ and $n=32$. The latter interpretation is favored by the lack of lower numbers in *Clibadium* and by the derived nature of lower numbers in most subtribes of the Heliantheae.

The closely related *Riencourtia* is reported for the first time in this paper, with $n =$ ca. 16.

GUARDIOLINAE.—The single genus *Guardiola* has usually been placed in the Melampodiinae because of the male disk flowers. Recently, Stuessy (1973, 1977) transferred the genus to the Coreopsidinae, with which it shares a number of characteristics. The chromosome number of $X=12$, based on counts of eight species (Van Faasen, 1973), seems to support this latter placement. Unfortunately, the genus differs from the Coreopsidinae in three of the most definitive features of that subtribe. The fact that $X=12$ is the base number of only specialized elements of the Coreopsidinae, but not the base of that whole subtribe, lessens the value of the number as evidence of close relationship.

ENHYDRINAE.—The subtribe consists of a single genus of specialized aquatics and is obviously the result of morphological reduction. There is a

superficial resemblance to some members of the Ecliptinae where the same chromosome numbers, 11 and 15, are also common, but details of the style and achene indicate there is no close relationship.

MONTANOINAE.—The single genus *Montanoa* has been placed in the broad and poorly defined subtribe Verbesininae that was considered the typical element of the tribe Heliantheae in the traditional systems of Bentham and Hooker (1873) and Hoffmann (1890–1894). The subtribe was interpreted much more narrowly by Stuessy (1977), but continued to include *Montanoa*. Anatomically, the achenes of *Montanoa* are totally distinct from those of the Verbesininae (included here in the Ecliptinae), and they are more like those of the Melampodiinae and Milleriinae. The chromosome number of $X=19$ is based on data from five species and seems stable. Polyploidy in the genus reaches $n=110$–120 (probably $12x$, $n=114$), the highest number reported for the Asteraceae (Funk and Raven, 1980).

RUDBECKIINAE.—The three genera of the subtribe form a closely related group with a probable base number of $X=18$–20. Both *Rudbeckia* and *Ratibida* have a series of numbers that can be interpreted as separate reductions from higher base numbers, but the single species of *Dracopis* seems to represent a derived element with $n=16$. Robinson's (1981) revised classification removes *Echinacea* from this group to the strictly defined Ecliptinae on the basis of anatomy. The transfer is supported by the chromosome numbers $n=11$ and 22 in the latter genus.

ZALUZANIINAE.—There are reports of $n=17$ and 18 for *Zaluzania* and $n=16$ for the recently resegregated *Hybridella* (Olsen, 1977). Emphasis on chromosome number has led Olsen (1979) to equate the $n=17$ of *Z. grayana* B. L. Robinson and Greenm. with the helianthine genus *Viguiera*, but partially fertile rays, a basal flange on the corolla, and details in resin ducts clearly mark the species as a *Zaluzania*. There is no particularly close relationship to the Helianthinae.

ECLIPTINAE.—The subtribe is interpreted here to include the Verbesininae, the Engelmanniinae,

and the Zinniinae. In view of patterns in other subtribes, a higher original base number is suggested here. The element containing *Verbesina*, *Podachaenium*, and the closely related series *Encelia-Enceliopsis-Flourensia-Geraea* reflects this original number, lower numbers not being seen in these genera. *Balsamorrhiza* and *Wyethia*, which also have $n=19$ or 20, represent a temperate element in this basically tropical subtribe. The higher number in the latter genus seems of passing interest in view of the ancestral aspect credited to the genus by Cronquist (1955).

The typical Ecliptinae, including *Calyptocarpus*, *Delilia*, *Eclipta*, *Wedelia*, and *Zexmenia*, seem to have a base number at or near 11 with some redoubling or tripling. The closely related *Synedrella* with $n=16$, 18, 19, and 20 may be the result of secondary polyploidy and subsequent secondary aneuploid loss. *Echinacea* has $X=11$, and both *Zinnia* and *Sanvitalia* seem to have lower base number from 8–12.

Numerous genera show an intermediate base number, such as *Melanthera*, *Steiractinia*, *Otopappus*, *Philactis*, *Helianthella*, *Heliopsis* (Fisher, 1957), *Borrichia* (Semple, 1977), *Perymenium* (Fay, 1978), and *Oyedaea* with $X=14$–16. The counts in *Philactis* and *Heliopsis* tend to confirm the artificial nature of the traditional Zinniinae. The $X=15$ of *Wollastonia* (King, 1964) seems to support removal of the genus from *Wedelia* (Fosberg and Sachet, 1980). *Lipochaeta* of Hawaii has been interpreted to include species related to *Wollastonia* (Gardner, 1977), but the former genus is limited here to the five species in the typical group having $X=26$. Gardner (1977) suggests two possible origins of this number: from a polyploid of $X=15$ with subsequent aneuploid loss from $n=30$ and from polyploidy of a hybrid between plants with $n=15$ and $n=11$.

Spilanthes seems to be on a separate descending series. Keil and Stuessy (1975) claim four base numbers for the genus, but allowing for miscounts and erratics, the counts resolve easily into $X=16$ (*Spilanthes*) and $X=13$ (*Acmella*). *Eleutheranthera*, with $n=15$ and 16, seems closely related to *Blainvillea*, with $n=8$, 17, and 39?, suggesting that the

higher number of the former genus might be a doubling of 8. On the same basis, the specialized temperate group containing *Engelmannia* might represent secondary polyploidy. Stuessy's (1973) suggested chromosomal history of the group might be correct, with *Engelmannia* representing a retained basic $X=9$, *Lindheimera* representing a derived $X=8$, *Chrysogonum* with $X=16$ being a polyploidy of the $X=8$, and *Berlandiera* with $X=15$ being a polyploid with aneuploid loss. Related to this group (Stuessy, 1977) is *Silphium*, with $X=7$. Of the present authors, Robinson and King consider the $X=9$ of *Engelmannia* as derived from much higher numbers, traces of the higher numbers still being evident in the closely related *Wedelia* series.

