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ABSTRACT

SYSTEMATICS OF THE GENUS GUARDIOLA (COMPOSITAE--HELIANTHEAE)

By

Paul Van Faasen

The genus *Guardiola* of the family Compositae, tribe Heliantheae, subtribe Melampodinae, is restricted almost entirely to western Mexico and extreme southeastern Arizona. Most of the species occupy disturbed habitats primarily between 1500 and 2000 meters elevation. *Guardiola* species are mostly perennial with annual herbaceous to lignescent stems arising from a woody caudex. However, subgenus *Rzedowskia*, recognized for the first time in this study, consists of one herbaceous annual species. Twelve species of the genus are recognized, one of which is described as new.

Chromosome numbers of $n = 12$ for eight *Guardiola* species are reported for the first time.

Breeding studies involving seven species of *Guardiola* reveal no barriers to production of F_1 hybrids in the laboratory. Although numerous F_1s were produced, few flowered even though they reached flowering age and size; thus F_1 sterility is suggested.

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Guardiola is thought to have originated in the southern Sierra Madre Occidental and the western Mexican transvolcanic belt because this area is the center of diversity and the most primitive species occur there. Geographic isolation is considered to be an important factor in speciation.

Cytological and morphological evidence suggest two lines of evolutionary development within subgenus *Guardiola*. One of these lines is characterized by plants with broad leaves and the other by narrow-leaved plants. Chemical evidence suggests two lines of evolutionary development within the narrow-leaved species group.

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(COMPOSITAE--HELIANTHEAE)

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INTRODUCTION

The genus _Guardiola_ consists of twelve species restricted to Mexico and southeastern Arizona. Traditionally it has been placed in the subtribe Melampodinae of the Heliantheae (Compositae). The species occur mostly in open, disturbed habitats and on rock outcrops between 1,500 and 2,000 meters elevation in oak-pine forests, the characteristic vegetation type at those elevations in the mountains of western Mexico. The greatest diversity of the genus is centered in the states of Jalisco, Michoacan, and southern Durango where the Sierra Madre Occidental, Sierra Madre del Sur, the trans-Mexican volcanic belt, the high plateau, and the Rio Balsas depression are juxtaposed near the Pacific coast. This is an area noted for both an extremely rich flora and numerous endemics (Rzedowski and McVaugh, 1966), and in which eight of the twelve species of _Guardiola_ occur.

The species of _Guardiola_ appear to be closely related, and the genus seems to have no close allies. This isolation has prompted doubt concerning the appropriateness of its taxonomic position among the Heliantheae. It is placed in the Melampodinae because of its pistillate ray florets and staminate disk florets, but the general aspect of the plant has suggested to some investigators (Gray, 1888; B. L. Turner, personal communication) a relationship with the Coreopsidinae.

Principal reasons for my undertaking a biosystematic study of Guardiola were the difficulty in determining specimens and a rather large accumulation of unidentified specimens in herbaria. Literature concerning the genus is very limited. Robinson's (1899) revision has been the only general account of the genus, and several species have been described subsequently. Furthermore, the newer methods applicable to systematic investigation, particularly chemical, cytological, and genetic approaches, appeared to have promise for the resolution of problems of evolutionary relationship and classification of the species.

Several aspects make Guardiola an ideal genus for systematic investigation. Its restricted distribution allowed field observations throughout most of its range during July and August of 1967. Eight of the twelve species were examined in the field, and living material of them was brought into the laboratory for experimental studies. The plants are easily cultured in the greenhouse, and ordinarily can be brought to flower from seed in four to six months. The hybridization experiments were facilitated by the fact that the plants bear heads containing functionally unisexual florets, pistillate ray and staminate disk florets, which are not self-compatible. Perhaps the least satisfactory aspects of *Guardiola* for study are those which must be based on herbarium specimens. The genus is still inadequately collected, with five species known from only one or two collections. In this study approximately 800 specimens from 14 herbaria were examined.

Solutions to all of the taxonomic problems in *Guardiola* are not in hand, primarily because of inadequate herbarium material. Although several recent studies have been conducted in western Mexico (e.g. Gentry, 1942; White, 1948; Rzedowski and McVaugh, 1966), major portions of this region have received the attention of few collectors and are poorly known floristically. Additional collections from these areas are essential to a more intensive systematic treatment of *Guardiola*. Likewise, additional field work is necessary to provide data and living material for species now known only from herbarium specimens. Detailed investigations on the reproductive biology of the species might also shed more light on their evolutionary relationships. In spite of these areas of ignorance, however, it is hoped that the present treatment will facilitate the determination of specimens and aid in the understanding of evolution in the genus.

HISTORICAL ACCOUNT

The genus _Guardiola_ is based on a specimen of _Guardiola mexicana_ collected between Ario de Rosales and Volcan Jorullo in Michoacan, Mexico, by Humboldt and Bonpland on or about September 19, 1803. The specimen was submitted to Professor Vincente Cervantes who recognized that it belonged to an undescribed genus, and who then named the genus after one of his most zealous and distinguished students, M. le Marquis de Guardiola. Humboldt and Bonpland subsequently (1808) described the genus along with many other taxa collected during that epic expedition to tropical America.

Hooker and Arnott (1838) described the genus _Tulocarpus_ on the basis of a specimen of _Tulocarpus mexicanus_ collected by Lay and Collie in the vicinity of Tepic, Nayarit, Mexico, during the course of Captain Beechey's voyage. Asa Gray (1850) recognized that this taxon was actually a species of _Guardiola_, and renamed it _Guardiola tulocarpus_. In the same and subsequent works, Gray described two new species of _Guardiola_, _G. atriplicifolia_, which he later relegated to synonymy (_G. mexicana_) and _G. platyphylla_; he also described two varieties of _G. tulocarpus_, var. _angustifolia_ and var. *arguta*. Another species, *G. rotundifolia*, was described by Robinson in 1894.

As Mexican specimens of *Guardiola* accumulated in the Gray Herbarium, B. L. Robinson recognized "the impossibility of bringing the diverse forms satisfactorily under the four or five hitherto recognized species." This led him to a study of the genus and in 1899 he published the only revision of *Guardiola*. In this revision he elevated the two varieties of *G. tulocarpus* described by Gray to specific level, described three new species, *G. carinata*, *G. odontophylla*, and *G. rosei*, and retained the four previously described species, thus recognizing a total of nine species. Robinson's 1899 revision is the only publication prior to this study which has attempted to present all of the taxonomic information concerning *Guardiola* in one paper. Since Robinson's revision, one new subspecies and four new species have been described in separate publications.

