

CHROMOSOME NUMBERS OF NEOTROPICAL MALPIGHIACEAE

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For some years I have been accumulating meiotic chromosome counts for neotropical Malpighiaceae, as time and materials made that possible. Some of those counts have been reported by me and my associates in scattered revisionary publications; the rest have never been published, and a number of those are the first counts in their genus. My purpose here is to report all those numbers in one place, and to comment on the systematic implications of some of them. This paper does not pretend to list all the chromosome numbers that have been published for neotropical Malpighiaceae, principally because I have not had the opportunity to verify the identity of the vouchers for most of those counts; some of those vouchers probably do not exist. However, I have included in Table 1 a few counts made and published by others but vouchered by specimens whose identification I have verified, plus one count whose voucher, although currently unavailable for verification, I am reasonably confident was identified correctly.

All of the counts made at the University of Michigan are from pollen mother cells undergoing meiosis; the pairs of chromosomes were stained in the usual acidic preparation with carmine or orcein and counted in squashed cells. Except where a publication is cited in a footnote, all these counts were made by me or Bronwen Gates, who did a number of chromosome counts, especially in the genus *Banisteriopsis*, when she was working in Malpighiaceae under my direction. All of the vouchers cited are deposited in the University of Michigan Herbarium (MICH) except where some other herbarium is cited. Where two or more vouchers are cited, that species was counted independently in material from each voucher. Except for cases where the voucher is followed by an asterisk (*), all of the counts made at the University of Michigan are documented by permanent microscope slides in my personal collection, which will afford the possibility of re-study and correction in the case of counts that might come into question. A star (*) denotes a collection for which I made the count in buds from greenhouse-grown plants derived from the voucher; all other counts made at Michigan were from buds collected from the original voucher.

DISCUSSION

SUBFAMILY BYRSONIMOIDEAE

When I proposed this subfamily (W. Anderson 1978), I used as one of the bases for the group its possession of chromosome numbers of $n = 6$ or multiples of 6. That generalization continues to be supported by most, but not all, of the counts recorded in Table 1. The genera cited in Table 1 that I would place in subfamily Byrsonimoideae are *Blepharandra*, *Byrsonima*, *Diacidia*, *Galphimia*, *Lophanthera*,

TABLE 1. Chromosome numbers of neotropical Malpighiaceae.

Genus + species	<i>n</i>	Voucher
<i>Aspicarpa</i>		
<i>brevipes</i> (DC.) W. R. Anderson	40	Anderson & Laskowski 3668*
<i>harleyi</i> W. R. Anderson	40	Anderson 11758
<i>humilis</i> Benth. ¹	40	Anderson & Laskowski 3584*
<i>hyssopifolia</i> A. Gray	40	Anderson 13321
<i>pulchella</i> (Griseb.) O'Don. & Lourt.	40	Anderson 11173
<i>schininii</i> W. R. Anderson	20	Anderson 11777
<i>Banisteriopsis</i>		
<i>acapulcensis</i> var. <i>llanensis</i> B. Gates	10	Gates 307*
<i>acerosa</i> (Nied.) B. Gates	10	Anderson 11177
<i>andersonii</i> B. Gates	10	Gates 351
<i>angustifolia</i> (Adr. Juss.) B. Gates	10	Anderson 11592; Gates 348
<i>argyrophylla</i> (Adr. Juss.) B. Gates	10	Anderson 11142; Gates 399
<i>campestris</i> (Adr. Juss.) Little	10	Gates 357
<i>cipoënsis</i> B. Gates	10	Gates 386
<i>hypericifolia</i> (Adr. Juss.) W. R. Anderson & B. Gates	10	Anderson 11548*
<i>laevifolia</i> (Adr. Juss.) B. Gates	10	Anderson 11143
<i>muricata</i> (Cav.) Cuatr.	20	Anderson 11148
<i>oxyclada</i> (Adr. Juss.) B. Gates	10	Anderson 11144
<i>pulchra</i> B. Gates var. <i>pulchra</i>	10	Anderson 11789
<i>valvata</i> W. R. Anderson & B. Gates	10	Anderson 12500
<i>vernoniifolia</i> (Adr. Juss.) B. Gates	10	Anderson 11490
<i>Barnebya</i>		
<i>harleyi</i> W. R. Anderson & B. Gates	(29) 30 ²	Guidon 2926
<i>Blepharandra</i>		
<i>hypoleuca</i> (Benth.) Griseb.	12	Holst 3839
<i>Bunchosia</i>		
<i>montana</i> Adr. Juss.	20	Anderson 13123
<i>Byrsonima</i>		
<i>basiloba</i> Adr. Juss.	12	Anderson 11423
<i>crassifolia</i> (L.) H. B. K.	12	Bawa 118 (MO) ³
<i>macrophylla</i> (Pers.) W. R. Anderson	12	Anderson 11565
<i>oblongifolia</i> Adr. Juss.	12	Anderson 11496
<i>rigida</i> Adr. Juss.	12	Anderson 11371
<i>sericea</i> DC.	12	Anderson 7630
<i>Callaeum</i>		
<i>macropterum</i> (DC.) D. M. Johnson	10	Daniel 1941 ⁴
<i>septentrionale</i> (Adr. Juss.) D. M. Johnson	10	Anderson & Laskowski 4046
<i>Camarea</i>		
<i>affinis</i> St.-Hil.	17	Anderson 11243
<i>axillaris</i> St.-Hil.	17	Anderson 9012
<i>ericoides</i> St.-Hil.	17	Anderson 11443 (NY), 11497
<i>hirsuta</i> St.-Hil.	17	Anderson 6849, 7948
<i>Cordobia</i>		
<i>argentea</i> (Griseb.) Nied.	9	Anderson 12359
<i>Diacidia</i>		
<i>rufa</i> (Maguire) W. R. Anderson	(23) 24 ⁵	Anderson 13373
<i>Dicella</i>		
<i>bracteosa</i> (Adr. Juss.) Griseb.	10	Anderson 11761
<i>Echinopterys</i>		
<i>eglandulosa</i> (Adr. Juss.) Small	10	Cochrane & Cochrane 8505
<i>eglandulosa</i> (Adr. Juss.) Small	20	Daniel 3359
<i>Ectopopterys</i>		
<i>soejartoi</i> W. R. Anderson	8	Soejarto et al. 4416

TABLE 1 continued.

