

TAXONOMIC STUDY OF CHRYSANTHELLUM (ASTERACEAE,
COREOPSIDEAE)

B. L. Turner

Department of Botany, University of Texas, Austin, TX,
78713, U.S.A.

ABSTRACT

An inclusive systematic study of Chrysanthellum is rendered. Eleven species are recognized: C. indicum, a highly variable, pantropical, weed with 3 continental varieties (var. indicum, Asia; var. afroamericanum, South America and Africa; var. mexicanum, North America) and var. madagascarense from Madagascar; C. americanum, largely restricted to the Caribbean Islands; C. pusillum, endemic to the Galapagos Islands; and 8, mostly localized, species confined to the mainland of tropical and subtropical North America. The species are all characterized by their herbaceous habit, alternate leaves, Kranz syndrome and linear, persistent, pales. Chrysanthellum is believed to be most closely related to Eryngiophyllum, a genus of only 2 closely related species endemic to Mexico. Several species are illustrated, diagrams showing relationships are presented, distribution maps for each taxon are portrayed and a new species, C. keilii, is proposed. Relationships of both Chrysanthellum and Eryngiophyllum to the Malasian genus, Neuractis are discussed.

Chrysanthellum is a genus belonging to the tribe Coreopsideae of the Asteraceae. It relates to a group of genera with alternate leaves which show the Kranz syndrome (Smith and Turner, 1975), and does not appear especially close to the large genera Bidens and Coreopsis with which it is often associated.

The type species of the genus, C. americanum, was described by Linnaeus in 1753 in his Species Plantarum from material obtained in the Caribbean Islands, but he placed this in the genus Anthemis. This species was subsequently (1807) positioned by Richards, along with C. procumbens, in its own genus, Chrysanthellum. The latter species, in time, proved synonymous with C. americanum and, until recently, only a few additional species were added, most of these relating to the widespread weedy species, C. indicum, which was first described by De Candolle in 1836. Indeed, in spite of the fact that 10 of the 11 species recognized in the present treatment occur in North America (the one exception, C. pusillum from the Galapagos Islands), Alexander (1955), in his

treatment for the North American Flora, recognized, or was familiar with, but two of these, C. americanum and C. indicum.

Mexico is especially rich in *Chrysanthellum* taxa, 10 of the 11 species are known to occur there. Steetz (1853) described the first mainland species for North America, C. integrifolium; this was followed by Greenman (1903) who added C. mexicanum (reduced to a variety of C. indicum by Turner); P.G. Wilson (1962) added C. involutum; McVaugh (1972) added C. filiforme; Strother (1976) added C. pilzii; and I have added the remainder of those recognized in the present paper.

At the present time I recognize 11 species in the genus: 1) a widespread pantropical weed, C. indicum, with 4 regional varieties; 2) C. americanum, itself a highly variable weedy taxon, largely confined to the Caribbean Islands, and much-confused with C. indicum; 3) C. pusillum, an endemic of the Galapagos Islands; the remaining 8 species are native to the mainland of North America, mostly narrow endemics of the Pacific slopes of Mexico.

CHROMOSOME COUNTS

Chromosome counts are available for only 6 of the 11 species of *Chrysanthellum* as follows

<u>Species</u>	<u>Count (n)</u>	<u>Reference or Voucher</u>
<u>C. indicum</u> var.		
<u>afroamericanum</u>	8	Olorode (1974; reported as <u>C. americanum</u>)
"	8	Turner et al. (1979)
"	8	Renard et al. (1983)
<u>C. indicum</u> var.	8	De Jong & Longpre (1963);
<u>mexicanum</u>	8	Powell & Turner (1963);
"	8	Keil & Stuessy (1975)
<u>C. keilii</u>	8	Keil 15222 (TEX)
<u>C. michoacanum</u>	ca 9,9	Keil 15327 (TEX)
<u>C. pilzii</u>	12	Strother 1094 (type)
<u>C. pusillum</u>	8	(Turner, unpubl.)

C. tamaulipense

8

Strother (1972);
reported as C.
involutum.

With the exceptions noted below, chromosome numbers have been obtained mostly from meiotic material with clear counts of $n=8$ pairs (which is the same as $2n=8$ pairs of authors). Chrysanthellum michoacanum has been reported to have $n=9$ pairs, but the camera lucida drawings documenting this number (attached to the voucher, TEX!) do not appear unequivocal and it is possible that the number is $n=8$ pairs, with univalents (or chromosomal fragments). Counts of $n=12$ pairs for C. pilzii appear to be unequivocal, this representing a fertile triploid on a base of $x=8$ or perhaps a tetraploid on a base of $x=4$.

GENERIC RELATIONSHIPS

Eryngiophyllum, a poorly known genus of only 2 species from the Pacific slopes of Mexico, is the closest relative of Chrysanthellum. Both have alternate leaves and show the Kranz syndrome and are distinguished largely by habitual features: Chrysanthellum is a tap-rooted annual or short-lived perennial with mostly cauline leaves whilst Eryngiophyllum is a rosette-forming, strongly perennial, herb with a woody, corm-like, tap root. Indeed, the 2 genera are so alike as to vegetative and floral features that I am inclined to combine the two, but have retained them pending chromosomal and chemical studies.

Past Eryngiophyllum one must look to South American genera (e.g., Isostigma, a largely Brazilian genus with alternate leaves and the Kranz syndrome) or perhaps to Neuractis, a small Malasian genus which Backer (1913) transferred to Chrysanthellum, and which was retained by Backer (1965) in his treatment of the Asteraceae of Java, a view rejected in the present paper, but one that speaks to the remote relationships of both Chrysanthellum and Eryngiophyllum.

SPECIES RELATIONSHIPS

Relationships among the 11 species recognized in the present paper are believed to be close. Three of these, C. americanum, C. indicum and C. pusillum, are especially close and can be recognized by their 2-nerved small ray ligules; the remaining 8 possess 4-8 nerved ligules and are more diverse. I have shown their hypothetical relationships in three diagrams: Fig. 1A., a "seat-of-the-pants" construct based on my intuitive "feel" of the

TABLE 1. Character states used in cladogram.

<u>Characters</u> (1)	<u>primitive</u> (0)	<u>advanced</u>
Gynecium		
1. Disk achenes	fertile	sterile
2. Ray achenes	straight	circinate
3. Ray achenes	unornamented	ornamented
4. Disk achenes	w/o wings	winged
5. Style branches of disk florets	unfused	fused
6. Achenes	monomorphic	dimorphic
7. Achene body	w/o neck	w neck
8. Pappus	present	absent
Androecium		
9. Anther appendages	well-developed	reduced
Corolla		
10. Ligules of ray	4-8 nerved	2-3 nerved
11. Disk color	all yellow	not so
12. Disk lobes	5-lobed	4-lobed
13. Ray ligules	yellow	cyanogenic
14. Ray ligules bifid	3-lobed	entire or
Involucre		
15. Bracts	present	absent
Leaves		
16. Shape	simple	dissected
17. Spinulose	not	yes
Habit		
18. Stems	erect	prostrate
19. Duration	perennial	annual
Other		
20. Chaff	well-developed	poorly dev.
21. Roots	tap-rooted	woody-crown
22. Phyllotaxy	alternate	subopposite
23. Ray floret no.	5-32	2-4
24. Achenes curled	adaxilly	abaxilly

Table 2. Character States used in Cladistic Analysis.

Species	Character States (from table 1)																								Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Chrysanthellum</i>	0	0	0	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	8
<i>indicum</i> ind.	0	0	0	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	8
<i>indicum</i> mex.	0	0	1	1	1	0	1	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	10
<i>indicum</i> aff.	0	0	1	1	1	0	1	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	10
<i>pusillum</i>	0	0	0	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	8
<i>americanum</i>	0	0	0	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	8
<i>perennans</i>	1	?	?	1	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	?	7	
<i>tamaulipense</i>	0	1	0	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	8
<i>keilii</i>	0	1	0	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	8
<i>involutum</i>	1	1	1	-	0	1	0	0	0	0	1	0	1	0	1	0	1	0	0	1	0	0	1	0	11
<i>pilzii</i>	1	0	0	-	1	-	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	8
<i>integrifolium</i>	1	0	0	-	1	-	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	8
<i>michoacanum</i>	1	0	0	-	1	-	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	8
<i>filiforme</i>	1	0	0	-	1	-	0	1	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	7
<i>Eryngiophyllum</i>																									
<i>pinnatisectum</i>	1	0	0	-	0	-	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	6
<i>rosei</i>	0	0	0	1	-	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	5
<i>Neuractis</i>																									
<i>leschenaultii</i>	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	1	0	0	1	0	0	0	0	7
<i>smithii</i>	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	0	1	0	0	1	0	8

? = character state unknown (immature)

0 = primitive

- = character absent

1 = advanced

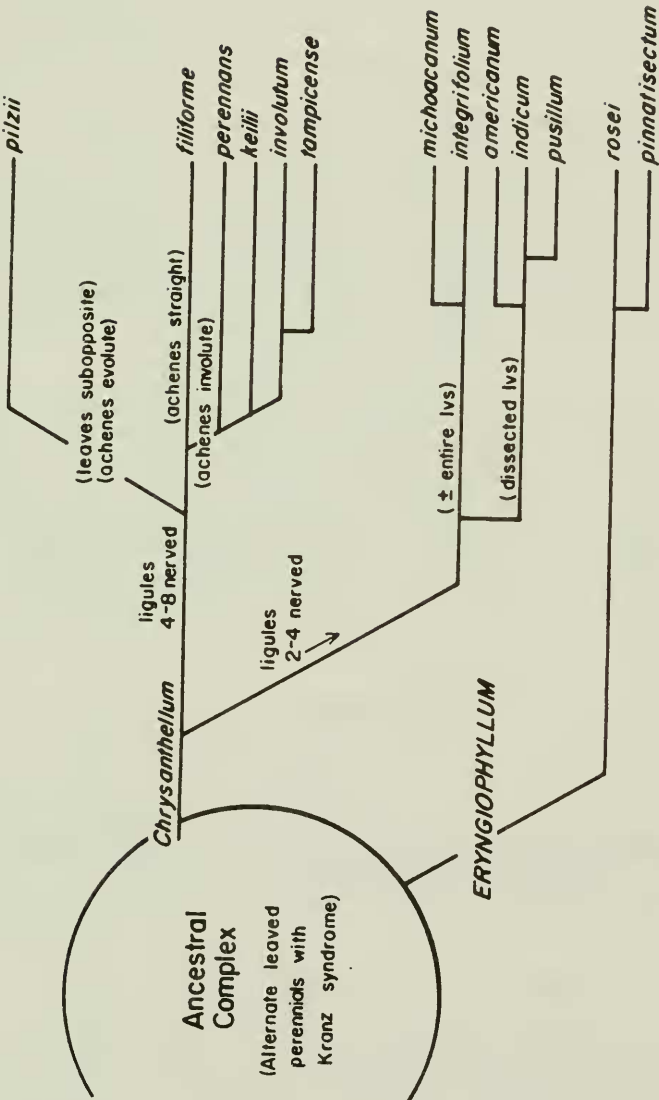


Fig. 1A. Hypothetical relationships of *Chrysanthellum* spp. (seat-of-the-pants-method)