The Andean genera *Monactis* and *Kingianthus* share high numbers of ca. 30–34. The new counts agree generally with the previous report of $n = $ ca. 30 for *Monactis wurdackii* H. Robins. (Turner et al., 1967, as *Monopholis jelskii* (Heiron.) Blake) and $n=32 + 2$ frag.. in *M. kingii* H. Robins. (as *M. flaverioides* H.B.K., Jansen and Stuessy, 1980). One species of *Monactis* has aborted anthers, and apomixis seems probable in both genera. The two genera form a closely related pair of obscure relationship to other members of the subtribe.

The report by Olsen (1979) of $n=18$ for *Kingianthus paniculata* (Turcz.) H. Robins. (as *Zaluzania sodiroi* Hieron.) conflicts with the present reports for the same species and conflicts with the otherwise consistent counts of ca. 30–34 for the generic pair. The Olsen count does conform with those of the Mexican genus *Zaluzania* of the subtribe Zaluzaniinae, in which Olsen placed the species.

NEUROLAENINAE.—The subtribe contains at least two distinctive elements represented by *Neurolaena* and *Calea*. The two totally different base numbers, based on numerous counts of both genera, reënforce the distinction. Because of trends seen elsewhere in the tribe, the lower numbers are regarded as the result of aneuploid loss from primitive polyploid ancestors. This seems to be confirmed in *Calea* by the lack of lower numbers and in the closely related *Brasilia* with $X=19$

(Turner et al., 1979). The $X=11$ of *Neurolaena* might represent aneuploid gain from $X=10$, but the genus is not so isolated in the subtribe as to suggest such a different history.

Previous treatments have associated both *Neurolaena* and *Calea* more closely with genera now placed in the Galinsoginae. *Neurolaena* has been closely linked with *Schistocarpha*, but basic differences were first suggested by Robinson and Brettell (1973b), and the lack of close relationship has been confirmed since by anatomical and chemical studies (Robinson et al., 1978; Robinson, 1979). The base numbers of the two genera have long been recognized as different, but with the present overview, the $X=8$ of *Schistocarpha* is seen to conform with other Galinsoginae, whereas the $X=11$ of *Neurolaena* is completely foreign to that subtribe.

Confusion in the case of *Calea* has resulted from the previous inclusion of the superficially similar genus *Alloispermum*. Anatomy and chemistry show that the two genera are not closely related (Robinson et al., 1978; Robinson, 1979). In spite of some shared numbers, the chromosome complements of the two genera also are fundamentally different. In *Calea*, $X=18$ and 19 are basic for the genus. In *Alloispermum*, the base is $X=8$ or 9, with $n=16$–18 derived by polyploidy.

Traditionally, *Unxia* has been placed in the subtribe Melampodiinae because of the male disk flowers and the lack of pappus. The genus proves to belong to the Neurolaeninae (Robinson, 1980) and shows the generally high chromosome number characteristic of the subtribe. The count of $n=16$ is based on the more widely distributed annual species *U. camphorata* L. f. The two suffruticose or fruticose Amazonian species, which are structurally more like *Calea*, have not been studied cytologically.

HELIANTHINAE.—The subtribe is considered by Robinson (1981) to be completely natural in the present interpretation, and the base number is obviously $X=17$. A few examples of descending aneuploid series are seen in *Viguiera* and *Sclerocarpus*. Feddema (1971) used the chromosome differences as a partial basis for the resurrection of

Aldama from the synonymy of *Sclerocarpus*. Eliasson (1974) has correctly interpreted the Galapagan genus *Scalesia*, with $X=34$, as being polyploid from $X=17$. There is a single report of $n=18$ in *Lagascea* by Chopde (1965), but all other counts for 10 of the 11 taxa are $n=17$ (Stuessy, 1978). There seems to be a polyploid series based on $X=15$ in *Alvordia*. The $n=17_{II}+11$ or $n=18$ in *Garcilassa* represents the first report for the genus and tends to confirm the position in the Helianthinae given by Robinson (1981).

Two occurrences of lower numbers in the subtribe present a problem of interpretation. They do not seem to represent an original condition in the subtribe, but neither are they connected with an evident aneuploid series. *Heliomeris*, recently resegregated from *Viguiera* by Yates (in herb.), is scarcely distinguishable except by details of the style and the nearly consistent $X=8$ based on counts of five species. One count of $n=9$ is cited by Keil and Pinkava (1976). In *Helianthopsis hypargyrea* (Blake) H. Robins, reports of $n=9$ and $n=17$ in this paper are accompanied by another report of $n=17$ for the closely related *H. pseudoverbesinoides* (Hieron.) H. Robins. The $n=9$ in *Helianthopsis* and the $X=8$ of *Heliomeris* must be interpreted as derived numbers within the subtribe, unless one accepts very unlikely relationships or unlikely parallelisms in chromosome number stabilization. Since the reduction in numbers seems so abrupt, we suggest that polyhaploidy or a closely related process is involved (Raven and Thompson, 1964; Ornduff, 1970; DeWet, 1971; Anderson, 1973). It would seem that the ancestrally polyploid chromosome complement in the Helianthianae is unusually susceptible to abrupt reversions to approximations of the diploid number.