MORPHOLOGY OF *GUARDIOLA*

Habit

Guardiola was originally described as an herbaceous annual by Humboldt and Bonpland (1808); this error was not completely refuted by Robinson in his 1899 revision. The plants, except the annual *G. pappifera*, are suffrutescent with a heavy woody caudex and taproot. The number of erect, subligneous to succulent, annual stems produced from the woody caudex varies, increasing with age.

Stems

The erect stems which arise from the basal, woody caudex are subligneous to herbaceous and succulent. The caudical thickening arises in the hypocotyl region, if that portion of the plant is at or below the surface of the soil subsequent to germination. In the greenhouse etiolated seedlings produced plants which were recumbent and did not develop a woody caudex. Older caudices exhibit seasonal or annual growth rings. In nature the opposite-leaved and usually profusely-branched erect stems die back at the end of the growing season, but under greenhouse conditions some stems survive as long as 15 months. Basal diameters of the stems range from 1.5 to 10 mm, and stem heights vary with the species from about 3 to 25 dm. The stems are green to reddish purple in color and may be uniformly colored or longitudinally lined by dark, resin-filled canals. The stems are glabrous below and often glaucous, but peduncles and axillary portions of inflorescence branches may bear some pubescence.

Roots

The plants normally have a woody taproot, the length of which varies with the habitat, and from which branch numerous secondary roots. The taproot may be only a few cm long in plants in clayey soil but may reach more than 2 dm in length in plants growing in cracks in rocks. The woody taproots exhibit seasonal or annual growth rings. *Guardiola pappifera* has a short annual taproot.

Leaves

The leaves are useful for distinguishing the species, even though there is some phenotypic plasticity. Leaf shape varies from linear-lanceolate to nearly orbicular and two species groups, the broad-leaved species (*G. rosei*, *G. carinata*, *G. rotundifolia*, *G. pappifera*, and *G. platyphylla*) and the narrow-leaved species (*G. mexicana*, *G. arguta*, *G. odontophylla*, *G. tulocarpus*,

G. thompsonii, G. stenodonta, and G. angustifolia) may be recognized on the basis of leaf shape. The leaves are sessile to petiolate with dentate to nearly entire margins. Hastate lobes are characteristic of some species. The texture varies from thin and herbaceous to subcoriaceous. Typically, there are three large veins extending from the base of the leaf blade, and the reticulate venation is often obvious. Most leaves have a rather heavy cuticle and little or no pubescence, although there may be some pilose pubescence on the petiole and lower leaf surface; G. pappifera has numerous papillose tubercles on the lower leaf surface.

Pubescence

The stems and leaves are usually glabrous and sometimes glaucous, although some individuals have sparse pilose pubescence on the lower leaf surface and petiole. The peduncles are often hirsute and the pubescence may extend onto the base of the involucre. Leaf trichomes are mostly spreading, while those of the peduncle and involucre base are mostly appressed. The achenes are usually sparsely pubescent.

Involucre

The involucres consist of three concave, thickened phyllaries which are distinct to the base and usually glabrous, although in some cases the bases of the phyllaries may bear appressed trichomes. *Guardiola carinata* is characterized by keeled phyllaries. The phyllaries are linear-lanceolate to lanceolate with acute tips which are sometimes recurved; the margins are somewhat scarious and entire. Upon maturation of the head, the phyllaries reflex allowing the achenes to fall to the ground. The phyllaries are usually lined with 10-20 dark, resin-filled canals.

Receptacle and Pales

The receptacles are 0.5 to 2 mm in diameter, slightly convex, and paleaceous. Two types of pales are found on the receptacle, an outer ring of thicker ones, each of which subtends a ray floret, and thin inner pales which subtend the disk florets. The outer pales, which reflex along with the phyllaries at the time the head matures, are structurally very similar to the inner pales which do not reflex on maturation of the achenes. The pales vary in shape from elliptic-lanceolate to linear-lanceolate. They are unlobed, and have entire margins and acute tips and those in *G. pappifera* may bear upward pointing trichomes on the inner surface.

Disk Florets

The disk florets have a vestigial ovary and are functionally male. The corollas are goblet-shaped, 5-lobed, and white. Pollen is produced in grass-green anthers which have apical appendages and rounded bases. The filaments of the anthers are so densely pubescent that the throat of the corolla is completely blocked by the filament pubescence. Surrounding the base of the style is a large nectary which produces copious nectar. The style is in all cases bifurcate, contrary to most species descriptions; however, the style branches are contained within the tube formed by the connate anthers and are only slightly exserted, thus giving the impression that the style is not cleft. At anthesis the disk florets are touch-sensitive and apparently rub pollen on the underside of insect pollinators as is described in the section on Crossing Studies. The disk corollas vary little in size or shape and provide no characters for distinguishing species. The number of disk florets per head varies, with advanced species having fewer florets per head than primitive species.

Ray Florets

The 1-5 ray florets per head are pistillate, fertile, and in a single series. The ray corollas are always white and vary somewhat in length and width. The tip of the ligule is usually 3-toothed, but occasional corollas are deeply lobed. The number of corolla veins varies from two to nine, with the normal number being four. Ray corolla vasculature and lobing are discussed further in the section on Ray Corolla Vasculature. Style branches are recurved, and the corolla tube is glabrous.

Achenes

Achenial characters have not proved taxonomically useful in *Guardiola* other than for distinguishing *G. pappifera* from the other species of the genus. Achene size, shape, color and pubescence may vary within a single head. The achenes are mostly obovate to oblong, and are somewhat flattened laterally; all taxa except *G. pappifera*, which has a pappus of 5 squamellate scales, lack a pappus. The achenes are usually spotted with cream or buff colored spots on a reddish-brown, brown, to dark gray background. The lower half is usually lighter in color than the upper half. Some achenes lack, or have few and poorly differentiated spots, thus appearing uniformly colored. All achenes are pubescent, but the density and extent of pubescence varies. The point of attachment of the achene to the receptacle is somewhat lateral rather than at the base of the achene. A large, water-absorbent callus, about 1 mm high, is present on the basal portion of the abaxial surface. The callus often extends around onto the adaxial surface of the achene. The callus may function in the germination process, in holding water for initiation of growth and/or for helping to keep the very hard seed coat damp and soft so it can be shed more easily when the cotyledons expand.