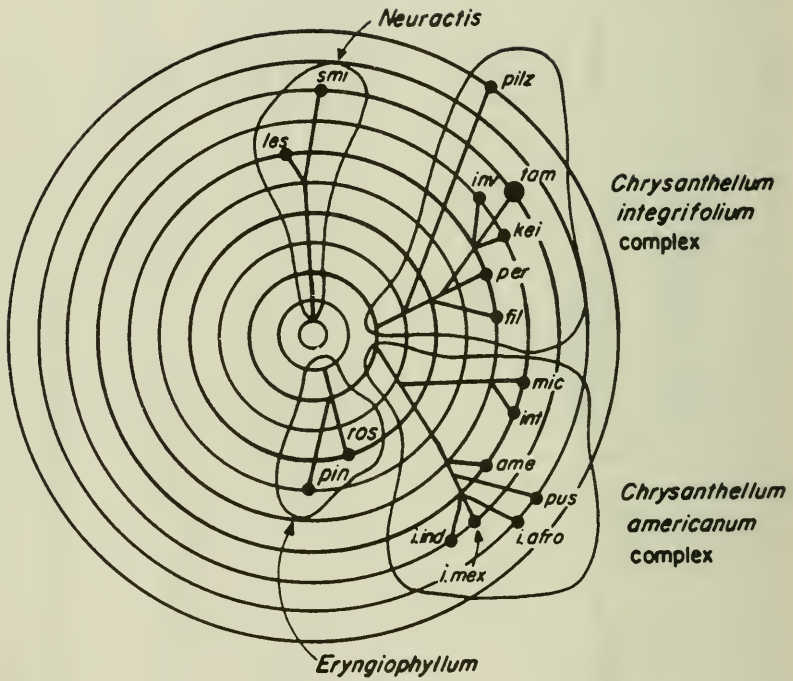


Fig. I.B. Hypothetical Relationships of *Chrysanthellum* spp. arranged in a Wagner-type diagram.

group based on my 40 or more years familiarity with character variability and species-relationships in the Asteraceae. Fig. 1B., a Wagner-type diagram based upon the characters shown in Table 1, the species arranged subjectively in concentric circles according to their additive positions; and 1c, a more formal cladistic analysis using the character states shown in Table 1.

Figures 1A and 1B suggest that within *Chrysanthellum* two phyletic lines exist, a group having ray ligules mostly reduced with 2-3 nerves centering about *C. americanum*, and a group having well-developed ligules with 4-8 nerves centering around *C. perennans*. The latter taxon, in particular, is believed to have retained characters which approach *Eryngiophyllum*, namely a perennial, rosulate habit, while *C. pilzii* with its subopposite leaves, evolute, ornate, disk achenes, and prostrate habit is believed to be the most advanced.

A parsimony analysis (PAUP, David Swofford, 198x) of the data presented in Table 2 resulted in 137 equal-length trees of 40 steps each. Figure 1C represents a strict consensus tree derived from 100 of these. *Chrysanthellum* is united as a monophyletic lineage by synapomorphies in characters 11 (1->0), 14 (0->1), and 15 (1->0). *Neuractis smithii* and *N. leschenaultii* are linked as sister taxa by synapomorphies in characters 8 (1->0), 9 (0->1), and 21 (1->0). The two species *Eryngiophyllum* lack a character in this data set to unite them as sister taxa.

ACKNOWLEDGEMENTS

This study is based upon the examination of approximately 840 sheets from the following herbaria (number of specimens shown in parenthesis): F (63), GH (96), GOT (1), K (127), LL (60), LP (42), MICH (44), MO (97), NY (106), TEX (66), UC (37), UNAM (15), US (84). I am grateful to the Directors for loan of materials. Linda Vorobik provided the illustrations and K. Nixon and G. Nesom helped with the cladistic analysis. Dr. J. Mears collected buds for the chromosome count of *C. pusillum*.

CHRYSANTHELLUM Rich. ex Persoon

Annual or rarely perennial prostrate to erect mostly glabrous herbs. Leaves predominantly alternate (superficially opposite in *C. pilzii*), simple to bipinnatisect. Heads terminal or axillary, heterogamous, radiate. Involucre 2-seriate, bracteate. Receptacle plane to convex, with membranous, persistent linear

florets fertile or functionally staminate throughout. Ray corollas pistillate, fertile, mostly yellow, 2-8 nervate. Disk corollas 4-5 lobate with well-marked tube and limb; often of 2 types, an outer, mostly yellow, series ca 1/2 the size of the inner florets, the latter usually with brown or reddish-brown, corollas. Anthers small, the appendages well-developed and acute. Style branches of ray florets filiform, acute, those of the disk well-developed with penicillate appendages 2-3 times the lengths of the stigmatic lines when fertile, or fused and merely bifid when sterile. Achenes dimorphic, those of the ray mostly clavate, epappose, unwinged, straight or variously recurved or coiled; disk achenes, when present, flattened, prominently winged, epappose or very rarely with 2 deciduous awns. Base chromosome number, $x=8$ or possibly $x=4$.

Type species. Chrysanthellum americanum (L.) Vatke

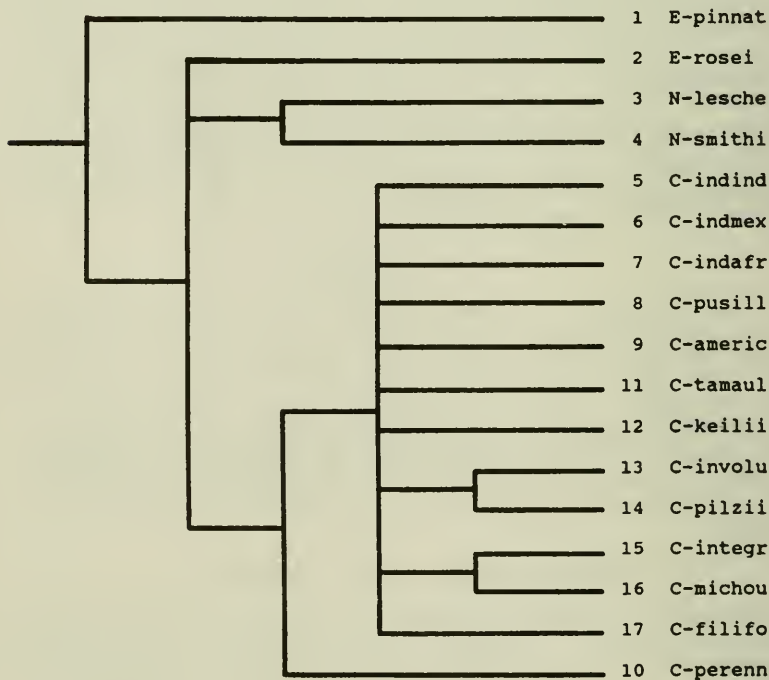


Fig. 1C. Cladistic analysis of Chrysanthellum, as discussed in text.

KEY TO SPECIES

- A. Ligule of ray florets with 2(3) well-developed veins (B)
- A. Ligule of ray floret with 4-8 rather equally well-developed veins (F)
- B. Ligules of the ray quite pronounced, 6-15 mm long; leaves simple, ovate to oblanceolate, toothed or rarely tri-lobed, but never pinnatisect with narrow divisions (C)
- B. Ligules of the ray short, inconspicuous, 1-5(6) mm long; leaves pinnately or ternately dissected, the divisions linear, 0.5-8.0 mm wide (D)
- C. Disk corollas brownish-black..... 1. *C. michoacanum*
- C. Disk corollas yellow.....2. *C. integrifolium*
- D. Involucres 2.0-3.0 mm long; plants of Galapagos Islands..
..... 3. *C. pusillum*
- D. Involucres (2.5)3.0-6.0 mm long; plants elsewhere (E)
- E. Leaves simple to variously lobed or dissected, the divisions broad, 2-8 mm wide; stems prostrate; ligules (3)4-5(6) mm long..... 4. *C. americanum*
- E. Leaves bi- or tripinnately dissected, the divisions narrow, mostly 1-2 mm wide; stems mostly erect (rarely prostrate); ligules 1-3 mm long..... 5. *C. indicum*
- F. Ray achenes straight or nearly so; disk florets "sterile"
.....6. *C. filiforme*
- F. Ray achenes circinate, incurved, outcurved, or coiled; disk florets fertile or "sterile" (G)
- G. Perennials; leaves tripartite with only occasional lobing; head single on an elongate peduncle from a basal rosette
..... 8. *C. perennans*
- G. Annuals; leaves variously bipinnatifid; heads several, not borne singly from a basal rosette (H)
- H. Leaves, especially the petioles, conspicuously pubescent with long, multicellular hairs; achenes outcurved at maturity, the inner surface markedly spiny-tuberculate..... 9. *C. pilzii*
- H. Leaves glabrous or nearly so; achenes incurved at maturity, the inner (adaxial) surface smooth or nearly so (I)
- I. Disk florets completely "sterile"; lower-most leaves tripinnatisect (parsley-like)..... 10. *C. involutum*
- I. Disk florets mostly fertile; lower-most leaves bipinnatisect (J)
- J. Achenes of the ray florets merely recurved ; disk florets brown or brownish-red..... 7. *C. keilii*
- J. Achenes of the ray florets circinate; disk florets yellow.
..... 11. *C. tamaulipense*

1. CHRYSANTHELLUM MICHOCANUM B. Turner, *Phytologia* 51: 292. 1982. Fig. 2.

TYPE: MEXICO. Michoacan: 11-13 km WSW of Apatzingan, along the road to Dos Aguas and Aguililla, ca. 300 m, 5-9 Sep 1972, J. V. A. Dieterle 4246 (holotype TEX!; isotype MICH!).