It is notable that Robinson (1981) places the Helianthinae close to the Galinsoginae and Dimeresiinae, two subtribes that show no present evidence of ancestral polyploid numbers. Two of the present authors, Robinson and King, believe the three subtribes all share a polyploid ancestry and probably also share the susceptibility to polyhaploidy or a related process. Powell reserves

judgment, especially on the Galinsoginae. An alternate proposal to that of Robinson and King is possible involving nonpolyploid ancestry for the Galinsoginae and Dimeresiinae and an independent polyploid development in the Helianthinae. Robinson and King believe such an interpretation places considerable weight on a few, mostly isolated subtribes specialized toward annual and short-lived perennial life-forms, and it does not adequately explain the preponderance of polyploidy in all other elements of the tribe Heliantheae.

GALINSOGINAE.—The subtribe as delimited by Robinson (1981) is regarded as natural, and it is one of the few in the tribe showing no relicts of higher base numbers. All higher numbers in the tribe are readily interpreted as polyploids from $X=8$ or $X=9$. As indicated in the previous paper of the series (Solbrig et al., 1972), the count of $n=4$ in *Sabazia* is from a specialized annual species. In *Alloispermum*, the only base number thus far reported is $X=9$ with the derived $n=17-18$ and ca. 27, but $X=8$ is well represented in counts of $n=16$, 24, and 32. There is general agreement on $X=8$ for *Galinsoga*. The $n=18$ reported by Nawaschin (1935) seems out of place, and Canne (1977a) makes the point that she has not seen the voucher. *Tridax* is credited with bases of $X=9$ and 10 by Powell (1965) with polyploids of 9 only.

The most recent of a series of studies of the Mexican genus *Cymophora*, with $n=8$, indicates that it should be kept separate from *Tridax* (Turner and Powell, 1977a), but the difference is based only on one count of one species (Turner et al., 1973). In aspect, *Tridax dubia* Rose, with $n=9$, is closer to *Cymophora*. An attempt by Powell to count the chromosomes of *Tridax venezuelensis* Arist. & Cuatr. (Venezuela: Distrito Federal, *Steyermark & Aristeguieta 122*, VEN, US) gave only approximate results, only three cells with rather sticky chromosomes, bivalents appeared heteromorphic, $2n =$ ca. 18. Canne (1977b) transferred the latter species to *Cymophora*, but the geographic disjunction plus other differences mentioned by Canne suggest a distinct phyletic line is involved.

DIMERESIINAE.—The subtribe consists of a sin-

gle, minute, annual herb from western North America having a chromosome number of $n=7$. *Dimeresia* seems to follow the pattern of annual habit correlating with reduced numbers.

COREOPSIDINAE.—The subtribe has been expanded recently by Stuessy (1977) and, with a few important omissions, the limits are regarded here as natural. The most common chromosome number in the subtribe is $n=12$, and Stuessy seems to regard this as the base number. In a study of the chromosome numbers of *Coreopsis*, which has implications for the whole tribe, Smith (1975) suggests a generic ancestor with $X=14$ and separate aneuploid reductions to various groups with $n=12$ and 13. The reduction series in the typical line includes $X=13, 10, 9, 7$, and 6. Smith suggests ultimate derivation of *Coreopsis* from plants with still higher chromosome numbers one to several aneuploid steps higher than *Coreopsis*. A high base number of $X=17-19$ is suggested for the tribe on the basis of the observations on the Coreopsidinae and the high numbers of other genera such as *Helianthus*, *Verbesina*, and *Rudbeckia*. In support of Smith, it is notable that within the Coreopsidinae higher numbers are characteristic of the distinctive genera *Hidalgoa* with $X=15$ and 16, *Dahlia* with 16, 17, and 18, and *Henricksonia* with $n=18$ (Turner, 1978), forming some of the most divergent elements in the subtribe.

The apparent restriction of $X=12$ to more derived elements of the Coreopsidinae lessens the significance of that number in the distinctive genus *Guardiola* as a basis for including it in the subtribe. Remarks on another omitted genus, *Guizotia*, may be found under the Milleriinae.

FITCHIINAE.—The subtribe contains only the Polynesian genus *Fitchia*. One chromosome count of $n=45$ has been reported for *F. speciosa* Cheesm. (Solbrig et al., 1972). Studies by Carlquist (1957) have shown basic similarities between the genus and the Coreopsidinae. The high number of chromosomes is correlated with an arborescent habit and large pollen. A base number of $X=15$ seems possible.

COULTERELLINAE.—The subtribe contains one species, *Coulterella capitata* Vasey & Rose, of south-

ern Baja California. A count of $n=18$ (Powell, pers. comm.) conforms to the general pattern of high numbers in the tribe.

PECTIDINAE.—Strother (1977), treating the group as a tribe, Tageteae, has provided a schematic diagram of relationships between the genera. The two basic groups are recognized as separate subtribes, Pectidinae with only *Pectis*, and Tagetinae with the remaining genera. In the Tagetinae three groups are recognized. The first, containing *Urbanella*, *Strotheria*, *Hymenatherum*, and *Hydropectis*, is credited with the greatest concentration of advanced characteristics combined with most of the chromosome numbers between $X=7$ and $X=9$. The genera of the second group include *Tagetes*, *Adenopappus*, *Adenophyllum*, *Dyssodia*, *Gymnolaena*, and *Schizotrichia*. These have $X=11-13$, except for *Dyssodia* with $X=7$ and 13. In the remaining group, the more advanced genera include *Porophyllum* with $X=11, 12$, and 15 and *Nicolletia* with $X=10$, while *Chrysactinia*, with $X=15$, is placed near the base. The scheme shows the general pattern seen in many other subtribes where lower numbers seem derived. The highest number, $X=15$, might be derived from lower numbers, but it is in a group of genera in which numbers below $X=10$ are notably absent. Of the present authors, Robinson and King believe the $X=15$ is representative of a more ancestral condition in the subtribe.