COTYLEDON VASCULATURE

Materials and Methods

Cotyledons of the seven species of which live material was available were removed from the seedlings by cutting them off as close as possible to the hypocotyl using a razor blade. They were fixed in 70% FAA for at least two days. Fixation was necessary because fresh cotyledons became softened so much during the clearing process that their handling was difficult during the rest of the procedures. The cotyledons were cleared for several hours to overnight in full strength Roman Cleanser Bleach and then washed in several changes of distilled water over 24 hours. The cotyledons were then placed on a microscope slide and covered with a second slide. These were placed in a petri dish and flooded with 95% alcohol. In this manner the cotyledons were held flat during the hardening taking place in the dehydration process, making them much easier to mount later on. After several hours in 95% alcohol the cotyledons were removed from between the slides and placed in 100% alcohol. Dehydration was completed and the cotyledons were then placed in a 1:1 mixture of xylene and 100% alcohol for several hours, stained with safranin, cleared in xylene, and mounted in piccolyte. After they had dried in the oven, drawings were made using a B & L microprojector.

Observations and Discussion

The cotyledons consist of a slender petiole and an expanded blade and are opposite on the seedling stem. The cotyledons are fairly large, ranging from about 15 to 40 mm in total length and averaging about 25 mm in total length. Six or eight petiole veins connect the vascular tissue of the hypocotyl with that of the vascular reticulum of the cotyledon blade. The number of cotyledon petiole veins is, with little variation, characteristic for a species.

Cotyledon petiole vein position and nomenclature and the two types of cotyledon petiole vasculature are illustrated in Figure 1. In both types there is a pair of midveins which retain their integrity and do not fuse, but run side by side through the cotyledon petiole and about one-quarter of the way into the cotyledon blade. At this point one of the veins, usually the right one as viewed from the adaxial surface of the cotyledon, veers away from its central position and assumes a position about one-third of the way toward the cotyledon margin. This vein branches and becomes part of the

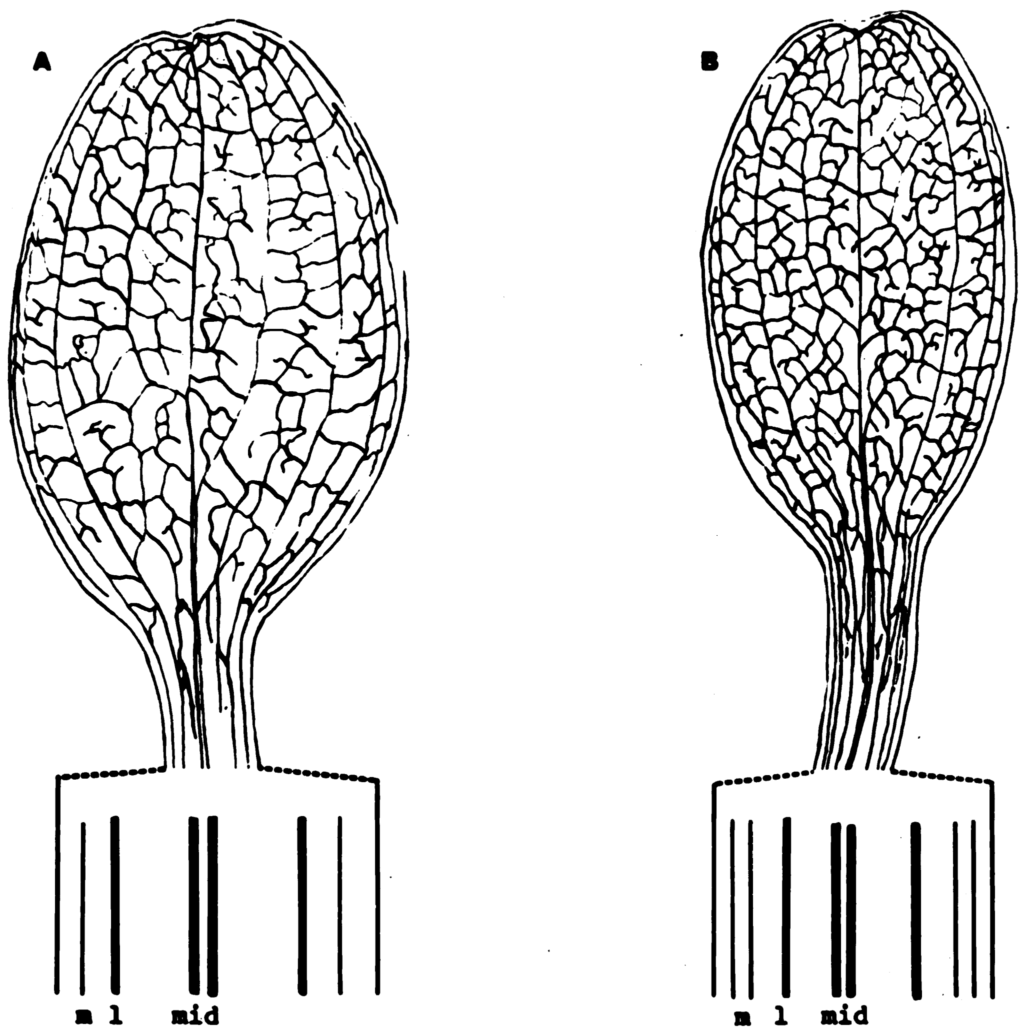

Figure 1. Guardiola cotyledon vasculature.
Petiole bases are enlarged to illustrate cotyledon petiole vasculature types. A. The one-marginal vein type (G. mexicana, Van Faasen 1569). B. The two-marginal vein type (G. angustifolia, Van Faasen 1783). Cotyledons x 7.5; petiole base x 25. Vein nomenclature: m, marginal vein; l, lateral vein; mid, mid vein.

vascular reticulum of the cotyledon blade. The double nature of the midvein is considered primitive (Thomas, 1970; Carlquist, 1957a) and is assumed to precede the fusion of these veins and formation of a single midvein.