Annual, glabrous, prostrate, succulent herbs with stems up to 40 cm long. Leaves finely denticulate to coarsely toothed, rarely trilobed or lyrate, up to 15 cm long (basal leaves); blades of rosette leaves, when simple, narrowly oval, broadest at the middle; mid-stem leaves usually with ovate blades (rarely obovate), broadest below the middle. Peduncles 8-14 cm long at maturity, swollen just below the head. Heads 10-20 mm across, ca. 10 mm high, subtended by 5 acuminate bracts, 3-5 mm long; involucre as in C. integrifolium except for the more narrowly ovate bracts, 5-7 mm long, 2-3 mm wide. Receptacle convex, the pales lanceolate, ca. 1/2 as long as the disk florets. Ray florets ca. 32, "orange-yellow"; ligules bidentate, (6)8-10 mm long, 1.0-1.5 mm wide, 2-nerved. Disk florets 2-34, "sterile", the smaller, outer-florets, yellowish-brown, with corollas 3-4 mm long, the larger, inner florets "brownish-red" or "dark brown", 3-8 in number at anthesis and nearly twice the size of the outer florets. Ray achenes clavate, 3-4 mm long, prominently 8-10 grooved or markedly 8-ridged at maturity.

Chromosome number, $2n = 9II$ (Keil 15237).

DISTRIBUTION (Fig. 6): Only a few collection sites are known, all near Apatzingan (Hinton et al. 12058, GH, NY, US; Keil 15237, ASU, ENCB, MEXU, TEX; McVaugh 17907, MICH). The plants reportedly occur in thorn forest, in open areas, and along roadsides. Flowering, Aug-Sep.

The Keil collections, cited above, are noteworthy for their smaller heads and ray florets, approaching those of C. integrifolium. But in other characters they are typical of C. michoacanum.

Chrysanthellum michoacanum can be readily distinguished from C. integrifolium by its leaves, larger heads with longer ray florets, shorter pales and, most notably, by the brownish-red disk florets, some of these (3-8) becoming much darker and nearly twice the size of the outer disk florets, which are presumably at the same or later stage of development. Florets of the latter type were not observed in the dry heads of C. integrifolium and its expression must reflect adaptation to particular pollinators since both floret-types seem to be functionally staminate or "sterile".

2. CHRYSANTHELLUM INTEGRIFOLIUM Steetz, in Seem., *Bot. Voy. Herald* 160. 1853. TYPE: PANAMA: In savannas about Panama. w/o date, Steetz 601. (holotype BM!).

Chrysanthellum americanum var. integrifolium (Steetz) Alexander, *N. Amer. Fl. II* 2: 148. 1955.



Fig. 2 *Chrysanthellum michoacanum*, from holotype.

Annual, glabrous, often succulent herbs, 5-30 cm tall, at first rosulate but soon forming prostrate branches. Leaves simple, oblanceolate, finely to coarsely toothed from above the middle. Peduncles 5-15 cm long at maturity, swollen just below the head. Heads 8-12 mm across, 5-8 mm high, subtended by 4 or subulate bracts, 3-4 mm long; involucre double, an outer series of ca. 5 elliptic to ovate, scarious-margined phyllaries, 5-6 mm long, 2-3 mm wide, these alternating with a similar inner series. Receptacle convex, the pales linear, ca. $\frac{2}{3}$ as long as the disk florets. Ray florets yellow, usually ca. 34 but often up to 55, the ligules bidentate, 5-6(7) mm long, 1.0-1.5 mm wide, 2-nerved. Disk florets ca. 35, yellow, (4-)5-lobed, "sterile", the tube ca. 1.5 mm long, the limb 3-4 mm long. Ray achenes clavate, 3-4 mm long, prominently 8-10 grooved, or markedly 8-ridged, at maturity.

Chromosome number undetermined.

DISTRIBUTION (Fig. 5): States of Veracruz, Oaxaca and Chiapas in Mexico; Honduras, El Salvador, Costa Rica and Panama. Reportedly common locally in full sun on wet clay soils at lower elevations (from sea level to 200 m). Flowering, Jul-Nov.

In spite of its locally weedy nature, the species is apparently relatively rare, to judge from the sparcity of collections in herbaria. Only one or two collection sites are known for each of the following: Veracruz (GH, NY), Chiapas (MICH), Oaxaca (ASU, MICH, TEX), El Salvador (F, MICH) and Honduras (F). While Guatemalan collections were not seen in the present study, it must surely occur in that country and perhaps other Central American Republics, for it appears to be quite common in Panama.

Alexander inexplicably treated this as a variety of Chrysanthellum americanum. The two taxa are distinguished by a number of vegetative and floral features, occupy different habitat types, are largely allopatric, and do not intergrade. The relationship of C. integrifolium is almost certainly with C. michoacanum and recent collections of the former from Oaxaca by Professor Keil seemingly reveal intergrades, (15555, ASU, ENCB, TEX) and additional study might justify treatment of C. michoacanum as a localized variety of C. integrifolium.

3. CHRYSANTHELLUM PUSILLUM Hook. f., Trans. Linn. Soc. London 20: 214. 1851. TYPE: ECUADOR: Galapagos Islands: Isabela (Albemarle), C. Darwin s.n. (holotype K!).

Chrysanthellum erectum Andersson, Kongl. Svensk. Vetenskapsakad. Hanl. 188. 1854. TYPE: ECUADOR: Galapagos Islands: Santa Cruz, 1853, Andersson 176 (holotype S!).

Chrysanthellum fagerlindii Eliasson, Svensk Bot. Tidskr. 61: 91. 1967. TYPE: ECUADOR: Galapagos Islands: San Salvador, 28 Apr - 2 May 1953, Fagerlind & Wilson 3426 (holotype S!).

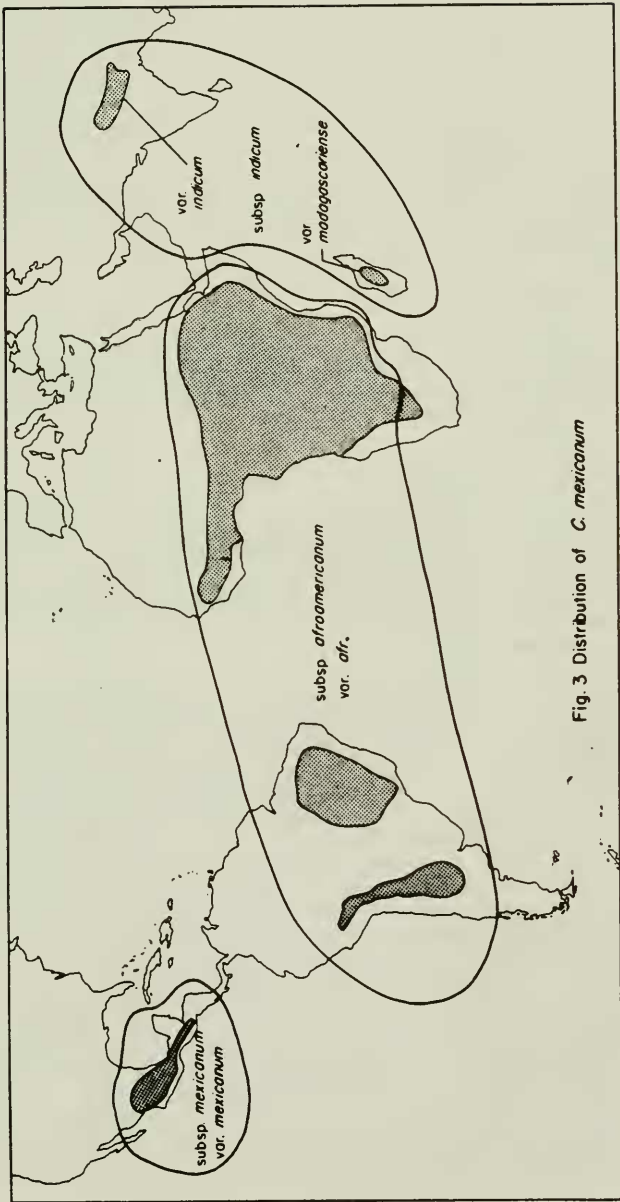


Fig. 3 Distribution of *C. mexicanum*

Annual, 5-30 cm high, at first rosulate, the peduncles elongate and arising from the center; primary stems erect, the secondary branches decumbent or ascending and richly floriferous. Leaves tritermately dissected, the divisions usually broad, but occasionally quite linear. Peduncles 1-11 cm long. Involucres 2.5-3.0 mm long, the involucre bracts ovate to ovate-lanceolate. Ray florets 5-23 (rarely more); ligules yellow, 2-3 mm long, 2-nerved and cleft at the apex. Disk florets yellow, mostly "sterile" but often fertile; corolla ca. 2 mm long, 4-lobed. Achenes of the ray florets clavate, 1.0-1.3 mm long, usually tuberculate at maturity (sometimes conspicuously so) or less often smooth; disk achenes slender, somewhat flattened with smooth, rounded, shoulders.

Chromosome number, $2n = 8 II$ (Turner, unpubl.)

DISTRIBUTION. Known only from the Galapagos Islands where it occurs in an array of sites, mostly disturbed. Collections have been seen from the following islands: Fernandina, Isabela, Rabida, San Cristobal, San Salvador, Santa Cruz, Santa Fe, and Santa Maria. Flowering, Jan-Apr.

I agree with Eliasson (1967) and Cronquist (1971) in relegating C. erectum to synonymy under this species. In spite of the variability in branching habit and achene sculpture, both between and within populations of this taxon, there appears to be but a single species. Perhaps the most striking variability is seen in the leaf segments, which are often quite linear (especially on San Cristobal Island), and in the tuberculate ray achenes, this latter feature also varying among populations.