<i>Galphimia</i>		
<i>angustifolia</i> Benth.	12	Lynch 710 (MO) ⁶
<i>glauca</i> Cav.	6	Anderson 13555; Breedlove 7072 (CAS) ⁷ , 19114 (CAS) ⁸
<i>gracilis</i> Bartl.	12	Fryxell & Anderson 3484; MacBryde & Herrera- MacBryde 63 (MO) ⁶
<i>Gaudichaudia</i>		
<i>albida</i> Schlecht. & Cham. sens. str.	40	Anderson & Laskowski 4259*; Anderson 13198
<i>albida</i> Schlecht. & Cham. sens. lat.	40	Anderson & Laskowski 3844#2*, 4147*, 4467*; Anderson 13216, 13224; Koch & Fryxell 83253
<i>chasei</i> W. R. Anderson	40	Anderson 12945
<i>cycloptera</i> (DC.) W. R. Anderson	40	Anderson & Laskowski 3669*, 4545**
<i>cynanchoides</i> H. B. K.	40	Anderson 12642
<i>diandra</i> (Nied.) Chodat	40	Anderson 13309; Daniel & Butterwick 3257
<i>galeottiana</i> (Nied.) Chodat	40	Anderson & Laskowski 4087*
<i>krusei</i> W. R. Anderson	40	Anderson 12868
<i>mcvaughii</i> W. R. Anderson	40	Anderson 12699
<i>subverticillata</i> Rose	40	Anderson & Laskowski 3698*
sp. aff. <i>cynanchoides</i> H. B. K.	80	Anderson & Laskowski 3645*; Anderson 12624
sp. aff. <i>cycloptera</i> (DC.) W. R. Anderson	80	Anderson & Laskowski 3925*; Anderson 13265
sp. aff. <i>diandra</i> (Nied.) Chodat	80	Anderson 12937
sp.	80	Anderson & Laskowski 3707*, 3714*, 4293*; Anderson 12990, 13031, 13148, 13316; Rzedowski 32522*
sp.	120	Anderson & Laskowski 4056*
<i>Heteropterys</i>		
<i>byrsonimifolia</i> Adr. Juss.	10	Anderson 11571
<i>campestris</i> Adr. Juss.	10	Anderson 11450, 11517
<i>coleoptera</i> Adr. Juss.	10	T. A. Silva 02 (R) ⁹
<i>escalloniifolia</i> Adr. Juss.	10	Anderson 11531
<i>sericea</i> (Cav.) Adr. Juss. in St.-Hil.	10	Anderson 11578
<i>Janusia</i>		
<i>anisandra</i> (Adr. Juss.) Griseb.	40	Anderson 9180, 11755
<i>californica</i> Benth.	10	Anderson 12553, 12539; Daniel 3373
<i>gracilis</i> A. Gray	20	Anderson & Laskowski 3520*, 4558*, 4559*
<i>guaranitica</i> (St.-Hil.) Adr. Juss.	19	Anderson 11136, 11174, 11176
<i>janusioides</i> (Adr. Juss.) W. R. Anderson sens. str.	20	Anderson 12517
<i>janusioides</i> (Adr. Juss.) W. R. Anderson sens. lat.	20	Anderson 11313
<i>lindmanii</i> (Skotts.) W. R. Anderson	20	Anderson 10614, 11090
<i>linearis</i> Wiggins	10	Anderson 12551
<i>mediterranea</i> (Vell.) W. R. Anderson	20	Anderson 7752, 11183
<i>occhionii</i> W. R. Anderson	20	Anderson 11151, 11175
<i>prancei</i> W. R. Anderson	20	Anderson 12334
<i>schwannioides</i> W. R. Anderson	20	Anderson 12514
<i>Jubelina</i>		
<i>magnifica</i> W. R. Anderson	10	Anderson 13361

TABLE 1 concluded.

<i>Lophanthera</i>		
<i>hammelii</i> W. R. Anderson	6	Schatz 1034 ¹⁰
<i>lactescens</i> Ducke	6	Anderson 11665
<i>Malpighia</i>		
<i>glabra</i> L.	10	Bawa 163 (MO) ¹¹
<i>Mascagnia</i>		
<i>cordifolia</i> (Adr. Juss.) Griseb.	20	Anderson 11246
<i>polybotrya</i> (Adr. Juss.) Nied.	10	Anderson 12944
<i>Mcvaughia</i>		
<i>bahiana</i> W. R. Anderson	10	Anderson 11740
<i>Peixotoa</i>		
<i>glabra</i> Adr. Juss.	10	Anderson 11549
<i>hispidula</i> Adr. Juss.	10	T. A. Silva 01 ⁹
<i>reticulata</i> Griseb.	[15] ¹²	Anderson 11790
<i>Peregrina</i>		
<i>linearifolia</i> (St.-Hil.) W. R. Anderson	19	Anderson 11764
<i>Pterandra</i>		
<i>egleri</i> W. R. Anderson	12	Anderson 10895
<i>Stigmaphyllon</i>		
<i>jatrophifolium</i> Adr. Juss.	10	Anderson 12371
<i>lalandianum</i> Adr. Juss.	10	Anderson 11610, 11666
<i>paralias</i> Adr. Juss.	10	Ormond 650 ⁹
<i>retusum</i> Griseb.	10	Fryxell & Anderson 3485
<i>Thryallis</i>		
<i>longifolia</i> Mart. ¹³	(29) 30 ²	Anderson 12515
<i>Verrucularia</i>		
<i>glaucophylla</i> Adr. Juss.	6	Anderson 13704

¹The taxonomy of *Aspicarpa* in North America is not fully resolved, and it is possible that *A. humilis* will ultimately fall into synonymy under *A. hirtella* L. C. Rich.

²The best figures indicate that the correct count is 30, but it is possible that I am consistently misinterpreting as two one pair whose halves are very loosely associated in late prophase.

³Bawa 1973.

⁴Baker & Parfitt 1986, under the name *Mascagnia macroptera*.

⁵No perfect figures were found. The best figures available show that n = at least 23, and probably 24.