On each side of the pair of midveins is another vein, the lateral vein, which is usually a little smaller than the midveins. The lateral veins extend the length of the petiole and upon entering the blade veer toward the margins of the blade. The lateral veins contribute branches to the vascular reticulum but do not become part of it.

Lateral to the above-mentioned petiole veins are either one or two small veins, the marginal veins. The number present differs with the species. The marginal veins extend the length of the petiole and then run near the margins of the cotyledon blade.

There are varying numbers of small interconnecting veins in the distal but not the proximal end of the cotyledon petiole (see Figure 1).

In the cotyledon blade is an interconnected reticulum of small veins which join the major veins or smaller branches from the major veins. A vascular plexus located just below the notched apex of the cotyledon blade is formed by the coalescence of a number of veins in the reticulum.

With the exception of *Guardiola thompsonii*, the cotyledon petiole vasculature is constant within those species investigated. *Guardiola arguta*, *G. mexicana*, and *G. rosei* and a few specimens of *G. thompsonii* all possess the one-marginal vein pattern as illustrated in Figure 1A. The other species investigated, *G. angustifolia*, *G. platyphylla*, *G. rotundifolia*, *G. tulocarpus*, and most specimens of *G. thompsonii* possess the two-marginal vein pattern as illustrated in Figure 1B. It may be more than coincidental that those species having the one-vein type of cotyledon petiole venation are considered to be the more primitive species, while the more advanced species mostly possess the two-vein type of vasculature. Therefore, proliferation of petiole veins is listed among the advanced characters on page 89. Viable seeds of the other taxa were not available for study.

There is a dearth of information concerning cotyledons in the recent taxonomic literature. Lee (1914) investigated seedling anatomy in about fifty species of Compositae and found five types of cotyledon vascular anatomy. More recently seedling anatomy has been investigated by Siler (1931) in *Helianthus* and *Arctium*, by Carlquist (1957a) in *Fitchia*, and by Anderson (1964) in *Petradoria*. The cotyledon vascular anatomy of *Guardiola* does not correspond to any of the types found by Lee or the other workers mentioned above, but is more complex than any of these patterns. However, Philips (1937) investigated germination and seedling development in *Cynara scolyma* and found a petiole vascular anatomy which corresponds to the *Guardiola* one-marginal vein type. No other reported vascular patterns correspond to the patterns found in *Guardiola*.

Since the number of marginal veins in the cotyledon petiole, with but one exception, was constant within each species investigated, it is not unreasonable to suspect genetic determination of this character. Cotyledons from hybrid plants were available for investigation of possible genetic control of the cotyledon petiole vasculature. Data obtained from this study are provided in Table 1, in which the results of species matings and their reciprocals may be seen. These data are summarized in Table 2.

A study of the data reveals that when two *Guardiola* plants of the same or different species, but each with the one-marginal vein pattern, were crossed, the progeny always had a one-marginal vascular pattern. Likewise, when the two parent plants both had the two-marginal vascular pattern, all offspring from that mating had the two-marginal vein pattern. The only exceptions to the above statements occurred when *G. thompsonii* was one of the parents. Then the results were variable and unpredictable (see Tables 1 and 2).

Table 1. --Cotyledon vasculature patterns in progeny from inter- and intra-specific matings.

Seed Parent	Pollen Parent: G. angustifolia (2)	G. mexicana (1)	G. platyphylla (2)	G. rosei (1)	G. rotundifolia (2)	G. tulocarpus (2)	G. thompsonii (1) & (2)
G. mexicana (1)	-----	27 F_1 * (1)-27	5 F_1 (1)-5	10 F_1 (1)-10	3 F_1 (2)-3	16 F_1 (1)-16	12 F_1 (1)-12
G. platyphylla (2)	-----	3 F_1 (2)-2 (1)-1 damaged	3 F_1 (2)-3	2 F_1 (2)-2	2 F_1 (2)-2	3 F_1 (2)-3	5 F_1 (2)-5
G. rosei (1)	1 F_1 (1)-1	3 F_1 (1)-3	2 F_1 (2)-2	7 F_1 (1)-7	2 F_1 (2)-2	-----	2 F_1 (2)-1 (1)-1
G. rotundifolia (2)	-----	1 F_1 (2)-1	1 F_1 (2)-1	2 F_1 (1)-2	1 F_1 (2)-1	1 F_1 (2)-1	-----
G. tulocarpus (2)	-----	9 F_1 (1)-9	3 F_1 (2)-3	-----	2 F_1 (2)-2	4 F_1 (2)-4	5 F_1 (1)-4 (2)-1
G. thompsonii (1) & (2)	-----	7 F_1 (1)-7	2 F_1 (2)-2	5 F_1 (1)-2 (2)-3	-----	6 F_1 (1)-1 (2)-5	4 F_1 (1)-4

*The data should be read as follows: From matings involving G. mexicana as the pollen parent and G. mexicana as the seed parent, 27 F_1 plants were produced of which 27 were of the one-marginal type and 0 were of the two-marginal type.

Table 2. --Summary of cotyledon vasculature in F_1 plants.

Seed Parent	Pollen Parent		
	1 marginal	2 marginals	G. thompsonii (1 & 2)
1 marginal	(1) - 47 * (2) - 0	(1) - 22 (2) - 7	(1) - 13 (2) - 1
2 marginals	(1) - 12 (2) - 5	(1) - 0 (2) - 20	(1) - 4 (2) - 6
G. thompsonii (1 & 2)	(1) - 9 (2) - 3	(1) - 1 (2) - 7	(1) - 4 (2) - 0

*The data in this square indicate that when the pollen parent is of the one-marginal type and the seed parent is of the one-marginal type, the progeny included 47 plants of the one-marginal type and 0 plants of the two-marginal type.

When two plants, one with the one-marginal pattern and one with the two-marginal pattern, were mated, the vasculature of the offspring was unpredictable. Sometimes the condition of the pollen parent was found in the F_1: in G. mexicana female (one-marginal) × G. rotundifolia male (two-marginal) all the F_1's had the two-marginal pattern. The progeny from reciprocal crosses was similar: in G. platyphylla (two-marginal) × G. rosei (one-marginal) all progeny from the cross and its reciprocal had the two-marginal pattern, or differed. In G. mexicana (one-marginal) × G. platyphylla (two-marginal), in both the cross and its reciprocal, the seed parent petiole vascular pattern was found in the F_1.