The two collections of Chrysanthellum fagerlundii (Fagerlund & Wilson 3426; 3440, S), both from Santiago Island, are enigmatic. The plants appear to be teratological forms of C. pusillum, the collectors apparently having obtained plants typical of the latter (F. & W. 3441, S) next to or near their collection 3440. What does seem clear is that the few plants known, while quite mature to judge from their much-branched habits, do not seem to produce fruiting material and their florets appear to be strangely reduced and irregular with 3-5 lobings, etc. Such anomalies are found nowhere else in the genus and extend to the involucre which is comprised of linear-lanceolate several-seriate bracts suggesting an atavistic reversion to some primordial developmental state. I have observed, very rarely, similar individuals among Texas populations of Gutierrezia (Asteraceae), the plants nearly always being small-headed, depauperate and sterile. Cronquist (1971) also does not accept C. fagerlundii as a "good" taxon, referring to it as "a minor form with very short rays and deeply cleft corolla, which will probably fail to persist...with the typical C. pusillum. The latter will probably swamp the incipient species in a few generations." Future field worker on Santiago Island should look for such forms to see if the present impressions are borne out, for Eliasson (1972)

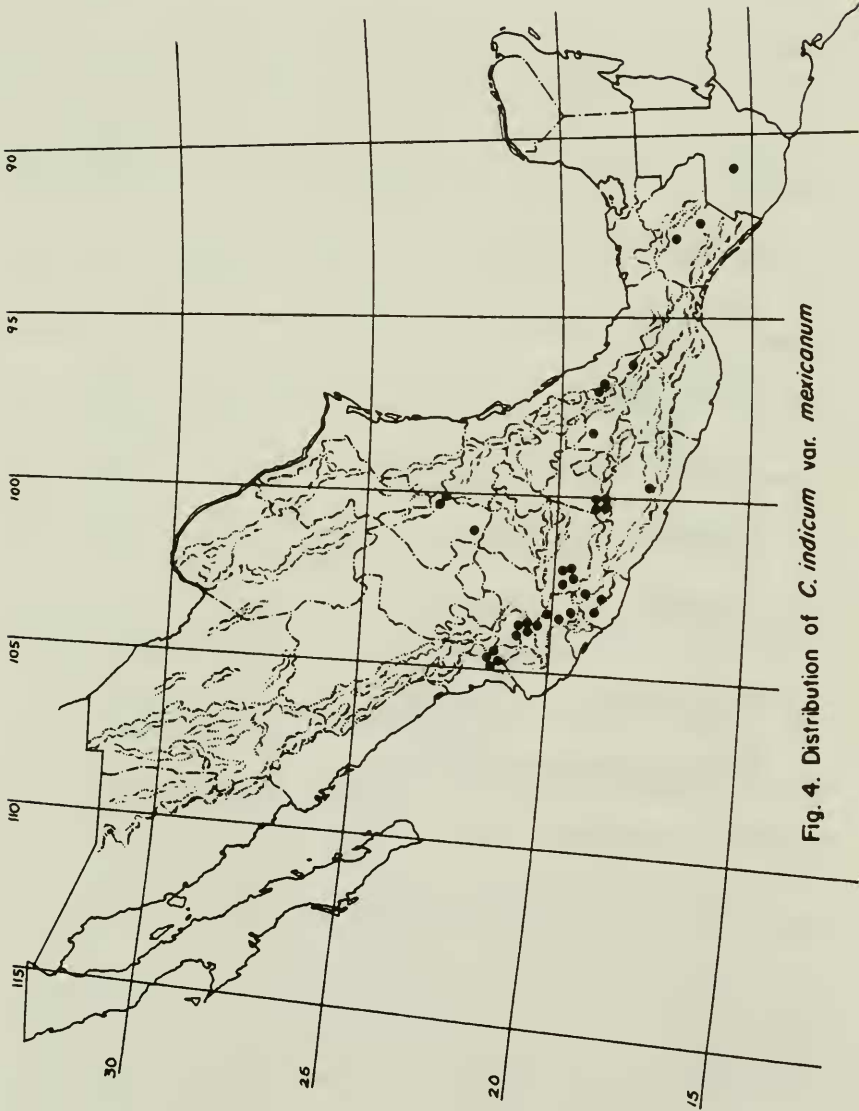


Fig. 4. Distribution of *C. indicum* var. *mexicanum*

seems quite convinced that the collections represent a good species. It would be quite helpful if achenes from such "forms" could be procured and germinated so as to see if the resultant plants breed true.

As to the origin of Chrysanthellum pusillum, I favor a relatively old introduction from some extinct populational source not too unlike C. indicum var. mexicanum. It has the chromosome number ($2n = 8 II$), reduced habit, and small, narrowly winged achenes of that taxon. In addition, highly "sterile" disk florets and tuberculate achenes are found in related taxa from the region where C. indicum occurs, suggesting that southwestern Mexico was the ancestral area from whence it dispersed.

4. CHRYSANTHELLUM AMERICANUM (L.) Vatke, Abh. Naturwiss Vereine Bermen 9: 122. 1885.

Anthemis americana L., Sp. Pl. 895. 1753. TYPE: JAMAICA. Sloane s.n. (holotype BM!).

Bidens apifolia L., Syst. ed. 10: 1203. 1760. TYPE: w/o locality or collector (holotype LINN!).

Verbesina mutica L., Sp. Pl., ed. 2. 1273. 1763. TYPE: w/o locality or collector (holotype LINN!).

Chrysanthellum procumbens Rich. ex Per., Syn. Pl. 2: 471. 1807. nom. superfl., illegit., TYPE: based on Verbesina mutica L.

Chrysanthellina fasciculata Cass., Dict. Sci. Nat. 25: 392. 1822. TYPE: Described from cultivated material, no specimens cited and place of origin unclear. The description fits C. americanum.

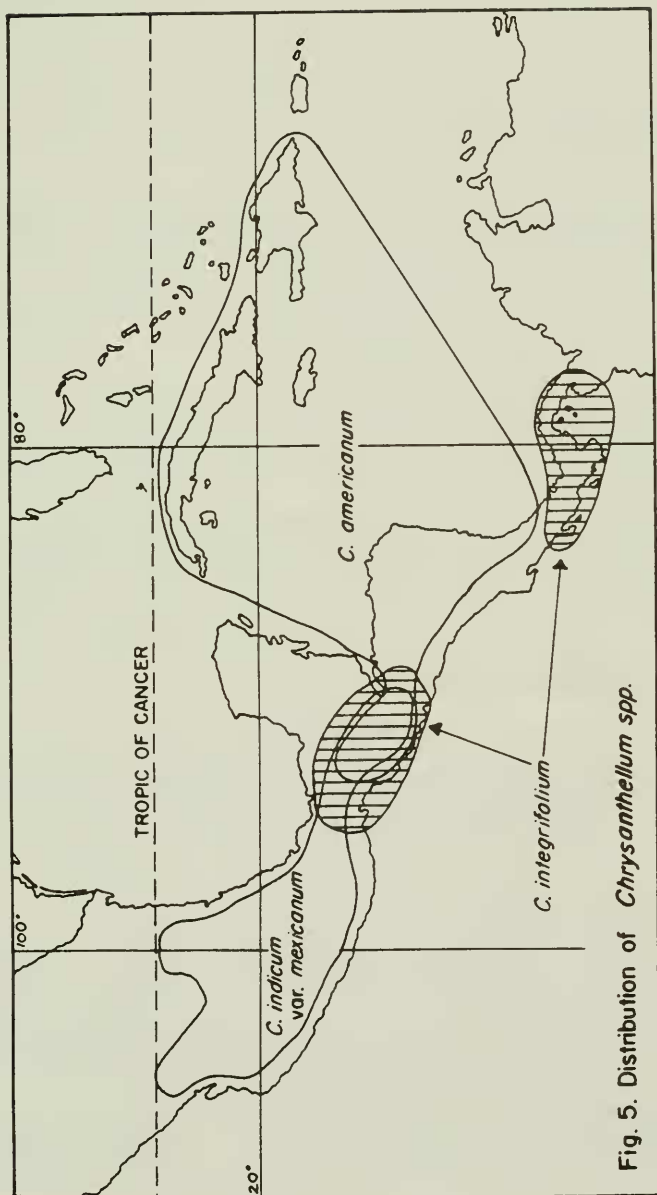
Chrysanthellina gracilis Cass., Dict. Sci. Nat. 25: 392. 1822. TYPE: As in the above. The description fits C. americanum.

Sebastiania heterophylla Bertol., Lucubr. 37. 1822. nom. superfl., illegit., TYPE: based on Anthemis americana L.

Collaea procumbens (Rich. ex Pers.) Spreng., Syst. 3: 622. 1826.

Chrysanthellum swartzii Cass. ex DC., Prodr. 5: 631. 1836. TYPE: JAMAICA. Swartz s.n. (holotype P; isotype SI!).

Prostrate or recumbent, glabrous, annual herbs. Leaves simple below to variously lobed or dissected, not decidedly pinnatisect. Peduncles, 3-6(7) cm long. Fruiting heads 6-9 mm across, 4-5(6) mm high, subtended by 4-6 linear bracts, 1-2 mm long. Involucre double, an outer series of 5 ovate phyllaries, 4-5 mm long, 3-4 mm wide, the margins scarious; inner series 5, similar to the outer but somewhat narrower. Ray florets 13-34, yellow, the ligules usually bidentate,

Fig. 5. Distribution of *Chrysanthellum* spp.

2-4(5) mm long, ca. 1 mm wide, with 2, or rarely 3, conspicuous nerves. Disk florets (4)5-lobed, most of them fertile, corolla orange-yellow to yellow (rarely white), ca. 1 mm long, the tube ca. 0.2 mm long; limb ca. 0.8 mm long, lobes acute, ca. 0.2 mm long. Ray achenes 2-3 mm long, columnar-clavate, with 3, or less often 2 sulci on the ad- and abaxial surfaces. Disk achenes linear-oblong, 2-3 mm long, ca. 1 mm wide, the faces bordered by a prominent, often rugose, cartilaginous, ciliate margin.

Chromosome number undetermined.

DISTRIBUTION (Fig. 5). Cuba, Hispaniola (Dominican Republic and Haiti) and Jamaica Islands; also Costa Rica, Guatemala, Honduras and southernmost Mexico (Chiapas) in continental North America. Mostly a weed in grassy fields and waste places at various elevations in the island areas but usually in pine and oak-pine woodlands and meadows of the lower montane regions (300-2000 m) on the mainland. Flowering, all seasons, according to rains.

This species, though quite distinct and fairly restricted in distributions, has long been confused with C. indicum. The latter is nearly pantropic but its range does not overlap that of C. americanum.