Strother (1969), in his treatment of "*Dyssodia*," discusses the apparent dibasic condition of the genus, where there is an enigmatic lack of intermediate numbers. Adjacent $n=8$ and $n=13$ populations of *Hymenatherum pentachaeta* DC. (as *Dyssodia*) are cited. Strother indicates the $n=13$ species in *Adenophyllum* (as *Dyssodia* subg. *Clomenocoma*) are more primitive, whereas the $n=7$ species are advanced. Strother comments further on the taxonomic remoteness of "*Dyssodia*" species with $n=7$ and $n=8$, a fact that makes the $X=4$ hypothesis of Johnston and Turner (1962) difficult to accept. Strother seems to favor low base numbers of $X=4$ and 5, but all extant populations are regarded as complex products of polyploidy and (subsequent?) aneuploidy. Higher numbers such as

$n=16$ and $n=26$ are accepted as the result of secondary polyploidy. Regarding the lack of intermediate numbers, Strother cites the study of *Gilia* (Grant, 1966), where hybrid lines showing a full range of numbers from $2n=36$–56, when selfed for nine generations, showed predisposition to revert to $2n=36$, 38, and 50.

FLAVERIINAE.—The review of structure by Robinson (1981) supports the association of *Flaveria* and *Sartwellia* (Gray, 1852; Rydberg, 1915) and the addition of *Haploesthes* from the Senecioneae (Turner and Johnston, 1961; Powell, 1978). On the basis of many counts, the three genera have a consistent $X=18$ (Turner, 1971, 1975; Powell and Powell, 1978; Powell, 1978). An interesting case of probable polyhaploidy with $n=9$ has been cited for *Flaveria campestris* Johnston (Anderson, 1973).

VARILLINAE.—The single genus *Varilla*, with $X=18$, conforms to the general concept of high basic chromosome numbers in the tribe. Details of structure tend to confirm the close relationship between *Varilla* and the Clappiinae that were parts of the somewhat amorphous subtribe Varilliinae proposed by Turner and Powell (1977b). Other paleaceous genera of the Heliantheae that were mentioned by Turner and Powell are of remote relationship. The paleae of *Varilla* are considered a secondary development from epaleaceous ancestry by Robinson (1981).

CLAPPIINAE.—The two epaleaceous genera *Clappia* and *Pseudoclappia* seem to belong to a larger natural group including the paleaceous genus *Varilla* and the epaleaceous subtribes Flaveriinae and Jaumeinae. The chromosome numbers of all four subtribes are in the general high range found throughout most of the tribe.

Keil and Stuessy (1977) indicate that the proper count for *Pseudoclappia arenaria* Rydb. is probably $n=19$. Powell and Powell (1977) report $n=19$ for *P. watsonii* Powell & Turner, but indicate the need for verification in both species.

JAUMEINAE.—As delimited here, the subtribe contains only one genus with two species. Both of the disjunct species in the genus share $X=19$ (Powell et al., 1975). The genera *Espejoa* and

Hypericophyllum, once included in the synonymy of *Jaumea*, are placed in the Chaenactidinae by Robinson (1981).

MADIINAE.—The subtribe has been well characterized in the past, and chromosome data are comparatively complete (Carlquist, 1959; Clausen et al., 1945). Solbrig et al. (1972) indicate that "the basic number in the Hawaiian Madiinae appears to be $n=14$, while in the Pacific Coast species, the most pervasive number is $X=7$, although $n=8$ and $n=9$ are also frequent." The common occurrence of $n=7$ along with $n=14$ suggests the latter is derived by polyploidy from the former in the subtribe. This impression is heightened by the fact that most occurrences of $n=14$ are in the geologically younger portion of the subtribal range. It is notable that the Hawaiian genera are more woody. The tendency for more shrubby habits in insular members of herbaceous groups is well known. A lesser example of perennial development is seen in a few North American Madiinae on the close offshore islands of California. Increased chromosome numbers are to be expected in such shrubby insular groups.

In spite of evidence from within the subtribe, the general trend in the Heliantheae would indicate derivation of the Madiinae from ancestors with higher numbers. Such continental representatives as *Calycadenia*, *Madia*, and *Raillardella* are interpreted here as aneuploid series from an original number of not less than $X=9$. The continuous series from $X=14$ downward in *Hemizonia* also might include relicts of higher ancestral numbers.

HYMENOPAPPINAE.—The present concept may be artificial, but any artificiality is within narrow limits. The revised alignment introduces no new problems in interpretation of the chromosome data, since the anomalous element, *Galeana* with $n=9$, has traditionally been placed adjacent to *Villanova* with $n=19$. The presence of higher numbers in three of the genera plus the example of other subtribes leads Robinson and King to consider the number in *Galeana* as derived.

PERITYLINAE.—The redelimitation of the subtribe by Robinson (1981) eliminates all elements

lacking distinct petioles and possessing striations on the achene. As such, all genera included by Powell and Turner (1974) with chromosome numbers lower than $X=18$ also are eliminated, except for the obvious declining aneuploid series in *Perityle* (Powell, 1968, 1969).