⁶MacBryde 1970.

⁷Kyhos 1966.

⁸Seavey 1975.

⁹Ormond et al. 1981.

¹⁰This count was made on buds of *Hammel* 13339, of which the voucher specimens were subsequently lost. *Schatz* 1034 is a fruiting specimen that was made later from the same tree as *Hammel* 13339, and can therefore serve as a voucher for this chromosome count.

¹¹Bawa 1973; voucher unavailable for verification.

¹²Meiosis is highly irregular, with anaphase figures only occasionally 15+15, more often 14+16 or 13+17. This species is probably a substerile triploid; most seed-set is apparently apomictic. See C. Anderson, 1982, pp. 65–66.

¹³The taxonomy of *Thryallis* needs study. This specific epithet is applied provisionally, with the understanding that the voucher may prove to represent an undescribed species when the genus is revised.

Mcvaughia, *Pterandra*, and *Verrucularia*. With one exception all the numbers in Table 1 for those genera are 6, 12, or 24. The exception is *Mcvaughia bahiana*, which has $n = 10$, the number characteristic of subfamily Malpighioideae. Nevertheless, I remain quite convinced that *Mcvaughia* belongs in subfamily Byrsonimoideae, for the reasons advanced when it was described (W. Anderson 1979), and I can only suppose that $n = 10$ in this genus was derived independently by aneuploid reduction from $n = 12$. Unfortunately we still have no count for *Burdachia*, the probable sister-genus of *Mcvaughia*.

The number $n = 6$ is the lowest known for the Malpighiaceae, and seems likely to be basal in the family (W. Anderson 1983). The plants showing that number are assignable to *Galphimia*, *Lophanthera*, or *Verrucularia*, all of which I placed in tribe Galphimieae in 1978. As I have recently pointed out (W. Anderson 1990b), *Lophanthera* and *Verrucularia* share several plesiomorphic morphological characters which, taken with their low chromosome numbers, suggest that they may be near the base of the phylogeny of the family. In the light of these observations it would be especially interesting to learn chromosome numbers for *Spachea*, the fourth genus of Galphimieae.

Anderson and Gates (1981) considered *Barnebya* to be fairly closely related to the Byrsonimoideae, in spite of its having winged fruits that resemble those common in subfamily Malpighioideae. The relationships of this problematic genus are not clarified by its chromosome number, which seems to be $n = 30$. That number is a multiple of both 6, which is basal in the Byrsonimoideae, and 10, which is basal in Malpighioideae, but in neither case can I postulate derivation of 30 through a series of doublings. *Barnebya* remains an intriguing enigma.

SUBFAMILY MALPIGHIOIDEAE

Most of the remaining genera in Table 1 form a more or less natural group, which must take the name Malpighioideae because it includes *Malpighia*, the type of the family. The group is characterized by derived pollen, winged fruits, a climbing habit, and a chromosome number based on $n = 10$, although all of these generalizations are contradicted by one or another of the genera listed here. *Banisteriopsis*, *Callaeum*, *Echinopterys*, *Heteropterys*, *Jubelina*, *Mascagnia*, *Peixotoa*, and *Stigmaphyllon* all fit fairly comfortably into this group and I shall say little more about them; their chromosome numbers are monotonously uniform, with only rare departures from diploid ($n = 10$) to tetraploid ($n = 20$), and therefore not very informative. *Aspicarpa*, *Camarea*, *Gaudichaudia*, *Janusia*, and *Peregrina* make up the tribe Gaudichaudieae, which is derived from *Banisteriopsis* and therefore clearly belongs in this subfamily too; this group is discussed in more detail below. *Cordobia* and *Ectopterys* are wing-fruited vines which, on the basis of their morphology, I place with confidence in this subfamily. They are not closely related to each other, so I interpret their chromosome numbers ($n = 9$ and 8, respectively) as independently derived through aneuploid reduction from ancestors with $n = 10$. *Malpighia* is derived in having a shrubby habit and fleshy fruits, but the pyrenes of the fruit show rudimentary winglets under the fleshy exocarp, and as I have said before (most recently in 1990a, pp. 50–51), *Malpighia* is so close to *Mascagnia* in most aspects of its morphology that it becomes increasingly difficult to maintain the two as separate genera, so *Malpighia* certainly must go into this subfamily with *Mascagnia*. Its chromosome number ($n = 10$) supports that placement.

The genera that remain unmentioned are *Bunchosia*, *Dicella*, and *Thryallis*, all of which I considered to have more or less uncertain affinities in 1978. At that time I was willing to assert that *Dicella*, in spite of its unwinged fruit, "certainly belongs with other vining genera. . . ." The chromosome number now available, $n = 10$, strengthens that claim, and for now, at least, I am content to leave *Dicella* in the Malpighioideae.

Bunchosia is a genus of trees and shrubs with fleshy fruits of a structure unique in the family. In 1978 I pointed out that *Bunchosia* shares a number of character-states with *Heladena*, a genus of vines bearing dry, unwinged, indehiscent cocci, and Lowrie (1982) stated that the two genera have very similar pollen. If that relationship is supported by additional evidence, and if *Heladena* is to be classified with other genera of vines with dry fruits, then *Bunchosia* may have to remain in the Malpighioideae, anomalous though it seems in that assemblage. The chromosome number reported here, $n = 20$, is consistent with such a disposition; no count has been reported for *Heladena*.

Thryallis, like *Barnebya*, remains an unsolved puzzle. As I noted in 1978, its habit, pollen, and stigmas suggest derivation from one of the wing-fruited vines that would fall in the Malpighioideae, but its links are not obvious and its unique derived character-states are most impressive. A chromosome number of $n = 30$ is as unhelpful as its other autapomorphies. Derivation directly from an ancestor with $n = 10$ or 20 is difficult to postulate, but a hybrid between a diploid and a tetraploid, followed by doubling in the progeny, could produce such an apparent hexaploid. We must hope that molecular studies now under way will shed some light on the relationships of isolated genera like *Thryallis*.