Neither the type of inheritance, nor for that matter the fact of genetic determination of cotyledon petiole vein patterns, is elucidated by this study. If F_2 plants can be produced, new information concerning this problem will be obtained. Nonetheless, this investigation reveals that with the exception of G. thompsonii the number of marginal veins in the cotyledon petiole of a species is constant.

RAY COROLLA VASCULATURE

Materials and Methods

Fresh heads were preserved in 70% FAA. Dried heads were softened in detergent water. Ray corollas were dissected out, cleared in 3% KOH for several hours to overnight, and rinsed in several changes of distilled water over three to four hours. Subsequent preparation was as described for cotyledons.

Observations and Discussion

Koch (1930a, b) investigated ray corolla anatomy in selected genera of Compositae and on the basis of the three venation patterns she found, characterized the Heliantheae Type, Aster Type, and Mutiseae Type of ray corollas. The Heliantheae Type ray corolla has 7 - 11 veins in the lamina. It is considered primitive in the family and the type from which reduced forms are derived (Cronquist, 1955). The Aster Type has four veins in the lamina, and the Mutiseae Type is bilabiate. In addition, Koch characterized the tribes of the Compositae by the ray corolla venation pattern found in each. Her venation types and tribal characterizations by venation type have been commonly cited (see e.g. Carlquist, 1957a; De Jong, 1965).

Examination of ray corolla vasculature in *Guardiola* revealed that even though the genus is a member of the Heliantheae, most species possess the Aster Type ray corolla vasculature (Figure 2A). I also found the Heliantheae Type venation in several species (Figure 2B), a reduction series in *G. angustifolia* (Figures 3A-D), and a variety of bizarre variations in corolla form and venation throughout the genus (Figures 3 E-H and Figure 4).

Only the Heliantheae Type ray corolla vein pattern has been found in *G. rosei*, primitive among the broad-leaved species, while in *G. platyphylla*, presumed to be derived from *G. rosei*, the Aster Type venation is most common and the Heliantheae Type occurs only occasionally. In other broad-leaved species only the Aster Type corolla has been found.

Among the narrow-leaved species *G. mexicana* is considered primitive and *G. tulocarpus* is believed to have been derived from it. In both of these species the Heliantheae Type corolla is found only occasionally and the Aster Type is most common. With the exception of occasional variants, all of the other narrow-leaved species possess only the Aster Type ray corolla.

It is widely accepted that fusion of five 3-veined petals gave rise to the gamopetalous, primitive disk corolla, a 15-veined,

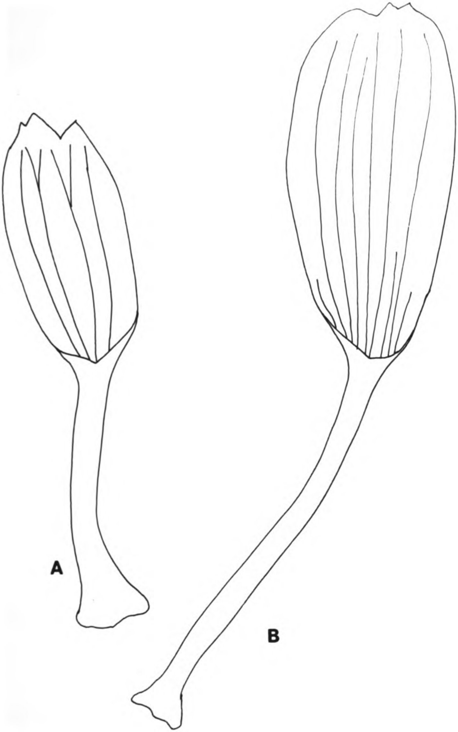

Figure 2. Vascular patterns in typical *Guardiola* ray corollas. A. Aster type venation, (*G. tulocarpus*, *Van Faasen 1759*, x 25). B. Heliantheae type venation, (*G. platyphylla*, *Van Faasen 1931*, x 25).