The island populations of Chrysanthellum were probably derived from relatively recent introductions from Central America, to judge from their morphological similarities, but it was presumably already established on Jamaica and Cuba at the time of European ventures into the region, for abundant, widespread, collections were obtained on these two islands by early collectors.

5. CHRYSANTHELLUM INDICUM DC.

Erect to prostrate, glabrous or nearly so, annual herbs up to 30 cm tall. Leaves bi- or tripinnatisect, 1-8 cm long. Peduncles 0.5-6.0 cm long, smooth or bearing scattered tuberculae. Heads 3-6 mm across, 2-6 mm high, subtended by 1 or 2 (rarely more) linear bracts. Involucre double, an outer series of 5(8) linear-ovate, phyllaries 2-5 mm long, 1-2 mm wide, the inner series similar but somewhat smaller. Ray florets 5-34 (modes at 5, 8, 13, 21 and 34), yellow or orange-yellow, the ligules usually bidentate, 1.0-2.5 mm long, 0.2-0.5 mm wide, 2-nerved. Disk florets fertile, 4- or rarely 5-lobed; corollas yellow, 0.8-1.3 mm long, the tube 0.2-0.3 mm long, limb 0.6-1.0 mm long. Ray achenes 2-4(5) mm long, compressed to columnar-clavate to cuboid, often corky-winged at maturity, smooth to ribbed on all faces, less often tuberculate. Disk achenes flattened, linear-oblong to oval, 2.3-5.0(6.0) mm long, 1-2 mm wide, the faces bordered with a narrow to broad callous margin (rarely absent), this being variously ciliate, tuberculate, erose or corky.

Chromosome number, $2n = 8$ II; $2n = 16$ (var. afroamericanum and var. mexicanum).

Four varieties in three subspecies are recognized and these are treated separately below.

Key to infraspecific taxa

A. Fruiting involucre 2-4 mm long; disk achenes bordered by a narrow cartilaginous margin (seemingly absent in var. madagascarense), 0.1-0.2 mm wide; ray florets 5-13; plants of Asia, Madagascar, Mexico, and Central America (B).

B. Involucral bracts 2.0-3.0 mm long; cartilaginous margin of disk achene either well developed (ca. 0.2 mm wide) or seemingly absent; plants of Asia or Madagascar subsp. indicum

C. Disk achenes with well-developed cartilaginous margins ca. 0.2 mm wide; plants erect (rarely prostrate); leaves much-dissected, mostly 2 cm long or more; India, Himalayan regions.....
.....5a. subsp. indicum var. indicum

C. Disk achenes with margins absent or poorly developed; plants prostrate; leaves not much dissected and mostly less than 2 cm long; Madagascar..... 5b. subsp. indicum var. madagascarense

B. Involucral bracts (2.5)3.0-4.0 mm long; cartilaginous margin of disk achene narrow, ca. 0.1 mm wide; plants of Mexico or Central America..... 5d. subsp. mexicanum

A. Fruiting involucre 4-5(6) mm long; disk achenes (at maturity) bordered by a well-developed, cartilaginous or corky wing 0.2-0.4 mm wide; ray florets (8)13-34; plants of Africa and South America..... 5c. subsp. afroamericanum

SUBSP. INDICUM

5a. CHRYSANTHELLUM INDICUM DC. var. INDICUM, PROD. 5: 631. 1836. TYPE: INDIA. Near Gajpur and Dukanaghur, Wallich 401 (also cited in Wallich's catalogue as no. 3291; not 3231 as given by DC) (holotype G-DC; isotype K!).

Erect to semi-erect glabrous annual herbs up to 25 cm tall. Leaves bi- or tripinnatisect, 1-6 cm long. Peduncles, at maturity, 0.5-2.5(3.0) cm long, bearing scattered tuberculae. Heads 4-5 mm across, 2.5-3.0 mm high, subtended by 1, or rarely 2, linear bracts, 2-3 mm long; involucre double, an outer series of 5, linear-ovate, phyllaries, 2.5-3.0 mm long, ca. 1.0 mm wide, the inner series of 5 similar but somewhat smaller phyllaries. Ray florets usually 8, yellow, the ligules bidentate, ca. 1.5 mm long, ca. 1.2 mm long, the tube ca. 0.3 mm long, limb ca. 0.9 mm long. Ray achenes ca. 2.5 mm long, columnar-clavate, the abaxial faces with two sulci. Disk achenes linear-oblong, 2.5-2.8 mm long, ca. 1.0 mm wide, the faces brownish, bordered with an irregularly undulate or erose, cartilaginous, eciliate (or nearly so) margin ca. 0.2 mm wide.

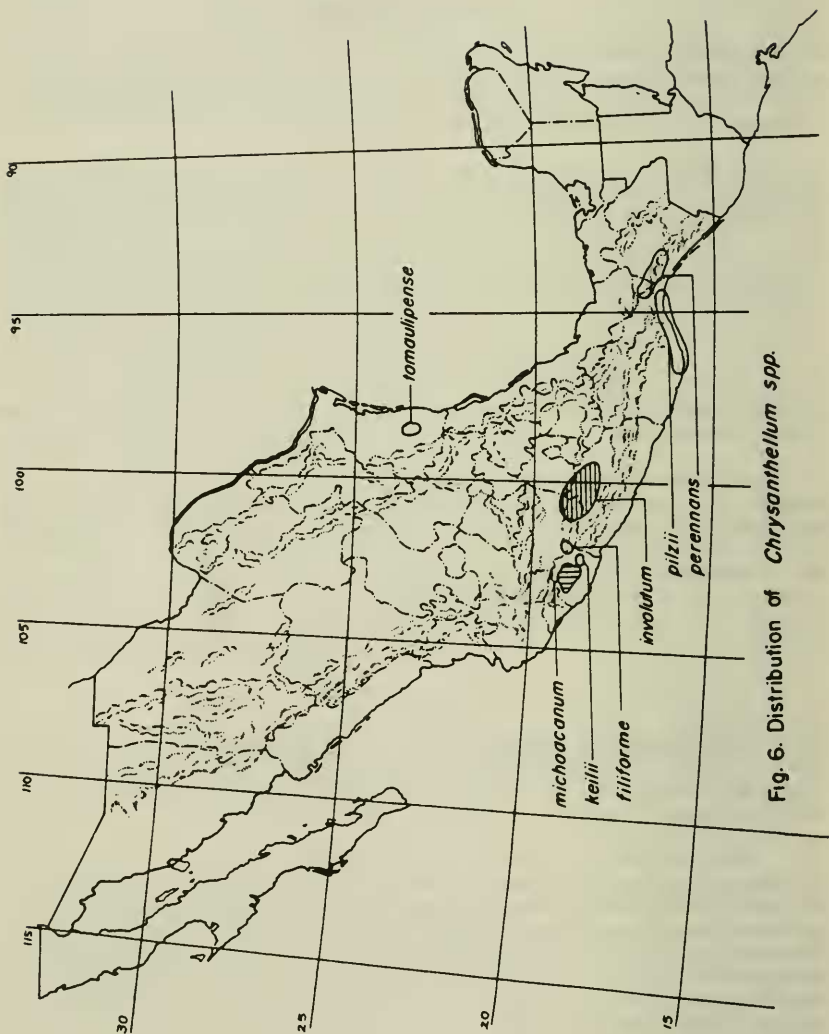


Fig. 6. Distribution of *Chrysanthemum* spp.

Chromosome number, unknown.

DISTRIBUTION (Fig. 3). Known only from India and adjacent Nepal, where it occurs in grassy places from 250 to 3500 m. Flowering, Aug-Oct.

With its small heads and relatively few ray florets, this variety much resembles var. mexicanum but it can be distinguished from the latter by its narrow-winged, nearly eciliate, disk achenes and generally shorter peduncles. Because of this resemblance it might have been reasonable to include var. mexicanum in the same subspecies with indicum but because of the distance separating their respective locales and the fact that the North American populations appear to have had a relatively more remote origin, perhaps relictual in the sense that it occupies the center of diversity of the genus, it seems more reasonable to assume that the Asian and Madagascar populations are convergent in the morphological characters that relate them to the Mexican populations. In short, phylogenetic reasoning suggests that propagules from montane North American populations, ancestral but similar to var. mexicanum, by long distance dispersal to the Andean regions, gave rise to var. afroamericanum; populations of the latter were presumably dispersed to Africa, India and Madagascar in relatively recent times, the latter two regions developing smaller-headed, less-winged fruits than is typical of the quite variable populations of var. afroamericanum on the African continent itself.

Inclusion of var. indicum and var. madagascarense in the same subspecies largely reflects emphasis upon head size and it might be that they should be recognized as sufficiently distinct so as to be treated as different subspecies. Enough material from Madagascar was not available to judge the constancy of the characters used to distinguish between these, but from the material at hand var. madagascarense seemed more distant from subsp. afroamericanum than from var. indicum.

Finally, it should be noted that some workers will surely say that var. indicum (and possibly var. madagascarense), being weedy, as are all the varieties, was probably introduced into India from Africa or South America during the past several hundred years and hence hardly worthy of subspecific rank. Perhaps so, but as noted in part by Hooker (1882) and wholly by Greenman (1903), the Indian populations have a combination of characters that readily distinguish them from the African and American populations, hence their recognition as a distinct taxon. However, taken on a worldwide basis, C. indicum is much too similar to selected African (and, as already noted, Mexican) populations to be accorded specific rank; indeed, if by chance an unlabeled Indian plant were transported to South American I would be hard-pressed to recognize this as anything more than an anomalous, few-flowered, small-fruited, form of afroamericanum, so much alike are they in their basic morphology.

Occasional specimens of var. indicum (Polunin et al. 5812, BM; Clarke 24919, BM) occur which have heads as large as those of var. afroamericanum, but their achenes and "tuberculate" peduncles are of the indicum-type, suggesting that the suite of subtle characters used to distinguish among the several infraspecific categories are relatively well-fixed, genetically speaking.

5b. CHRYSANTHELLUM INDICUM var. MADAGASCARENSE B. L. Turner, var. nov.

Chrysanthellum indicum var. indicum accedens sed marginibus cartilaginibus achem debile evolutis, foliis parvioribus minus dissectis. TYPE: CENTRAL MADAGASCAR. "Bessileo: an Strotknen Stellen der, Flugel." Mar 1881, J. M. Hildebrandt 3943 (holotype US!; isotype K!).