TRIBE GAUDICHAUDIEAE

Adrien de Jussieu first recognized this group in 1840 and later (1843) refined his concept to one that matches mine, although the generic nomenclature has changed somewhat. I place here the genera *Aspicarpa*, *Camarea*, *Gaudichaudia*, *Janusia*, and *Peregrina*, all of which are represented in Table 1. These genera share a reduced androecium and a terminal capitate stigma; most members of the tribe have only one style and produce a carpophore at the base of each carpel, and many (some species in every genus except *Peregrina*) produce cleistogamous flowers in addition to chasmogamous flowers (W. Anderson 1980). The group seems likely to have originated in the genus *Banisteriopsis*, which hardly differs from some species of *Janusia* except for possessing a full complement of stamens and, usually, three styles. Chromosome numbers are much more interesting in this tribe than in most other Malpighiaceae, showing evidence of both aneuploidy and recurrent cycles of polyploidy.

Janusia comprises two rather different groups, approximately 12–15 species in South America (section *Janusia*) and three species in North America (section *Metajanusia* Niedenzu). The latter are all natives of the deserts of northwestern Mexico and the adjacent United States. They are *J. californica* and *J. linearis*, which are both diploid ($n = 10$), and *J. gracilis*, a tetraploid with $n = 20$. The three are very similar morphologically; the diploids have broad and narrow leaves, respectively, and the tetraploid has leaves of intermediate width. It is also intermediate between the diploids in most other characters (Table 2), and has few if any uniquely distinguishing character-states of its own, which leads me to suggest that *J. gracilis* is an allotetraploid derived, perhaps more than once, from a hybrid

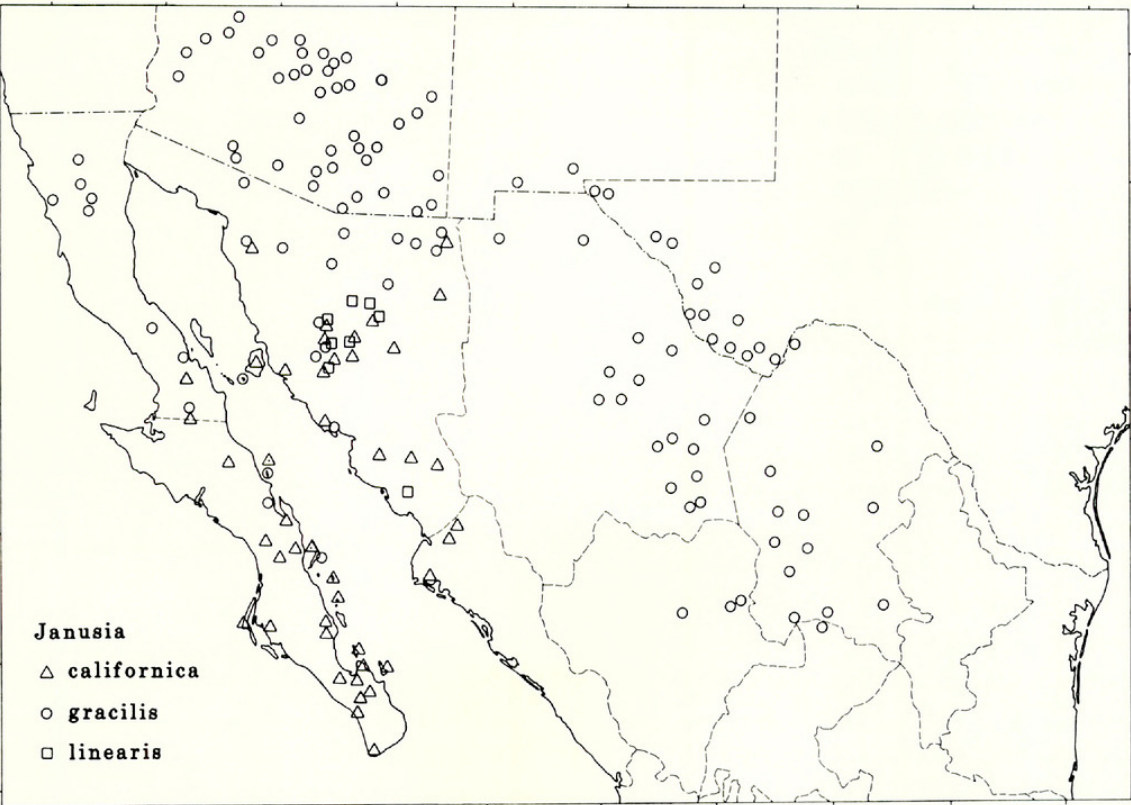


FIG. 1. Distribution of *Janusia* in North America.

between *J. californica* and *J. linearis*. All three species in this little complex occur sympatrically in western Sonora, but the putative allotetraploid has a range that far exceeds the range of either diploid (Fig. 1). Pairing is strictly normal in meiosis in all three species.

TABLE 2. Morphological characters in *Janusia* section *Metajanusia*.

	<i>J. californica</i>	<i>J. gracilis</i>	<i>J. linearis</i>
Leaf length/width	1.2–2.5	4–10	12–40
Leaf margin	toothed	toothed	entire
Sepal length (mm)	1.7–2.5	2.0–2.5	2.5–3.0
Sepal vesture	glabrous	hairy	hairy
Style length (mm)	1.5–1.9	1.9–2.3	2.1–3.0

The other species of *Janusia* in Table 1 occur in central and southern Brazil, as well as Paraguay, Argentina, and Bolivia. Most have $n = 20$, but *J. guaranitica* has $n = 19$ and *J. anisandra* has $n = 40$. These counts suggest that section *Janusia* is probably a clade based on an ancestor that was already tetraploid relative to $x = 10$ in *Banisteriopsis*, that $n = 19$ in *J. guaranitica* is aneuploid from $n = 20$, and that *J. anisandra* is tetraploid relative to $n = 20$ at the base of the clade. At this time I have no basis for suggesting that the doubling in *J. anisandra* may have been associated with hybridization. All of the species of *Janusia* section *Janusia* that I have studied cytologically show only normal pairing in meiosis.