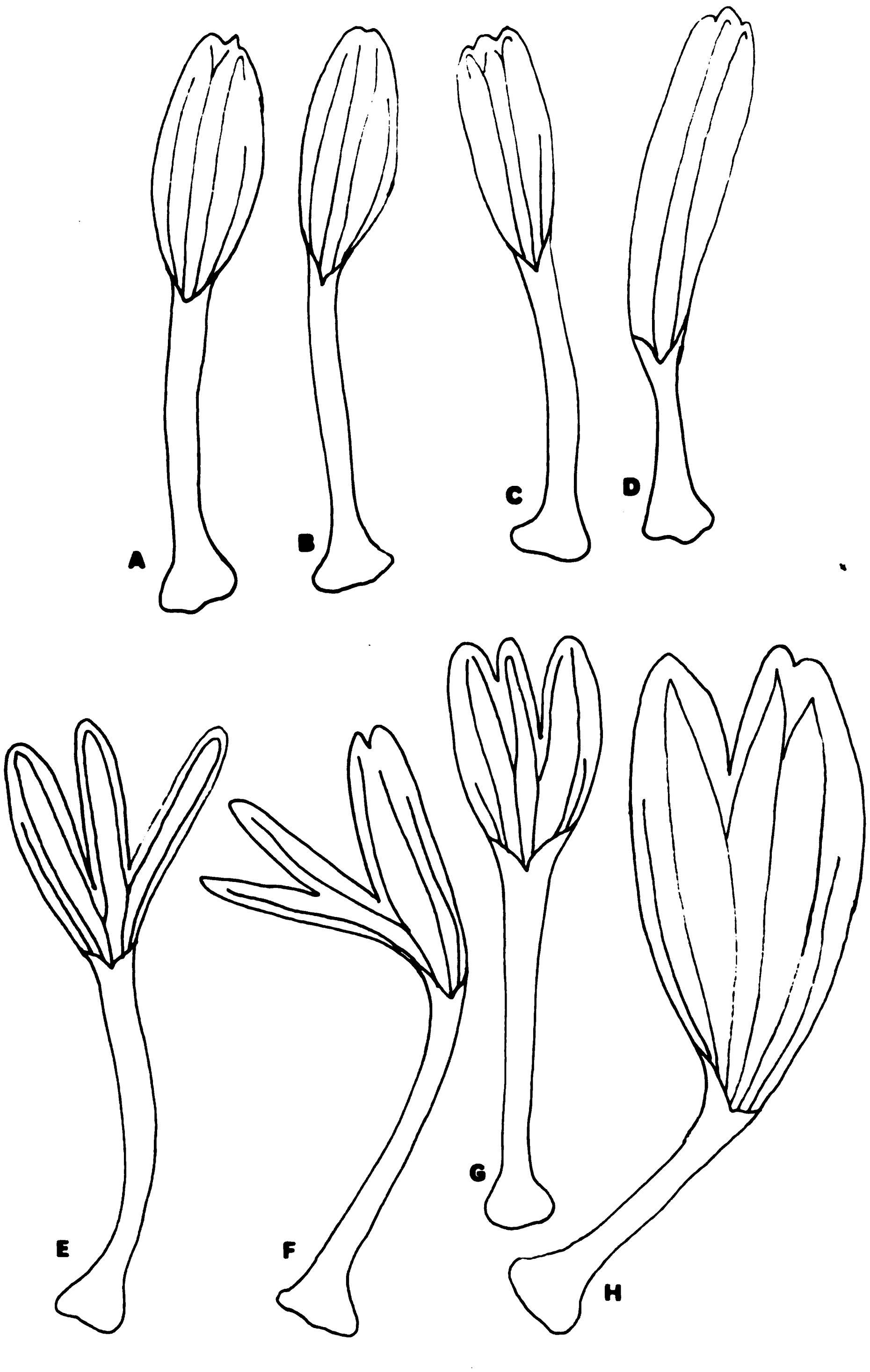

Figure 3. Variations in Guardiola ray corolla vascular patterns. A-D. Reduction series in G. angustifolia, A. Van Faasen 1777. B. Van Faasen 1776. C, D. Van Faasen 1783. E-H. Miscellaneous ray corolla variations, E. G. tulocarpus, Van Faasen 1785; F. G. tulocarpus, Van Faasen 1796; G. G. tulocarpus, Van Faasen 1785; H. G. mexicana, Van Faasen 1601. (All x 14).

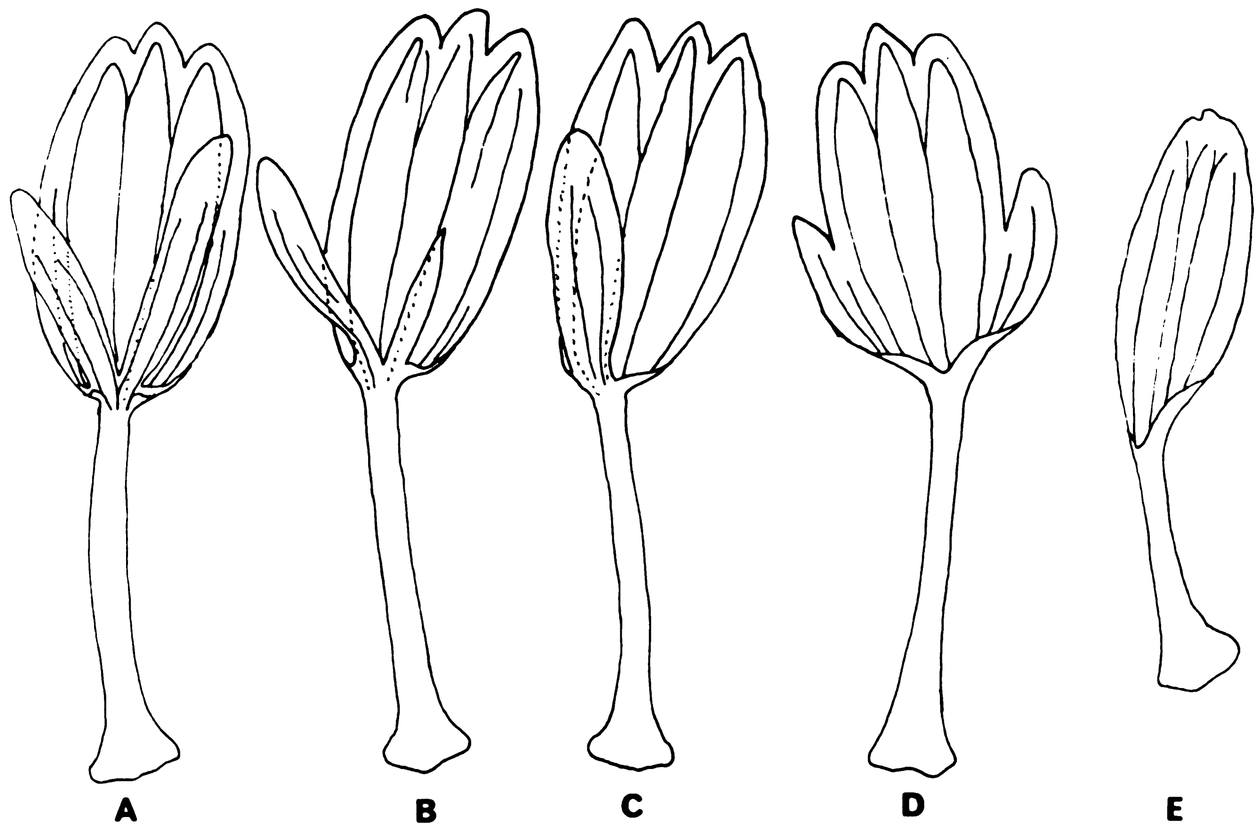

Figure 4. Teratologies in *Guardiola* ray corollas. A. Lamina plus two vascularized small lobes. B. Lamina plus two lobes, one reduced and non-vascularized, the second with only portions of veins. C. Lamina plus one vascularized lobe. D. A 5-lobed lamina. E. A typical Aster type lamina. (All from *G. tulocarpus*, *Van Faasen* 1797; all x 12.5)

5-lobed corolla. Subsequent evolution by reduction of the number of veins resulted in a 10-veined corolla produced by fusion of pairs of lateral veins. Vein branching in the disk corolla may have originated in this step. Subsequent loss of the mid-veins resulted in the 5-veined disk corolla most common in the Compositae today.