BAERIINAE.—The subtribe as presented seems to be a natural group. The distribution of chromosome numbers indicates a common ancestor of $X=10$. *Eatonella*, with $X=19$, seems close to *Lembertia* and apparently is derived from a polyploid of $X=10$. The higher numbers in *Lasthenia*, an obviously specialized genus, are also likely to be of polyploid origin (Ornduff, 1966). It is the evidence of related subtribes that causes Robinson and King to believe the $X=10$ is derived, in turn, from higher numbers, rather than being a direct reflection of the original $X=10$ of the subfamily Asteroideae.

CHAENACTIDINAE.—The subtribe is interpreted broadly to include the Bahiinae, although the latter group forms a rather distinctive element within the subtribe. The obviously related subseries *Bahia*, *Florestina*, *Palafoxia*, *Platyschkuhria*, and *Schkuhria* has a rather consistent $X=10–12$. Since aneuploid decrease is more likely, the $X=12$ is presumed to represent the ancestral number of the series. The typical Chaenactidinae have a mixture of higher and lower numbers with the $X=19$ of *Arnica*, *Hulsea*, *Psathyrotopsis*, *Venegesia*, and *Whitneya* representing the primitive condition. The $n=16$ of *Chamaechaenactis* also seems a relict of originally higher numbers. The series of numbers in *Chaenactis*, however, seems to indicate that the $n=18$ in some specimens of *C. douglasii* (Hook.) Hook. & Arn. is of polyploid origin from $X=6$.

The $n=9$ for one species of *Hypericophyllum* (Powell et al., 1975) tends to support its separation from the genus *Jaumea*, with which it has often been placed.

The genus *Arnica*, one of a series of Heliantheae that has been traditionally placed in the Seneci-

oneae, is clearly in this subtribe. The structural, chemical, and cytological reasons for excluding the "Arniceae" from the Senecioneae are summarized by Nordenstam (1977), with a subsequent note of interest by Robins (1977).

GAILLARDIINAE.—The subtribe is closely related to the typical element of the Chaenactidinae, especially to such genera as *Arnica* and *Psathyrotopsis*. In the present group, however, the higher base numbers are more consistently retained. The most obvious reduction series is in the closely knit generic group with *Helenium*, *Hymenoxys*, and *Tetraneuris*. Within *Helenium*, section *Hecubaea* is considered most primitive by Bierner (1972). Both species of the section are now known to have chromosome numbers of $n=17$ (Keil and Stuessy, 1977).

Trichoptilium with $X=13$ is regarded here as a product of a separate reduction series in the relationship of *Psathyrotes* with $X=17$.

MARSHALLIINAE.—There is a single chromosome report for *Marshallia graminifolia* (Walt.) Small with $n=9$ (Jones, 1970).

The genus *Marshallia* traditionally has been placed in the Heliantheae, but recently the position has been questioned, and a position in or near the Eupatorieae has been suggested (Stuessy, 1977; Turner and Powell, 1977b). Robinson (1981) rejects a relationship to the Eupatorieae and cites characters that place the genus definitely in the Heliantheae-Inuleae relationship. The latter position is supported by chemistry (Bohlmann et al., 1979). Robinson retains the genus as a subtribe in the Heliantheae isolated from the rest of the tribe. Improved understanding of the Inuleae may eventually show that *Marshallia* is better accommodated in that tribe. Tails of short to medium length are present on the anthers of some species.

At best, *Marshallia* is isolated from other members of the Heliantheae and probably does not share the ancestry of higher base numbers that is evident in most other subtribes.

Literature Cited

Anderson, L. C.
  1973. *Flaveria campestris* (Asteraceae): A Case of Polyhaploidy or Relic Ancestral Diploidy? *Evolution*, 26: 671–673.
Anderson, L. C., D. W. Kyhos, T. Mosquin, A. M. Powell, and P. H. Raven
  1974. Chromosome Numbers in Compositae, IX: *Haplopappus* and Other Astereae. *American Journal of Botany*, 61:665–671.
Baagøe, J.
  1974. The Genus *Guizotia* Cass. (Compositae): A Taxonomic Revision. *Saertryk af Botanisk Tidsskrift*, 69: 1–39.
  1977. Taxonomical Application of Ligule Microcharacters in Compositae, 1: Anthemideae, Heliantheae, and Tageteae. *Saertryk af Botanisk Tidsskrift*, 71: 193–223.
Baker, H. G.
  1967. The Evolution of Weedy Taxa in the *Eupatorium microstemon* Species Aggregate. *Taxon*, 16:293–300.
Bennett, M. D.
  1972. Nuclear DNA Content and Minimum Generation Time in Herbaceous Plants. *Proceedings of the Royal Society of London*, series B, *Biological Sciences*, 181: 109–135.
Bentham, G., and J. D. Hooker
  1873. Ordo CXXXVIII, Compositae. *Genera Plantarum*, 2(1):163–533, 536–537.
Bierner, M. W.
  1972. Taxonomy of *Helenium* sect. *Tetrodus* and a Conspectus of North American *Helenium* (Compositae). *Brittonia*, 24:331–355.
Bohlmann, F., C. Zdero, R. M. King, and H. Robinson
  1979. New Prenylflavanoids from *Marshallia grandiflora*. *Phytochemistry*, 18:1246, 1247.
Canne, J. M.
  1977a. A Revision of the Genus *Galinsoga* (Compositae: Heliantheae). *Rhodora*, 79:319–389.
  1977b. A New Combination in *Cymophora* (Compositae: Heliantheae; Galinsoginae). *Madroño*, 24:190, 191.
Carlquist, S.
  1957. The Genus *Fitchia* (Compositae). *University of California Publications in Botany*, 29(1):143 pages.
  1959. Studies on Madinae: Anatomy, Cytology, and Evolutionary Relationships. *Aliso*, 4:171–236.
Chopde, V. P.
  1965. Chromosome Numbers in Some Flowering Plants. *Science and Culture*, 31:30.