Aspicarpa and *Camarea* are reduced in both stature and the ornamentation of their fruits. *Camarea* occurs only in southern South America; *Aspicarpa* is both there and in Mexico and the adjacent United States. Plants of both genera are suffrutescent or have trailing, almost herbaceous stems from a perennial base; they

usually do not climb, although a few populations in Mexico with very long stems trailing among shrubs show some weak tendency to twine. The ancestral samara as found in *Banisteriopsis* and *Janusia* has been reduced to a nutlet bearing rudimentary winglets or irregular outgrowths. The two genera differ morphologically in the details of their androecia. Chromosome numbers are $n = 20$ or 40 in *Aspicarpa*, 17 in *Camarea*. These suggest that *Aspicarpa* and *Camarea* may have diverged from a common ancestor with $n = 20$, *Camarea* representing a clade set apart by an early aneuploid reduction to $n = 17$, most extant species of *Aspicarpa* being tetraploid relative to that ancestor. Of the species of *Aspicarpa* listed in Table 1, the first, third, and fourth, all tetraploid, are Mexican; the other three, including the only known diploid, are South American from the same area as *Janusia* section *Janusia*.

Peregrina is a monotypic genus of southern Brazil and Paraguay that has a habit and androecium like those of some species of *Aspicarpa* but a samara with a well-developed lateral wing like that found in *Gaudichaudia* (see below). It is obviously close to all of the other genera in the tribe but will not fit happily in any of them, which was my reason for segregating it as a genus (W. Anderson 1985). Its sole species has 19 pairs of chromosomes, presumably through aneuploid reduction from $n = 20$ in an ancestor near the branch from *Janusia* section *Janusia* that gave rise to *Aspicarpa*. It is interesting to note that *Janusia guaranitica* also has $n = 19$, but the two species are otherwise so dissimilar that it would hardly be parsimonious to suggest a close relationship between them; they are much more likely to have reached $n = 19$ through independent reductions.

GENUS GAUDICHAUDIA

This is a genus of at least ten and perhaps 25 species, mostly Mexican but with a few species extending into Central America and one reaching Colombia and western Venezuela. The genus seems almost certain to have diversified in Mexico, with the plants now in Central America and northwestern South America representing a relatively recent extension of the genus's range southward, not remnants of ancestral immigrants from central or southern South America. Most species of *Gaudichaudia* are vines, but a few are shrubby. They resemble *Janusia* spp. in their androecium and gynoecium, and the well-developed carpophore of their samaras. Most species have the cleistogamous flowers peculiar to this tribe, which are two-carpellate and therefore produce only two samaras, unlike the chasmogamous flowers, which are three-carpellate (W. Anderson 1980). *Gaudichaudia* is distinguished by its eglandular leaves and its samaras, which have the lateral wing well developed and the dorsal wing rudimentary, the opposite of the situation in *Janusia*.

Of the many chromosome numbers now available for *Gaudichaudia*¹⁴, most

¹⁴In addition to the chromosome counts listed for *Gaudichaudia* in Table 1, I have made a number of attempts that produced figures not good enough to yield a definite count but good enough to tell the approximate ploidy level of the plant. In all my work on this genus, I have seen no evidence of aneuploidy, and I now suspect that all gaudichaudias are euploid. I list here seven very rough counts in *Gaudichaudia*, in the belief that they may be of value to future students of the genus. Anderson & Laskowski 4236, diploid, *G. albida* Schlecht. & Cham. sens. str.; Anderson & Laskowski 4206, diploid, *G. albida* Schlecht. & Cham. sens. lat.; Anderson 13285, diploid, *G. cynanchoides* H. B. K.; Koch & Fryxell 82218, diploid, *G. mcvaughii* W. R. Anderson; Anderson & Laskowski 3926, tetraploid, *G. sp. aff. cycloptera* (DC.) W. R. Anderson; Anderson 13291, tetraploid, *G. sp.*; Anderson 13286, hexaploid, *G. sp.*

are either $n = 40$ or $n = 80$; $n = 120$ also occurs. I assume that the ancestor of the genus had 40 pairs of chromosomes, tetraploid with respect to some ancestor in *Janusia* section *Janusia* and octoploid relative to a more remote ancestor in *Banisteriopsis*. In the comments that follow I shall use "diploid" to refer to plants with $n = 40$, "tetraploid" for plants with $n = 80$, and "polyploid" for plants with $n =$ either 80 or 120.

The diploids in *Gaudichaudia* are mostly assignable to morphologically recognizable species, which is evident from Table 1. Their fruits include three rather different types, which Niedenzu (1928) used to divide the genus into subgenera and sections, and I shall use the same three sections as a framework for my comments here.

Section *Gaudichaudia* comprises species in which all three samaras from a chasmogamous flower, and both samaras from a cleistogamous flower if such flowers are present, are alike and have a symmetrical orbicular, ovoid, or obovoid shape (Fig. 2a). Of the diploid species in Table 1, the ones that fall in section *Gaudichaudia* are *G. chasei*, *G. cycloptera*, *G. cynanchoides*, *G. krusei*, *G. mcvaughii*, and *G. subverticillata*. *Gaudichaudia chasei*, *G. krusei*, *G. mcvaughii*, and *G. subverticillata* are especially intriguing because they all lack cleistogamous flowers, all produce three styles instead of one, and none is an aggressive colonizer like many gaudichaudias; in addition, *G. krusei* and *G. subverticillata* are small shrubs, not vines. If it were not for the convincing links through *Janusia* to an origin in *Banisteriopsis*, I would suppose three styles and a lack of cleistogamous flowers to be ancestral character-states in this genus, but in the light of what we know about the rest of the tribe that seems unlikely, so perhaps these species represent a clade in which the cleistogamous flowers were lost, probably in correlation with a shift away from weediness, and the three styles of a remote ancestor became able to be expressed once again. The other two species in Table 1, *G. cycloptera* and *G. cynanchoides*, bear cleistogamous flowers and are more aggressive plants, but rather different in their ecology, with *G. cycloptera* more likely to be found in mesic places and *G. cynanchoides* often, but not always, found in drier and more disturbed shrubby habitats.