Additional specimens examined: MADAGASCAR. Angavo, 19 Oct 1931, M. R. Decary 7285 (K, US); Ankatso, 2 Feb 1921, Decary 240 (K).

DISTRIBUTION (Fig. 3). Known only from a few, mostly poorly-preserved specimens from the highland regions of Central Madagascar where it reportedly grows prostrate, although one collection (Decary 240) shows the plant to be at least weakly ascending. Flowering, Feb-Mar.

As noted in the discussion of var. indicum, collections of var. madagascarense available to me appear quite distinct and additional material might show the taxon to be deserving of subspecific recognition.

Subsp. AFROAMERICANUM B. L. Turner, *Phytologia* 51: 291. 1982.

Similar to the subspecies indicum but differing in its larger fruiting involucre (4-6 mm long); disk achenes with more prominent, well-developed, cartilaginous wings or corky margins, 0.2-0.4 mm wide; and ray florets mostly 13-34 (very rarely 8).

Chromosome number, $2n = 16$ II.

The subspecies is comprised of but a single variety.

5c. CHRYSANTHELLUM INDICUM var. AFROAMERICANUM B. L. Turner, *Phytologia* 51: 291. 1982. TYPE: ARGENTINA. Prov. Cordoba., Dept. Colon; Rio Ceballos, 15 Mar 1944, C. A. O'Donnell & J. M. Rodrigues V. 501 (holotype A!; isotypes F! UC!).

Adenospermum tuberculatum H. & A., *Hookers J. Bot.* 3: 318. 1841. TYPE: ARGENTINA: Prov. Cordoba, Cordoba. "On hillsides and hard dry soils", w/o date, L. Tweedie 1107 (not 1109 as cited) (lectotype K!). In the original description a collection by Gillies from Cordoba was also cited; I choose to typify the name with the Tweedie collection.

Hinterhubera kotschy Sch.-Bip. ex Hochst., Flora 24: 419. 1841. TYPE: ABYSSINIA; "Ad montem Cordofanum Arasch cool locis prinis humide", 14 Oct 1839, pl. exs. Kotschy 175 (isotypes BM!, MO!, NY!, K!, L!).

Plagiocheilus erectus Rusby, Mem. Torrey Bot. Club 4: 212. 1895. TYPE: BOLIVIA. Cochabamba, 1891, A. M. Bang 965 (holotype US!; isotype US!).

Chrysanthellum boliviense Sch.-Bip., Bull. Soc. Bot. France 12: 82. 1865. Nomen nudum.

Chrysanthellum weberbaueri Chung, Phytologia 14: 321. 1967. TYPE: PERU. Prov. Tayacaja: Valley of the Mantaro below Colcabamba, 1900-2000 m, Mar 1931, A. Weberbauer 6465 (holotype F!; isotypes GH!, S!, US!).

Chrysanthellum tuberculatum (H. & A.) Cabrera, Bol. Soc. Argent. Bot. 15: 117. 1973.

Chrysanthellum argentinum Ariza & Cerana, Bol. Soc. Argentina Bot. 22: 267. 1983 (holotype, as shown by the illustration provided with the original description!).

DISTRIBUTION (Fig. 3). Mostly montane or moderately elevated regions of South America and Africa where it occurs as a weed along paths, in gardens and disturbed areas generally; possibly introduced into Africa from South American in relatively recent times. Flowering most all seasons, depending upon rain.

An exceedingly variable, weedy taxon, especially on the eastern side of the Andes in northern Argentina, Bolivia, and Peru where it is undoubtedly native. Chrysanthellum tuberculatum is a sporadic form of the variety possessing tuberculate ray (and often disk) achenes; such plants occur throughout the American region. Cabrera (1973) correctly noted the relationship of the South American material to be with C. indicum and C. mexicanum and not C. americanum where most workers positioned these plants.

The Peruvian C. weberbaueri is a form with squat, much-thickened, somewhat tuberculate ray achenes, but otherwise scarcely different from typical afroamericanum; individuals of the latter occur in the same region with the former suggesting that this character is quite polymorphic. Indeed a similar, but not so striking, variability is found in African populations in which the ray achenes may be smooth or tuberculate, etc. Also noteworthy in both African and South American plants is the occasional occurrence of poorly developed, but distinct, awns at the apex of the disk achenes, much in the manner of Bidens or Isostigma.

Ariza and Cerana recognized Chrysanthellum argentinum largely by

the presence of well-developed wings on the ray achenes. In northcentral Argentina populations occur in which individuals have both ray and disk achenes essentially monomorphic or heteromorphic (i.e., disk achenes winged and the ray achenes unwinged). Indeed, the development of wings on ray achenes should not require much of a genetic change and I suggest that the considerably polymorphic variation which I found during my own field work in this region is due to such variation. In any case additional work will be needed to show that C. argentatum is an isolated gene pool growing within the bounds of C. indicum var. afroamericanum. Personally, I suspect that the former are weakly differentiated populations in which only a few genes for wing expression on the ray achenes have become partially fixed. Experimental crosses and progeny studies will be needed to resolve the problem.

Brazilian populations are also quite variable, especially the disk achenes, which often possess very narrow, ciliate, cartilaginous margins similar to those found in var. mexicanum. Similar forms also occur rarely in African populations; expression of this character is apparently regulated by a relatively simple genetic system. The larger heads, more numerous flowers, and the occurrence of individuals within these same populations with winged achenes typical of var. afroamericanum, show that the origin or closest affinity of the Brazilian populations must lie with the South American-African taxon and not var. mexicanum. Considering its weedy nature and the paucity of material collected in the Brazilian area it seems likely that these populations were introduced into this region from Andean populations in relatively recent times.

Wild (1967) and Milne-Redhead (1948) treated the African specimens of Chrysanthellum indicum as C. americanum, as did workers before them. They report collections from the countries of Malawi, Mozambique, Rhodesia and Zambia. In December of 1975 I examined African specimens at BM and K and in December of 1982 from MO. The earliest year of collection is given in parenthesis for the following countries:

Angola (1857)	Kenya (1915)	Southwest Africa (1907)
Burundi (1972)	Malawi (1974)	Sudan (1929)
Cameroun (1964)	Mozambique (1944)	Tanzania (1932)
Eritrea (1902)	Nigeria (1899)	Uganda (1912)
Ethiopia (1838)	Rhodesia (1912)	Upper Volta (1972)
Guinea (1949)	Senegal (1938)	Yemen[Arabian Peninsula] (1977)
Ivory Coast (1967)	South Africa (1906)	Zaire (1950)

Thus, if introduced into Africa during historic times, Chrysanthellum indicum probably found first-footing in the Abyssinian highlands of East Africa, subsequently spreading to the more western and southern lower montane regions. Indeed, populations from Ethiopia are exceedingly variable and some of these with small heads and nearly wingless achenes could as readily be annotated as var. indicum.

Subsp. MEXICANUM (Greenm.) B. L. Turner, *Phytologia* 51: 291. 1982.

The subspecies is represented by a single taxon, var. mexicanum.

5d. CHRYSANTHELLUM INDICUM var. MEXICANUM (Greenm.) B. Turner, *Phytologia* 51: 291. 1982.

Chrysanthellum mexicanum Greenm., *Proc. Amer. Acad. Arts* 39: 114. 1903. TYPE: MEXICO. Jalisco: Banks of ravines near Guadalajara, 10 Sep 1890, C. G. Pringle 3259 (lectotype GH!; isolectotypes ENCB!, F!, K!, MICH!, MO!, NY!, S!, UC!).

Coreopsis diffusa M. E. Jones, *Contr. Western Bot.* 18:73. 1933. TYPE: MEXICO. Jalisco: La Barranca, Guadalajara, 7 Nov 1930, M. E. Jones 27720 (holotype POM). As noted by Morton (1945), Sherff was the first to relegate this to synonymy under this taxon.

Similar to, but differing from, the var. indicum in possessing longer peduncles and longer leaves but especially by the somewhat larger disk achenes with narrower, more ciliate, cartilaginous margins. As noted by Greenman in his original description, var. mexicanum bears a close resemblance to var. indicum; this was also recognized by Cabrera (1973). I agree with both these authors and after examining a broad suite of specimens from throughout the world find it most reasonable to treat the largely continental isolates as weak, but distinct, varieties, most of which are sufficiently differentiated so as to be accorded the rank of subspecies.

DISTRIBUTION (Fig. 4). Mostly montane or moderately elevated subtropical regions of Mexico and Guatemala where it occurs as a weed along paths and roadways, especially in shallow wet depressions. Flowering, Jul-Oct.