Clausen, J., D. D. Keck, and W. M. Hiesey
  1945. Experimental Studies on the Nature of Species, II: Plant Evolution through Amphiploidy and Autoploidy with Examples from the Madiinae. *Carnegie Institution of Washington Publication*, 564: 174 pages.
Coleman, J. R.
  1968. Chromosome Numbers in Some Brazilian Compositae. *Rhodora*, 70:228–240.
  1970. Additional Chromosome Numbers in Brazilian Compositae. *Rhodora*, 72:94–99.
Cronquist, A.
  1955. Phylogeny and Taxonomy of the Compositae. *The American Midland Naturalist*, 53:478–511.
Cuatrecasas, J.
  1976. A New Subtribe in the Heliantheae (Compositae): Espeletinae. *Phytologia*, 35:43–61.
DeWet, J.M.J.
  1971. Reversible Tetraploidy As an Evolutionary Mechanism. *Evolution*, 25:545–548.
Eliasson, U.
  1974. Studies in Galapagos Plants, XIV: The Genus *Scalesia* Arn. *Opera Botanica*, 36: 117 pages.
Fay, J. J.
  1978. Revision of *Perymenium* (Asteraceae-Heliantheae) in Mexico and Central America. *Allertonia*, 1:235–296.
Feddema, C.
  1971. Re-establishment of the Genus *Aldama* (Compositae-Heliantheae). *Phytologia*, 21:308–314.
Fisher, T. R.
  1957. Taxonomy of the Genus *Heliopsis* (Compositae). *The Ohio Journal of Science*, 57:171–191.
Fosberg, F. R., and M. H. Sachet
  1980. Systematic Studies of Micronesian Plants. *Smithsonian Contributions to Botany*, 45: 40 pages.
Funk, V. A., and P. H. Raven
  1980. Polyploidy in *Montanoa* Cerv. (Compositae, Heliantheae). *Taxon*, 29:417–419.
Gardner, R. C.
  1977. Chromosome Numbers and Their Systematic Implications in *Lipochaeta* (Compositae: Heliantheae). *American Journal of Botany*, 64:810–813.
Grant, V.
  1966. Selection for Vigor and Fertility in the Progeny of Highly Sterile Hybrids in *Gilia*. *Genetics*, 53:757–775.

Gray, A.
  1852. Plantae Wrightianae. *Smithsonian Contributions to Knowledge*, 3(4): 146 pages.
Hoffman, O.
  1890–1894. Compositae. *In* H.G.A. Engler and K.A.E. Prantl, editors, *Die natürlichen Pflanzenfamilien*, 4(5): 87–391.
Hsu, C. C.
  1967. Preliminary Chromosome Studies on the Vascular Plants of Taiwan (I). *Taiwania*, 13:117–129.
Jansen, R. K., and T. F. Stuessy
  1980. Chromosome Counts of Compositae from Latin America. *American Journal of Botany*, 67:585–594.
Johnston, M. C., and B. L. Turner
  1962. Chromosome Numbers in *Dyssodia* (Compositae: Tageteae) and Phyletic Interpretations. *Rhodora*, 64:2–15.
Jones, S. B., Jr.
  1970. Chromosome Numbers in Compositae. *Bulletin of the Torrey Botanical Club*, 97:168–174.
  1977. Vernonieae: Systematic Review. *In* Heywood, Harborne, and Turner, editors, *The Biology and Chemistry of the Compositae*, chapter 17:503–521. London and New York: Academic Press.
Keil, D. J., and D. J. Pinkava
  1976. Chromosome Counts and Taxonomic Notes for Compositae from the United States and Mexico. *American Journal of Botany*, 63:1393–1403.
Keil, D. J., and T. F. Stuessy
  1975. Chromosome Counts of Compositae from the United States, Mexico, and Guatemala. *Rhodora*, 77:171–195.
  1977. Chromosome Counts of Compositae from Mexico and the United States. *American Journal of Botany*, 64:791–798.
King, R. M.
  1964. Chromosome Numbers of Thailand Compositae. *Phytologia*, 11:217, 218.
King, R. M., D. W. Kyhos, A. M. Powell, R. H. Raven, and H. Robinson
  1976 [1977]. Chromosome Numbers in Compositae, XIII: Eupatorieae. *Annals of the Missouri Botanical Garden*, 63:862–888.
Nawaschin, M.
  1935. [Citation.] *In* G. Tischler, Die Bedeutungen der Polyploidie für die Verbreitung der Angiospermen, erläutert an der Arten Schleswig-Holsteins, mit Ausblicken auf andere Florengebiete. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 67:1–36.
Nordenstam, B.
  1977. Senecioneae and Liabeae: Systematic Review. *In* Heywood, Harborne, and Turner, editors, *The*