Section *Zygopterys* (Nied.) Nied. contains the single species *G. galeottiana*. As in the preceding section the samaras of a fruit are all symmetrical and alike, but in this case their shape is rather different. It is more or less Y-shaped, with three rounded lobes, two upper and one lower, with a deep division between the two upper lobes and a constriction at the waist between the lower lobe and the two upper lobes (Fig. 2b). This section can be seen as intermediate between the other two; it resembles section *Gaudichaudia* in having all the samaras of a fruit alike, but its samara is somewhat like the anterior samara of section *Tritomopterys* in shape. *Gaudichaudia galeottiana* is a weedy species of dry habitats, and relies heavily on cleistogamous flowers for seed set.

Section *Tritomopterys* Adr. Juss. includes *G. albida* and several closely related species whose taxonomy is not yet fully resolved, as well as *G. diandra*. All the plants in this section have both chasmogamous and cleistogamous flowers, and they are often more or less weedy. The three samaras of a chasmogamous flower are all different. The one from the anterior carpel, which lies on the flower's plane of symmetry, is V- or Y-shaped, with the upper lobes longer and more tapered than in *G. galeottiana* and the lower lobe relatively less developed. The samaras coming from the two lateral carpels of the same flower are one-sided, having the anterior upper lobe of the wing well developed and the other rudimentary or undeveloped. The two lateral samaras are mirror-images of each other, i.e., one

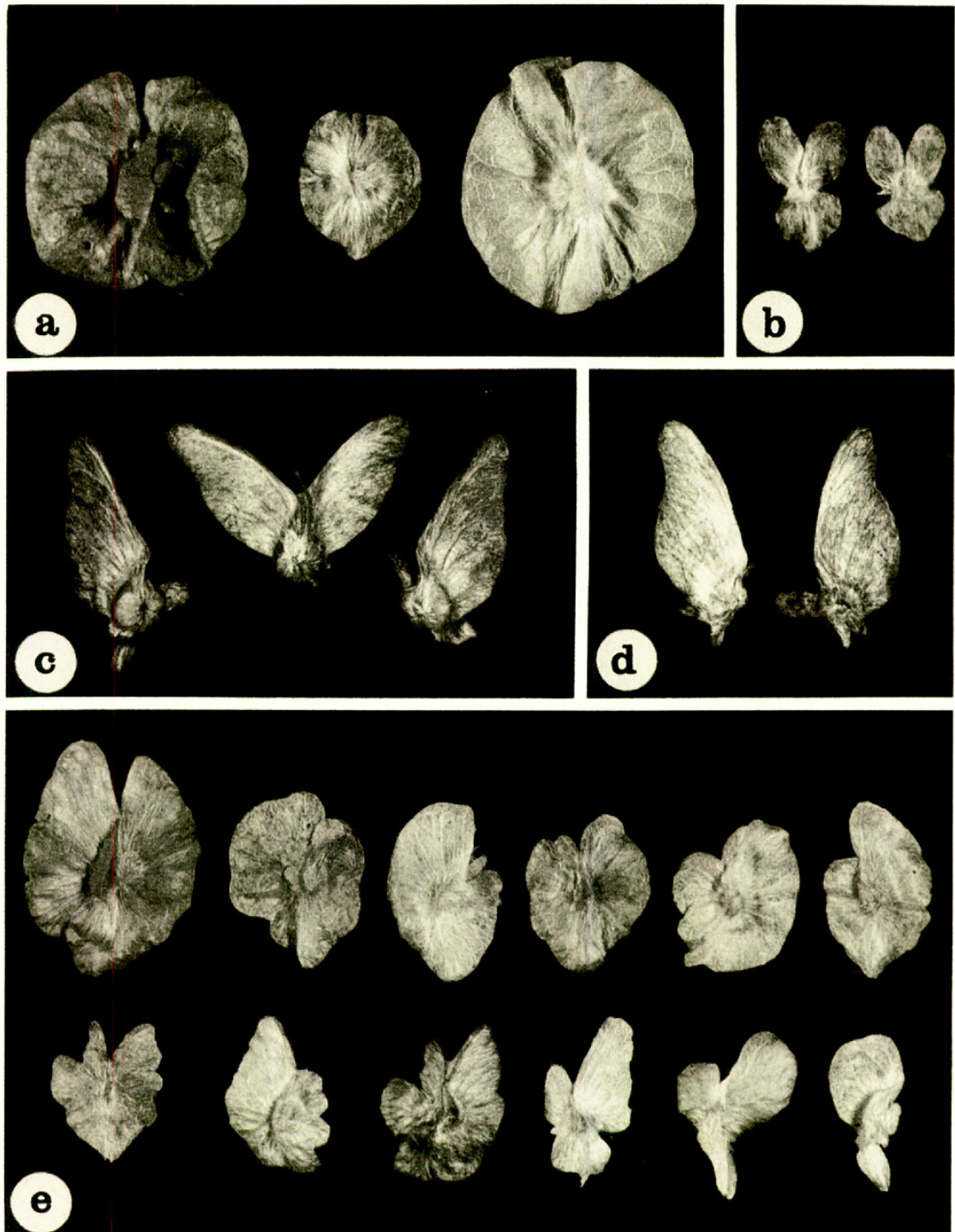


FIG. 2. Samaras of *Gaudichaudia*, all $\times 1.75$. a, section *Gaudichaudia*; left to right: *G. mcvaughii* (A 12699, from a chasmogamous flower), *G. cynanchoides* (A 13285, from a cleistogamous flower), *G. cycloptera* (A & L 4510, from a cleistogamous flower). b, section *Zygopterys*, *G. galeottiana* (A & L 4087, both from cleistogamous flowers). c & d, section *Tritomopterys*, *G. diandra* (A & L 3649); c, three samaras from a single chasmogamous flower, the central one from the anterior carpel; d, two samaras from a single cleistogamous flower. e, known or probable polyploids, *G. spp.*; upper row, left to right: A 13291, A 13031, A 12661, A & L 4108#5, A 13316, A 12624; lower row, left to right: A & L 4293, A & L 4056, A & L 3867, A 13320, A 13138, A 12990; all from cleistogamous flowers. Abbreviations of collectors: A = Anderson; A & L = Anderson & Laskowski.

has its right side developed and the other has its left side developed (Fig. 2c). As noted above, the cleistogamous flowers in this tribe usually have only two carpels, and the one that is missing is the anterior carpel, so as one might expect, the two samaras produced by a cleistogamous flower in species of section *Tritomopterys* are one-sided (Fig. 2d).