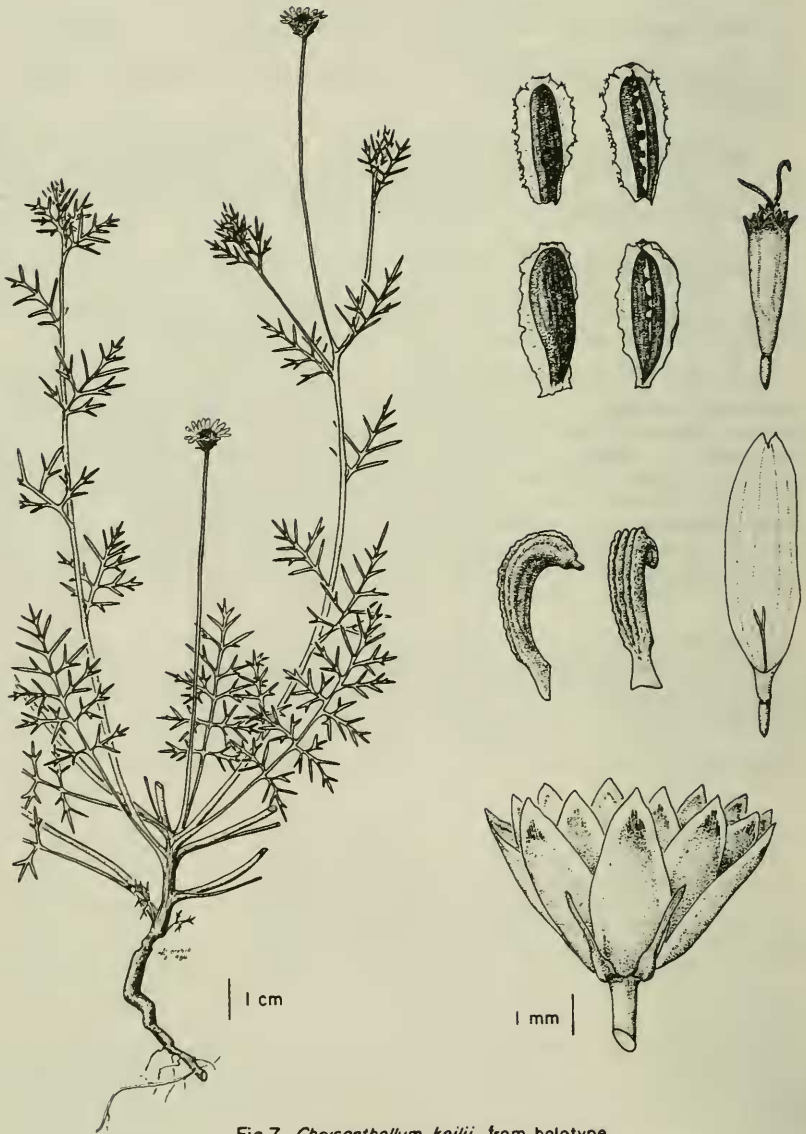


Fig.7 *Chrysanthellum keilii*, from holotype

6. CHRYSANTHELLUM FILIFORME McVaugh, Contr. Univ. Michigan Herb. 9: 412-413. 1972. TYPE: MEXICO. Michoacan: Summit of Canon el Marques, ca. 8 km N of Nueva Italia, ungrazed hillsides in Bouteloua grassland, 450-500 m, 19 Sep 1958, McVaugh 18030 (holotype MICH!; isotypes ENCB!, LL!, MICH!, NY!).

Slender, delicate, erect, glabrous annuals, 10-40 cm tall. Leaves, 2-9 cm long, pinnately dissected with narrowly linear divisions. Peduncles, at maturity, 7-12 cm long. Heads 1.2-1.8 cm across, 6-8 mm high, subtended by 3-4 bracts ca. 2 mm long; involucre double, an outer series of 5, scarious-margined, lanceolate phyllaries, 4-5 mm long, 1.5-2.0 mm wide, an inner series of 5(8) similar phyllaries. Ray florets 8-15, "orange", the ligules 5-7 mm long, ca. 2 mm wide, 4-5(6) nerved, obtuse or emarginate. Disk florets 20-30, brownish-red, "sterile", the tube 1.0-1.5 mm long, limb 3-4 mm long, 5(4) lobed. Ray achenes clavate, slightly incurved, 3.5-4.0 mm long, abaxially, 6-8 sulcate.

DISTRIBUTION. Known only from the type collection, cited above.

As noted by McVaugh in his original description, the species is quite distinct, being closer to Chrysanthellum americanum than to C. indicum. Actually, with the exception of C. keilii, C. filiforme, with its 4-5 nerved ligules, pinnately dissected leaves and somewhat incurved achenes, seems to stand closer to C. involutum than it does to C. michoacanum, its closest taxon among the C. americanum complex. The relationship of C. filiforme to C. keilii is discussed under the latter.

7. CHRYSANTHELLUM KEILII B. L. Turner, sp. nov. Fig. 7.

C. filiforme McVaugh accedens sed achaeniis florum radiatorum florumque aliorum fecundorum valde incurvis.

TYPE: MEXICO. Michoacan: 0.3 mi E of Antunez along highway 120; 8.7 mi W of Cuatro Caminos in areas of cultivation with thorn forest; "locally common in bottom of ditch", 1100 ft, 29 Aug 1981, D. Keil 15222 (holotype TEX!; isotypes ASU!, ENCB!, MEXU!).

Slender, erect, glabrous annual, 20-50 cm tall. Leaves, 3-15 cm long, pinnately dissected with narrowly linear divisions. Peduncles, at maturity, 7-18 cm long. Heads 1.0-1.5 cm across, 6-8 mm high, subtended by 3-5 bracts ca. 2 mm long; involucre double, an outer series of 5, scarious-margined, lanceolate phyllaries, 5-6 mm long, 1.5-2.5 mm wide, an inner series of 5(8) similar phyllaries. Ray florets 21-32, orange, the ligules 4.0-6.5 mm long, 2.0-3.0 mm wide, 4-nerved, obtuse or with a small notch. Disk florets 20-40, brown, mostly fertile, the tube 0.5-2.0 mm long, limb 2.0-4.5 mm long, 5-lobed. Ray achenes strongly incurved, 4-5 mm long, ca. 1 mm in diameter, rugose and 2-4 sulcate along the outer surface, the inner surface smooth; disk achenes somewhat spoon-shaped, 3.5-4.0 mm long, the body black, ca. 1 mm wide, smooth and glabrous on the outer

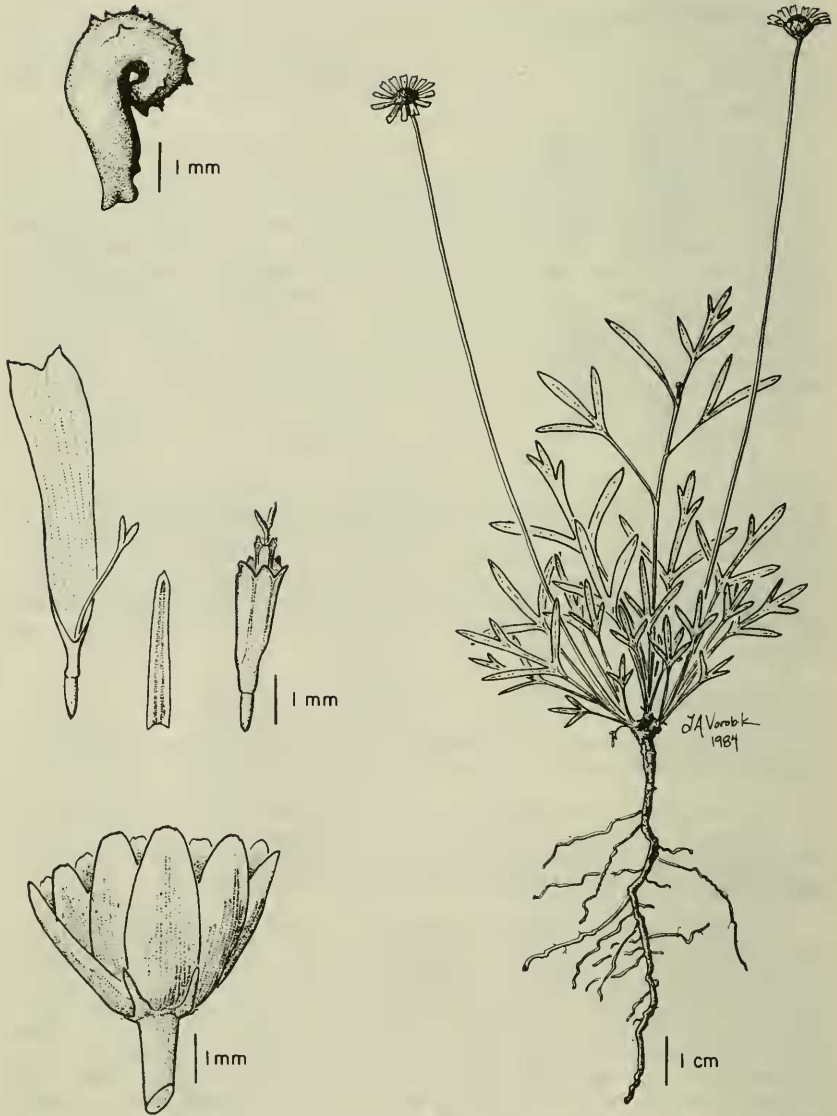


Fig.8 *Chrysanthellum perennans*, from holotype

surface but with a warty mid-vein on the inner surface, bordered on both sides by a white cartilaginous erose wing about 0.5 mm wide.

Chromosome number, $2n = 8$ II (Keil 15222).

Additional collection. MICHOACAN: 8 mi S of Cuatro Caminos along highway 37; 2.4 mi N of El Capirio; thorn forest with short grass understory, "scattered in short grass, rocky area", 900 ft, 31 Aug 1981, D. Keil 15249 (ASU, TEX).

I propose this species with considerable hesitation since in habit, floral morphology and general geography it is like C. filiforme. However, the latter has fewer ray florets which produce nearly straight achenes and, as noted by McVaugh, it has completely "sterile" disk florets.

Such differences characterize species in other member-pairs of *Chrysanthellum* (e.g., C. americanum vs C. integrifolium; C. involutum vs C. tamaulipense; C. involutum vs C. indicum, etc.). Nevertheless, it is possible that relatively few genes regulate the sterility of what otherwise appear to be functional disk florets, including the remarkable transformation of ray florets. Thus McVaugh's disk-sterile, C. filiforme, with its nearly straight ray achenes, may be populational forms vicariously derived from what I have here described as C. keilii. Only additional field and experimental work can resolve the problem but it seems noteworthy that all of the 16 individuals from the two cited populations of C. keilii possessed fertile disk achenes and incurved ray achenes.

The taxon is named for Dr. David Keil, Professor at the University of California and avid scholar of the genus *Pectis*. Along with Dr. Melissa Luckow, he collected the fine set of specimens upon which the present species is based.

8. CHRYSANTHELLUM PERENNANS Turner, *Phytologia* 51: 293. 1982. Fig. 8. TYPE: MEXICO. Oaxaca: Along the Pan-American Highway, 22 km NW of Zanatepec, 100 m elevation or less; high dense vegetation, 10 Jul 1958, R. M. King 463 (holotype LL!; isotype MICH!).

Small, erect, glabrous perennial with well-developed, corky tap roots, with new growth producing from its crown up to four rosettes, each bearing but a single, elongate peduncle. Leaves merely tripartite with occasional secondary lobing, the lobes linear to lanceolate, 3-20 mm long, 1-3 mm wide. Peduncles at maturity, 15-20 cm long or longer. Heads ca. 15 mm across, ca. 6 mm high, subtended by 3-5 acuminate, prominently ciliate bracts, 1.0-1.5 mm long; involucre double, an outer series of 5, lanceolate, scarious-margined phyllaries, 5-6 mm long, 2-3 mm wide, an inner series of ca. 5 similar phyllaries. Ray florets ca. 13, "orange", the ligules ca. 8 mm long, 2 mm wide, 6-7 nerved and deeply cleft (ca. 2 mm). Disk florets presumably "sterile", "brown-orange", 5-lobed, the tube ca. 0.8 mm long, limb 2.0-2.2 mm long. Achenes immature.