Biology and Chemistry of the Compositae, chapter 29: 799–830. London and New York: Academic Press.
Norlindh, T.
  1977. Calenduleae: Systematic Review. *In* Heywood, Harborne, and Turner, editors, *The Biology and Chemistry of the Compositae*, chapter 34:961–987. London and New York: Academic Press.
Olsen, J. S.
  1977. Re-establishment of the Genus *Hybridella* (Asteraceae: Heliantheae). *Madroño*. 24:29–36.
  1979. Systematics of *Zaluzania* (Asteraceae: Heliantheae). *Rhodora*, 81:449–501.
Ornduff, R.
  1966. A Biosystematic Survey of the Goldfield Genus *Lasthenia*. *University of California Publications in Botany*, 40: 92 pages.
  1970. Pathways and Patterns of Evolution: A Discussion. *Taxon*, 19:202–204.
Ornduff, R., T. Mosquin, D. W. Kyhos, and P. H. Raven
  1967. Chromosome Numbers in Compositae, VI: Senecioneae II. *American Journal of Botany*, 54:205–213.
Ornduff, R., P. H. Raven, D. W. Kyhos, and A. R. Kruckeberg
  1963. Chromosome Numbers in Compositae, III: Senecioneae. *American Journal of Botany*, 50:131–139.
Payne, W. W., P. H. Raven, and D. W. Kyhos
  1964. Chromosome Numbers in Compositae, IV: Ambrosieae. *American Journal of Botany*, 51:419–424.
Powell, A. M.
  1965. Taxonomy of *Tridax* (Compositae). *Brittonia*, 17: 47–96.
  1968. Chromosome Numbers in *Perityle* and Related Genera (Peritylinae-Compositae). *American Journal of Botany*, 55:820–828.
  1969. Taxonomy of *Perityle* section *Pappothrix* (Compositae-Peritylinae). *Rhodora*, 71:58–93.
  1972. Artificial Hybridizations in the Subtribe Peritylinae (Compositae-Helenieae). *American Journal of Botany*, 59:760–768.
  1978 [1979]. Systematics of *Flaveria* (Flaveriinae-Asteraceae). *Annals of the Missouri Botanical Garden*, 65: 590–639.
Powell, A. M., and J. Cuatrecasas
  1970. Chromosome Numbers in Compositae: Colombian and Venezuelan Species. *Annals of the Missouri Botanical Garden*, 57:374–379.
Powell, A. M., and R. M. King
  1969. Chromosome Numbers in the Compositae: Colombian Species. *American Journal of Botany*, 56:116–121.
Powell, A. M., and S. A. Powell
  1977. Chromosome Numbers of Gypsophilic Plant Species of the Chihuahuan Desert. *SIDA*, 7:80–90.

1978. Chromosome Numbers in Asteraceae. *Madroño*, 25: 160–169.

Powell, A. M., and B. L. Turner
1974. A Generic Conspectus of the Subtribe Peritylinae (Asteraceae-Helenieae) and Reassessment of Its Tribal Position. *American Journal of Botany*, 61:87–93.

Powell, A. M., D. W. Kyhos, and P. H. Raven
1974. Chromosome Numbers in Composite, X. *American Journal of Botany*, 61:909–913.
1975. Chromosome Numbers in Compositae, XI: Helenieae. *American Journal of Botany*, 62:1100–1103.

Rabakonandriana, E., and G. D. Carr
1981. Intergeneric Hybridization, Induced Polyploidy, and the Origin of the Hawaiian Endemic *Lipochaeta* from *Wedelia* (Compositae). *American Journal of Botany*, 68:206–215.

Raven, P. H.
1975. The Bases of Angiosperm Phylogeny: Cytology. *Annals of the Missouri Botanical Garden*, 62:724–764.

Raven, P. H., and D. W. Kyhos
1961. Chromosome Numbers in Compositae, II: Helenieae. *American Journal of Botany*, 48:842–850.

Raven, P. H., and H. J. Thompson
1964. Haploidy and Angiosperm Evolution. *American Naturalist*, 98:251, 252.

Raven, P. H., O. T. Solbrig, D. W. Kyhos, and R. Snow
1960. Chromosome Numbers in Composite, I: Astereae. *American Journal of Botany*, 47:124–132.

Robins, D. J.
1977. Alkaloids of the Compositae. *Compositae Newsletter*, 5:1–11.

Robinson, H.
1976. Studies in the Heliantheae (Asteraceae), VII: Notes on the Genus *Monactis*. *Phytologia*, 34:33–45.
1979. A Study of the Genus *Schistocarpha* (Heliantheae: Asteraceae). *Smithsonian Contributions to Botany*, 42: 20 pages.
1980. Studies in the Heliantheae (Asteraceae), XXV: A New Species of *Unxia*. *Phytologia*, 46:289–292.
1981. A Revision of the Tribal and Subtribal Limits of the Heliantheae (Asteraceae). *Smithsonian Contributions to Botany*, 51.

Robinson, H., and R. D. Brettell
1973a. Tribal Revisions in the Asteraceae, II: The Relationship of *Trichospira*. *Phytologia*, 25:259–261.
1973b. Tribal Revisions in the Asteraceae, V: The Relationships of *Neurolaena*, *Schistocarpha*, and *Alepidocline*. *Phytologia*, 25:439–445.
1973c. Tribal Revisions in the Asteraceae, IX: The Relationship of *Ischnea*. *Phytologia*, 26:153–158.
1974. Studies in the Senecioneae (Asteraceae), V: The Genera *Psacaliopsis*, *Barkleyanthus*, *Telanthophora*, and *Roldana*. *Phytologia*, 27:402–439.

Robinson, H., and R. M. King
1977. Eupatorieae: Systematic Review. *In* Heywood, Harborne, and Turner, editors, *The Biology and Chemistry of the Compositae*, chapter 15:437–485. London and New York: Academic Press.

Robinson, H., F. Bohlmann, and R. M. King
1978. Chemosystematic Notes on the Asteraceae, I: New Correlations in Subtribes of the Heliantheae. *Phytologia*, 41:50–54.