It is also widely accepted that the primitive Compositae were discoid and that ray florets were derived from disk florets. Cronquist (1955) suggests that ray florets evolved early in the evolution of the family and that reduction in both ray and disk florets occurred simultaneously. It seems then that there is no reason to restrict the ancestral ray floret to the 5-veined disk corollas we see today. It seems likely that ray florets could also have been derived from the primitive 10- or 15-veined disk corollas. If this was the case, then there should be three ancestral types for ray florets, namely 5-, 10-, and 15-veined disk corollas, with the 15-veined disk corolla ancestral to the other two types of disk corollas. Subsequent evolutionary reduction in each of these lines would yield three separately derived reduction series, the latter stages of which would converge and merge morphologically. Figure 5 is a visualization of these possible evolutionary sequences.

If some of the teratologies seen in Guardiola ray corollas are atavistic, they suggest that Guardiola reflects ancestors which

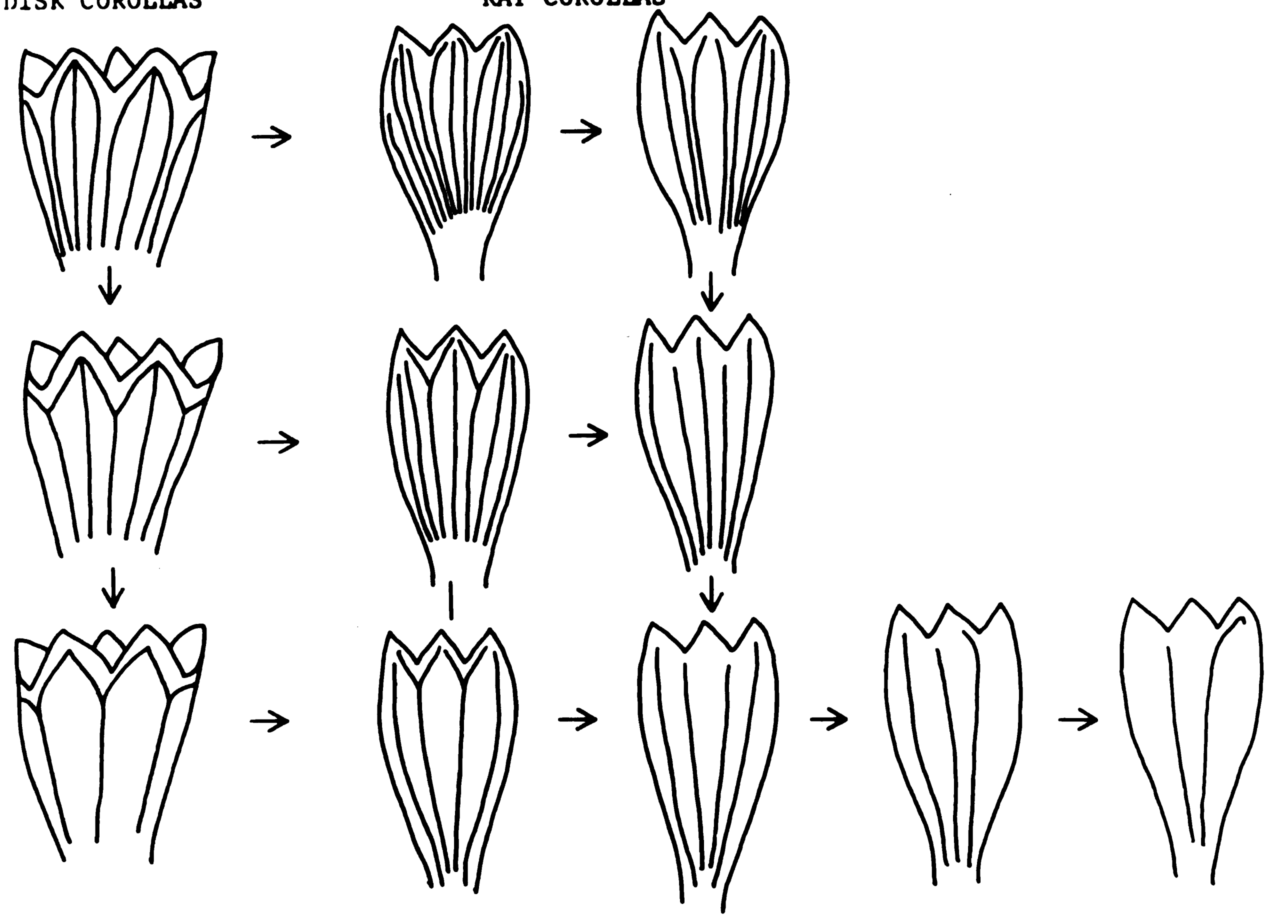

Figure 5. Possible evolution of ray corollas in Guardiola.

had 10-veined disk corollas from which the ray florets were derived in a reduction series as illustrated in Figure 5. If, however, there is proliferation of veins as occurs in Helianthus and Fitchia (Carlquist, 1962), then no sequence can be deduced readily.

One plant (G. tulocarpus, Van Faasen 1797) produced a remarkable array of ray corollas (Figure 4). Some appear very similar to Mutisieae Type bilabiate corollas as illustrated by Koch (1930b) and Carlquist (1957b), which Koch states are merely modified disk corollas and not a stage intermediate in the derivation of the ray corolla from the disk corolla. If the teratologies seen in this specimen are atavistic, then the rays from this plant of Guardiola present a clear series between the two kinds of corollas.

Guardiola and the other members of the Melampodinae present a special problem in that all have fertile ray but sterile disk florets. Therefore, the ray and disk florets must be rather highly derived forms since the ray florets had to have been evolved from the discoid head prior to evolution of female sterility in the disk florets. However, among the numerous Guardiola heads examined, I found two which each had a ray floret bearing one anther. In addition, advanced species of Guardiola with reduced numbers of ray florets usually have typical disk florets replacing ray florets in the outer floret whorl. These disk florets mature along with the ray florets a day or two ahead of the rest of the disk florets. These two facts suggest that in Guardiola ray and disk florets are to a considerable extent morphogenetically similar.

CYTOLOGICAL STUDIES

Materials and Methods

Meiotic Chromosome Numbers

Buds were collected in Carnoy's 6:3:1 (absolute alcohol: glacial acetic acid: chloroform) in Mexico and were maintained at ambient temperatures until returned to East Lansing. No deleterious effects were noted from this procedure. Buds from greenhouse-grown plants were fixed and refrigerated at once. Squash preparations were made in acetocarmine and chromosomes were examined using phase contrast microscopy at an initial magnification of about 1600 diameters. Meiotic chromosome counts were obtained from cells undergoing microsporogenesis. Drawings were made using a Zeiss drawing apparatus.