DISTRIBUTION (Fig. 6). Known only the type locality where it is reportedly uncommon in sandy soil, and a single collection from Mpio. Cintalapa, Oaxaca, in pine-oak woodlands. Flowering Jul-Sep.

Additional collection: OAXACA: Mpio. Cintalapa, 23 km W of Las Cruces along road to La Mina Microwave Station, 870 m, 10 Sep 1981, Breedlove 52903 (CAS, TEX).

This is the only perennial taxon in the genus and is readily recognized by the elongate peduncles that arise singly from each rosette. Unfortunately, the collections available do not have mature heads so that the shape of the achene is unknown. These will probably prove to be circinate to some degree, to judge from the position of the corolla upon the somewhat oblique ovary, for it is positioned off-center towards the abaxial side.

9. CHRYSANTHELLUM PILZII Strother, Madrono 23: 358. 1976. TYPE: MEXICO. Oaxaca: ca. 1 km E of Salina Cruz, beach sand, 22 Jul 1971, J. Strother 1094 (holotype UC!; isotype TEX!).

Sparsely pubescent, annual herbs, 10-15 cm high; rosulate at first but soon forming prostrate stems. Leaves petiolate, arranged in nearly opposite pairs, the "pairs" separated by internodal lengths of 5-7 cm; blades tripartite, 2.0-3.0 cm long, 1.5-2.0 cm wide, the divisions variously lobed. Peduncles up to 9 cm or longer. Heads ca. 15 mm across, 8 mm high, subtended by 5, acuminate, prominently ciliate, bracts ca. 3 mm long; involucre double, an outer series of ca. 8, broadly lanceolate, scarious-margined, phyllaries, 5-6 mm long, 2-3 mm wide, an inner series of ca. 8 similar phyllaries. Ray florets ca. 13, yellow, the ligules ca. 6 mm long, 3-4 mm wide, 5-8 nerved, bidentate, the sinus shallow (0.5 mm or less). Disk florets brownish-yellow, functionally staminate, the tube ca. 0.8 mm long, limb 2.2-3.4 mm long. Ray achenes outcurved, the adaxial surface conspicuously echinate and marginally grooved, the abaxial surface depressed and smooth, ca. 6 mm long, 4 mm wide and 2 mm thick.

Chromosome number, $2n = 12 II$.

DISTRIBUTION (Fig. 6). Known only by a few collection from coastal dunes of eastern Oaxaca, 3-10 m. Flowering Mar-Jul.

Additional collections: OAXACA. Salina Cruz, 15 Jul 1946, Morley 680 (UC); Distr. Juguila, Trailer Park "Carrizalillo", Puerto Escondido, 10 m, 20 Mar 1983, Tenorio L. et al. 3578 (MEXU, TEX).

In spite of its restriction to what might appear to be relatively recently formed habitats (sand dunes), this is a remarkably distinct taxon. In habit it looks, at first glance, like a Bidens, especially in the superficially "paired" spacings of its alternate leaves, but it is best recognized by its large, prickly-tuberculate, evolute achenes. Its relationship is undoubtedly with the multinervate series, presumable near C. involutum or C. perennans.

10. CHRYSANTHELLUM INVOLUTUM P. G. Wilson, Hooker's Icon. Pl. 36: tab. 3587. 1962. TYPE: MEXICO. Mexico State, District Temascaltepec: on hill at Palmar, 9 Aug 1934, G. B. Hinton et al. 6977 (holotype K!; isotypes LL!, MICH!, NY!, UC!, US!).

Erect to ascending (rarely subsulate) glabrous, annual herbs. Leaves bi- or tripinnatisect, up to 12 cm long. Peduncles, at maturity, 6-15 cm long. Heads 4-16 mm across, 6-7 mm high, subtended by 2-4 linear bracts, 2-4 mm long; involucre double, an outer series of ca. 8, elliptic to oval phyllaries, 4-6 mm long, 2-3 mm wide, an inner series of ca. 5, linear to oblong phyllaries, 4-5 mm long, 0.5-1.3 mm wide. Ray florets 18-21, yellow, the ligules 6-7 mm long, 2-3 mm wide, 4-5 nerved and bidentate. Disk florets yellow, "sterile", the tube 0.8-1.0 mm long, limb 2.8-3.1 mm long. Ray achenes circinate-involute, the outer surface rugose and nerved at maturity, the inner surface smooth, ca. 0.8 mm wide, 2-3 mm in diameter.

DISTRIBUTION (Fig. 6). Limestone hills in states of Mexico, Michoacan, and Guerrero. Flowering, Aug-Sep.

The species was originally known from only 7 Hinton collections cited by Wilson in his original description, duplicates of which are widely distributed. An excellent drawing accompanying this description depicts nicely the important features of the plant, except that of the functionally staminate florets, which is commented upon by Wilson as "peculiar for the subtribe Coreopsidinae as the disk florets are always sterile." Actually, completely sterile disk florets were recorded for Chrysanthellum integrifolium nearly a century earlier by Steetz (1856) in his original description of that species. It is also found in several additional species, some of which are quite closely related to species with fructiferous disk achenes (e.g., C. filiforme and C. keilii).

The only collections of C. involutum, besides those of Hinton mentioned above, are those of Keil 15368, 15371 (both from the vicinity of Arcelia, Guerrero, 6 Sep 1981, ASU).

Chrysanthellum involutum superficially resemble C. indicum var. mexicanum but its closest relationship is presumably with C. tamaulipense, which is vegetatively similar to C. involutum and possesses circinate ray achenes, but has at least some of the disk florets in each head quite fertile. This is not so for C. involutum, as determined by my examination of 100 or more heads from 50 or more plants.

11. CHRYSANTHELLUM TAMAULIPENSE Turner, Phytologia 51: 292. 1982. Fig. 9. TYPE: MEXICO. Tamaulipas: 6 mi. N of Aldama on the road to Soto la Marina, "Weedy growth in bottom of small arroyo through the basalt uplands.", 25 Sep 1960, J. Crutchfield & M. C. Johnston 5726 (holotype TEX!).



Fig. 9 *Chrysanthellum lamaulipense*, from holotype

Prostrate glabrous annual herbs. Leaves bipinnatisect, 2-6 cm long. Peduncles slender, at maturity 4-12 cm long. Heads 12-15 mm across, 5-6 mm high, subtended by 2-4 linear bracts, 2-4 mm long; involucre double, an outer series of 5, narrowly ovate, scarious-margined, phyllaries 4-5 mm long, 1.5-2.0 mm wide, the inner series similar but somewhat smaller. Ray florets ca. 21, yellow, the ligules ca. 6 mm long, 1.2-2.0 mm wide, 4-nerved, obtuse or indistinctly notched. Disk flowers yellow, at least some of them quite fertile, 5(4)-lobed, the tube ca. 1 mm long, limb ca. 2 mm long. Ray achenes circinate, the abaxial surfaces rugose at maturity, the inner surfaces smooth, ca. 0.8 mm wide, 1.8-2.0 mm in diameter. Disk achenes narrowly elliptic, ca. 4 mm long, 2 mm wide, bordered with conspicuous, erose, often ciliate, corky wings.

Chromosome number, $2n = 8$ II.

DISTRIBUTION (Fig. 6). Known only from the holotype and one additional collection (Tamaulipas: 2.4 mi N of Aldama, 16 Sep 1964, Strother 544, TEX).

The species is undoubtedly closely related to Chrysanthellum involutum but is readily distinguished by its smaller, less petiolate, mid-stem leaves, generally smaller floral parts and especially by its quite fertile disk florets. In all these characters C. tamaulipense approaches C. indicum but its circinate, marginal achenes and 4-nerved ligules place it nearer C. involutum.

EXCLUDED SPECIES

Chrysanthellum smithii Backer = Neuractis smithii (Backer) B. Turner, comb. nov.--based on Chrysanthellum smithii Backer, Bull. Jard. Bot. Buitenzorg 12:39. 1913.

Chrysanthellum leschenaultii (Cass.) Backer ex Koster = Neuractis leschenaultii Cass.

LITERATURE CITED

- Alexander, E.J. 1955. Chrysanthellum, in N. Amer. Fl. ser II. 2:147-149.
- Backer, C.A. 1965. Chrysanthellum, in Fl. Java 2:166. 1965.
- Cabrera, A.L. 1973. Notas sobre tipos de compuestas sudamericanas in herbarious Eureopas. Bol. Soc. Argentina Bot. 15:113-125.
- De Jong, D.C.D. and E.K. Longpre. 1963. Chromosome studies in Mexican Compositae. Rhodora 65:763. 1963.
- Eliasson, V. 1967. Studies of Galapagos plants. IV. The genus Chrysanthellum. Svensk Bot. Tidskr. 61:88-92.
- _____ . 1972. Studies in Galapagos plants XIII. Bot. Notiser

125:320-322.

- Keil, D.J. and T.F. Stuessy. 1975. Chromosome counts of Compositae from the United States, Mexico and Guatemala. *Rhodora* 77:171-195.
- McVaugh, R. 1984. Chrysanthellum, in *Flora Novo-Galiciana* 12:223-228.
- Milne-Redhead, E. 1948. Chrysanthellum in Tropical African plants. XX. *Kew Bull.* 1948:466.
- Morton, C.V. 1945. Mexican phanerogams described by M.E. Jones. *Contr. U.S. Natl. Herb.* 29:129.
- Olorode, O. 1974. Chromosome numbers in Nigerian Compositae. *Bot. J. Linn. Soc.* 68:329-335.
- Powell, A.M. and B.L. Turner. 1963. Chromosome numbers in the Compositae. VII. *Madrono* 17:128-140.
- Renard et al. 1983. in *Bull. Jard. Bot. Nat. Belg.* 53:342-371.
- Smith, B.N. and B.L. Turner. 1975. Distribution of Kranz syndrome among Asteraceae. *Amer. J. Bot.* 62:541-545.
- Strother, J. 1972. Chromosome studies in western North American Compositae. *Amer. J. Bot.* 59:242-247.
- Wild, H. 1967. Chrysanthellum. *Kirkia* 6:34-35.