If that were all one encountered in *Gaudichaudia* there would be no great difficulty to its systematics, but in fact many plants will not fit into one of the three morphologically defined sections. It is common to find populations whose fruits are extremely variable and intermediate between the three sections that accommodate the diploid species. These fruits range from being very close to those of section *Gaudichaudia* through every conceivable degree of lobing to ones that are very close to those of section *Tritomopterys*, and in some cases one can find a large portion of that spectrum of variation in a single population, and even on a single plant (Fig. 2e). These plants with intermediate fruits are always vines, they always bear cleistogamous as well as chasmogamous flowers, and they are often aggressive weeds, being especially common in shrubs in overgrazed pastures and along disturbed roadsides. In every case where I have been able to count the chromosomes of plants with such intermediate samaras they have been polyploids, mostly tetraploid with $n = 80$, occasionally hexaploid with $n = 120$ (see Table 1). This correlation between morphology and ploidy level has led me to the obvious hypothesis that the polyploids with intermediate fruits have resulted from hybridization between the diploids with consistent fruits. That hybridization may have happened at the diploid level, followed by restoration of fertility to sterile hybrids through doubling of the chromosomes. These plants would be preadapted for such a scenario through possession of cleistogamous flowers. A single tetraploid plant could produce large quantities of samaras through self-fertilization in the cleistogamous flowers, and thus have a much higher probability of surviving than must usually be the case when a single tetraploid appears among a swarm of diploid hybrids. It is also possible that hybridization has occurred at the tetraploid level, between autotetraploids arising spontaneously among the diploids. That would be consistent with the fact that some tetraploids are morphologically nearly indistinguishable from diploids, and it would help to explain why the variation among the fruits fills the gaps between the diploids so completely, because tetraploid hybrids derived from tetraploid "species" should be able to backcross freely to their parents. The cytological history of the tribe Gaudichaudieae, as reviewed above, suggests that autopolyploidy followed by complete diploidization has happened repeatedly in this group of plants. I have certainly seen no sign of reproductive irregularity in any plant of *Gaudichaudia*; pairing is always perfect at meiosis, fruit-set is heavy, and germination of the fruits is ready and abundant.

The sections of *Gaudichaudia* are not evenly distributed through Mexico (Fig. 3). Section *Gaudichaudia* is mostly central and western, section *Zygopterys* has a restricted distribution in Puebla and Oaxaca, and section *Tritomopterys* extends south and east from western and eastern Mexico, but avoiding the driest part of the Central Plateau, throughout southern Mexico and into Central America and northwestern South America. Sections *Gaudichaudia* and *Zygopterys* are not sympatric, but section *Tritomopterys* has large areas of sympatry with both of them, and of course we have no way of knowing what the distributions of these groups may have been in past times. When we look at the distribution of the probable diploids as compared to the distribution of probable polyploids (Fig. 4), we find that they co-occur today over much of south-central Mexico, but the polyploids