Rydberg, A.
1915. (Carduales), Carduaceae, Helenieae, Tageteae. *North American Flora*, 34:81–180.

Sanders, R. W.
1977. Taxonomy of *Rumfordia* (Asteraceae). *Systematic Botany*, 2:302–316.

Semple, J. C.
1977. Chromosome Numbers and Karyotypes in *Borrichia* (Compositae). *Systematic Botany*, 2:287–291.

Smith, E. B.
1975. The Chromosome Numbers of North American *Coreopsis* with Phyletic Interpretations. *Botanical Gazette*, 136:78–86.

Solbrig, O. T.
1977. Chromosomal Cytology and Evolution in the Family Compositae. *In* Heywood, Harborne, and Turner, editors, *The Biology and Chemistry of the Compositae*, chapter 9:267–281. London and New York: Academic Press.

Solbrig, O. T., L. C. Anderson, D. W. Kyhos, and P. H. Raven
1969. Chromosome Numbers in Compositae, VII: Astereae III. *American Journal of Botany*, 56:348–353.

Solbrig, O. T., L. C. Anderson, D. W. Kyhos, P. H. Raven, and L. Rudenberg
1964. Chromosome Numbers in Compositae, V: Astereae II. *American Journal of Botany*, 51:513–519.

Solbrig, O. T., D. W. Kyhos, A. M. Powell, and P. H. Raven
1972. Chromosome Numbers in Compositae, VIII: Heliantheae. *American Journal of Botany*, 59:869–878.

Strother, J. L.
1969. Systematics of *Dyssodia* Cavanilles (Compositae: Tageteae). *University of California Publications in Botany*, 48: 88 pages.
1977. Tageteae: Systematic Review. *In* Heywood, Harborne, and Turner, editors, *The Biology and Chemistry of the Compositae*, chapter 27:769–783. London and New York: Academic Press.

Stuessy, T. F.
1971. Chromosome Numbers and Phylogeny in *Melampodium* (Compositae). *American Journal of Botany*, 58: 732–736.
1972. Revision of the Genus *Melampodium* (Compositae: Heliantheae). *Rhodora*, 74:1–70, 160–219.

1973. A Systematic Review of the Subtribe Melampodiinae (Compositae, Heliantheae). *Contributions from the Gray Herbarium*, 203:65–80.

1977. Heliantheae: Systematic Review. *In* Heywood, Harborne, and Turner, editors, *The Biology and Chemistry of the Compositae*, chapter 23:621–671. London and New York: Academic Press.

1978. Revision of *Lagascea* (Compositae, Heliantheae). *Fieldiana: Botany*, 38:75–133.

1979. Cladistics of *Melampodium* (Compositae). *Taxon*, 28:179–195.

Subramanyan, K., and N. P. Kamble

1967. [Citation.] *In* IOPB Chromosome Number Reports, XII. *Taxon*, 16:350.

Tobgy, H. A.

1943. A Cytological Study of *Crepsis fuliginosa, C. neglecta*, and Their F₁ Hybrids and Its Bearing on the Mechanism of Its Phylogenetic Reduction in Chromosome Number. *Journal of Genetics*, 45:67–111.

Tomb, A. S., K. L. Chambers, D. W. Kyhos, A. M. Powell, and P. H. Raven

1978. Chromosome Numbers in the Compositae, XIV: Lactuceae. *American Journal of Botany*, 65:717–721.

Turner, B. L.

1971. Taxonomy of *Sartwellia* (Compositae Helenieae). *SIDA*, 4:265–273.

1975. Taxonomy of *Haploesthes* (Asteraceae-Senecioneae). *Wrightia*, 5:108–115.

1977. Summary of the Biology of the Compositae. *In* Heywood, Harborne, and Turner, editors, *The Biology and Chemistry of the Compositae*, chapter 42:

1105–1118. London and New York: Academic Press.

1978. [Citation.] *In* IOPB Chromosome Number Reports, LXII. *Taxon*, 27:533.

Turner, B. L., and M. C. Johnston

1961. Chromosome Numbers in the Compositae, III: Certain Mexican Species. *Brittonia*, 13:64–69.

Turner, B. L., and R. M. King

1962. A Cytotaxonomic Survey of *Melampodium* (Compositae-Heliantheae). *American Journal of Botany*, 49:263–269.

Turner, B. L., and A. M. Powell

1977a. Taxonomy of the Genus *Cymophora* (Asteraceae: Heliantheae). *Madroño*, 24:1–6.

1977b. Helenieae: Systematic Review. *In* Heywood, Harborne, and Turner, editors, *The Biology and Chemistry of the Compositae*, chapter 25:699–737. London and New York: Academic Press.

Turner, B. L., W. L. Ellison, and R. M. King

1961. Chromosome Numbers in the Compositae, IV: North American Species, with Phyletic Interpretations. *American Journal of Botany*, 48:216–223.

Turner, B. L., A. M. Powell, and J. Cutrecasas

1967. Chromosome Numbers in Compositae, XI: Peruvian Species. *Annals of the Missouri Botanical Garden*, 54:172–177.

Turner, B. L., A. M. Powell, and T. J. Watson, Jr.

1973. Chromosome Numbers in Mexican Asteraceae. *American Journal of Botany*, 60:592–596.

Turner, B. L., J. Bacon, L. Urbatsch, and B. Simpson

1979. Chromosome Numbers in South American Compositae. *American Journal of Botany*, 66:173–178.

Van Fassen, P.

1973. [Citation.] *In* IOPB Chromosome Number Reports, XL. *Taxon*, 22:291.