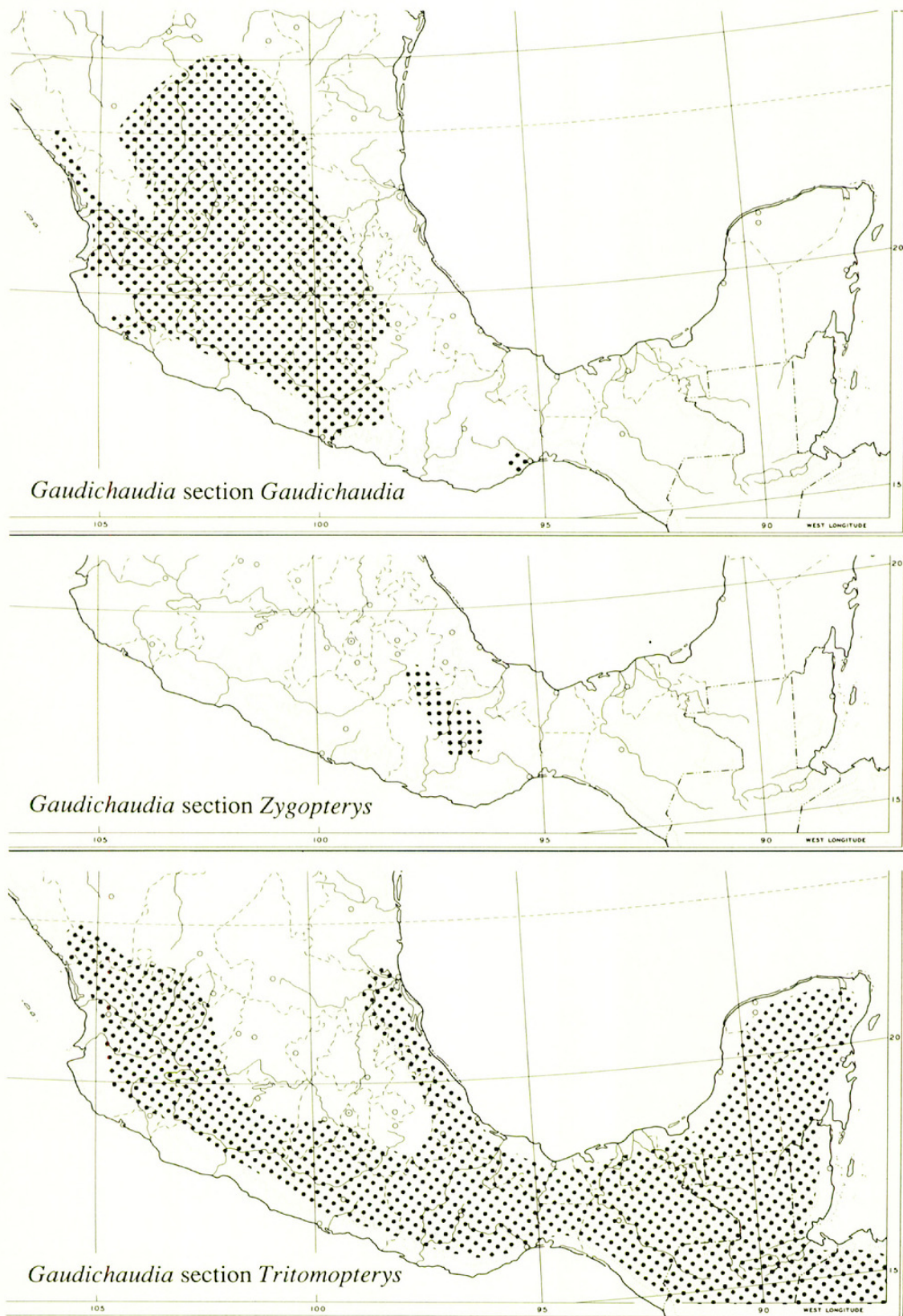
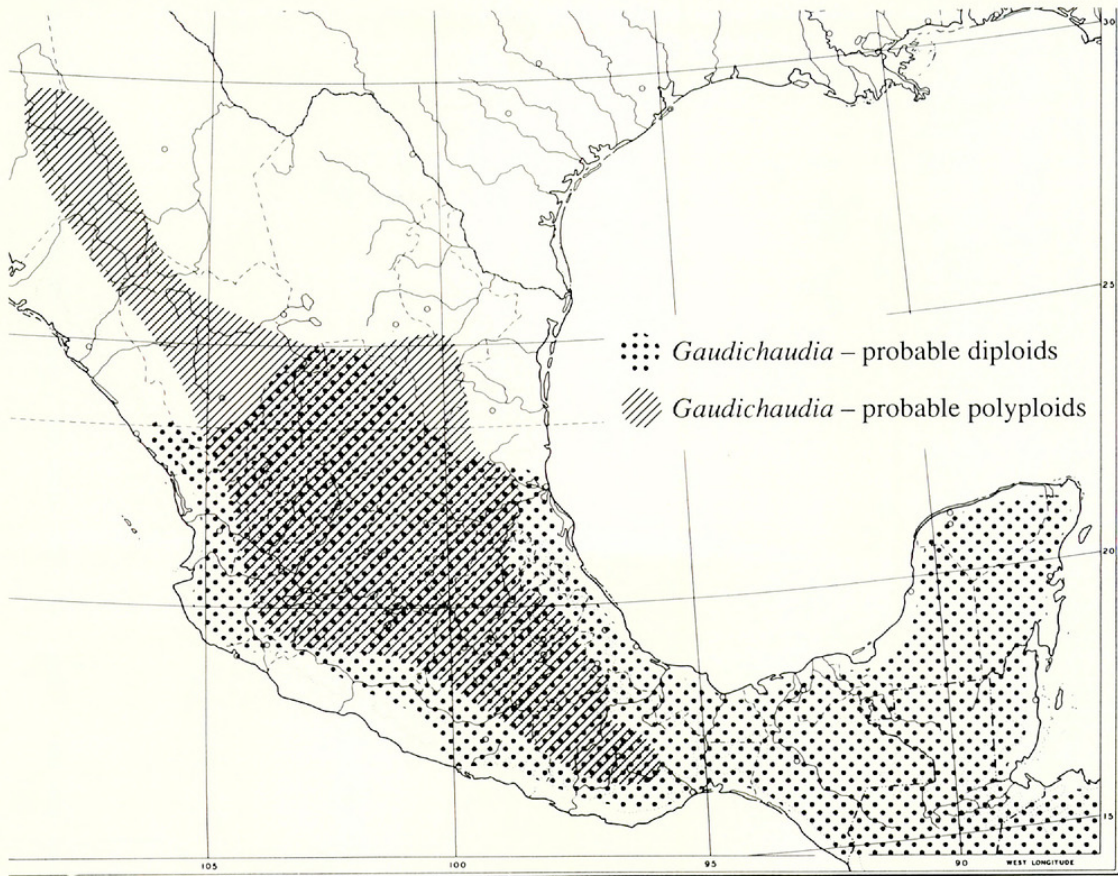


FIG. 3. Distribution of the sections of *Gaudichaudia*; not shown is the continuation of section *Tritomopterys* through Central America into northwestern South America.

FIG. 4. Distribution of *Gaudichaudia* in Mexico.

have expanded farther north into Mexico than any diploid, and there is no hint from morphology that any of the plants found east and south of the Isthmus of Tehuantepec are likely to be polyploids or of hybrid origin.

Chromosome numbers in *Gaudichaudia* have pointed the way toward at least a preliminary understanding of a very complex situation. It seems likely that frequent hybridization has produced the morphological complexity and that polyploidy plays an essential role in the stabilization of those hybrids. Cleistogamous flowers, which were presumably an earlier adaptation for a pioneer habit, probably facilitated the survival of polyploids, and the chasmogamous flowers, which keep some outcrossing available even to plants which depend mostly on cleistogamy for seed-set, enabled backcrossing and further rounds of hybridization, with each new fertile hybrid able to perpetuate itself indefinitely through self-fertilization in the cleistogamous flowers. This process may well be continuing today. It would be especially interesting to investigate the relationship between an aggressively colonizing habit, disturbance caused by humans, and the evolution of the many populations of putative hybrids. It may be that there is a tight correlation between such recent disturbance and the success of these hybrids, and that the hybrids cannot persist in the absence of such disturbance. As for the systematics of the polyploids, that is still to be resolved, as is evident from Table 1. Given their excessive variability, it will probably never be possible to divide them up into the kind of tidy species that taxonomists prefer. We may have to recognize several broadly-defined taxa of convenience, based perhaps on a few relatively reliable characters and our best understanding of their probable origins. Much remains to be done in this perplexing genus.

ACKNOWLEDGMENTS

Bronwen Gates contributed both counts and preparations for subsequent counting by me, and I am grateful for her cheerful assistance. George Rogers photographed the samaras of *Gaudichaudia diandra*. This work was supported by a series of grants from the National Science Foundation to the University of Michigan and, before that, to the New York Botanical Garden; the most recent such grant was BSR-8700340 to the University of Michigan. The following colleagues sent buds fixed in the field for study in Ann Arbor or fruits for cultivation, and I send special thanks to all of them: T. S. Cochrane, T. F. Daniel, L. Emperaire, P. A. Fryxell, B. E. Hammel, B. K. Holst, S. D. Koch, J. Rzedowski, and D. D. Soejarto.

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