Somatic Chromosomes

Root tips were collected in Carnoy's 6:3:1 which produced better results than did Carnoy's 3:1 (absolute alcohol: glacial acetic acid). Pretreatment for even one hour in either p-dichlorobenzene or 8-oxyquinoline shortened the chromosomes so much that it was impossible to interpret chromosome morphology. For this reason untreated cells were used in this study. Root tip squashes were prepared according to the procedure outlined by Van Faasen (1963). Examination and drawing of cells undergoing mitosis were as described above for meiotic chromosomes.

Observations

The meiotic chromosome number of all *Guardiola* species counted was *n* = 12. These counts are listed in Table 3 and selected meiotic configurations are illustrated in Figure 6.

Meiotic chromosomes are relatively small and nearly uniform in size, although they are slightly larger in the broad-leaved than in the narrow-leaved species.

All of the cells in which I was able to determine the number of somatic chromosomes present contained 24 chromosomes. Idiograms of the somatic chromosomes of the seven *Guardiola* species examined are found in Figure 7 and measurements of the same are in Table 4.

The somatic chromosomes of the *Guardiola* species studied are very small and vary in length from approximately 1.7 microns to approximately 4.3 microns. No satellites were observed on any of the chromosomes.

Table 3. --Meiotic chromosome numbers in Guardiola.

Taxon	n Number	Collection Data
G. rosei	12	DURANGO: One mile W of Llano Grande, Km. 1024-1043 of Mexico rt. 40, Van Faasen 1859.
	12	DURANGO: 16 miles E of Llano Grande, Km. 1024-1025 of Mexico rt. 40, Van Faasen 1891.
	12	DURANGO: 20 miles E of Llano Grande, Km. 1019 of Mexico rt. 40, Van Faasen 1906.
G. rotundifolia	12	JALISCO: 4 miles NW of Tequila, Van Faasen 1784.
G. platyphylla	12	ARIZONA: Pima County, Bear Canyon, Van Faasen 1931.
	12	ARIZONA: Pima County, Sabino Canyon, Van Faasen 1932.
	12	ARIZONA: Santa Cruz County, 12 mi. W of Nogales on road to Ruby (Arizona rt. 289), Van Faasen 1933.
	12	ARIZONA: Cochise Co., one mile W of east gate to Coronado National Monument, Van Faasen, 1934.

Table 3. --Continued.

Taxon	$\underline{n}$ Number	Collection Data
G. mexicana	12	GUERRERO: Km. 153 along Mexico rt. 95, 20 miles NE of Taxco, *Van Faasen 1568*.
	12	GUERRERO: 2 mi. NW of Taxco on Mexico rt. 95, *Van Faasen 1569*.
	12	MEXICO: 45 miles W of Toluca on road to Valle de Bravo, near Juantepec, *Van Faasen 1601*.
	12	MICHOACAN: About 10 miles E of Morelia, Km. 291-292 of Mexico rt. 15, *Van Faasen 1649*.
	12	MICHOACAN: 27 miles W of Morelia, Km. 354 of Mexico rt. 15, *Van Faasen 1650*.
	12	MICHOACAN: Mexico rt. 15, Km. 401-402, 5 mi. W of Zacapu, *Van Faasen 1688*.
	12	MICHOACAN: Mexico rt. 37 about 9 miles S of Carapan, *Van Faasen 1701*.
	12	JALISCO: 4 miles NW of Tequila, *Van Faasen 1785*.
G. arguta	12	DURANGO: Near Revolcaderos, Km. 1142 of Mexico rt. 40, *Van Faasen 1822*.

Table 3. --Continued.

Taxon	n Number	Collection Data
G. tulocarpus	12	MICHOACAN: 4 miles S of Los Reyes, Van Faasen 1757.
	12	JALISCO: One mile S of Tecalitlan, Mexico rt. 110, Km. 135, Van Faasen 1759.
	12	JALISCO: 8 miles SW of Autlan, Mexico rt. 80, Km. 1044, Van Faasen 1774.
	12	JALISCO: 10 miles E of Tequila, Mexico rt. 15, Km. 713, Van Faasen 1782.
	12	JALISCO: 44 miles NW of Tequila, Mexico rt. 15, Km. 769, Van Faasen 1795.
	12	NAYARIT: One mile NW from Michoacan border along Mexico rt. 15, Van Faasen 1796.
	12	NAYARIT: One mile W of village of Santa Isabella, Mexico rt. 15, Km. 851-852, Van Faasen 1797.
	12	NAYARIT: 2 miles S of Laguna Santa Maria on road to Santa Maria del Oro, Van Faasen 1800.
	12	NAYARIT: 10 miles S of Tepic, Van Faasen 1802.

Table 3. --Continued.

Taxon	$\underline{n}$ Number	Collection Data
	12	NAYARIT: 10 miles NW of Tepic, Mexico rt. 15, Km. 1018, Van Faasen 1813.
	12	NAYARIT: 11 miles NW of Tepic, Mexico rt. 15, Km. 1019, Van Faasen 1814.
G. thompsonii	12	MICHOACAN: 12 miles S of Uruapan along Mexico rt. 37, Van Faasen 1727.
	12	MICHOACAN: 20 miles S of Uruapan along Mexico rt. 37, Van Faasen 1756.
G. angustifolia	12	JALISCO: La Barranca, 5 miles NE of Guadalajara, Van Faasen 1776.
	12	JALISCO: 10 miles N of Guadalajara on Mexico rt. 41, Van Faasen 1777.
	12	JALISCO: 2 km. NW of Tequila, Van Faasen 1783.

Figure 6. Meiotic chromosomes of _Guardiola_.
A. _G. rosei_, _Van Faasen 1859_; B. _G. rotundifolia_, _Van Faasen 1784_; C. _G. platyphylla_, _Van Faasen 1934_; D. _G. mexicana_, _Van Faasen 1649_; E. _G. arguta_, _Van Faasen 1822_; F. _G. thompsonii_, _Van Faasen 1727_; G. _G. tulocarpus_, _Van Faasen 1782_; H. _G. angustifolia_, _Van Faasen 1783_; all first meiotic divisions ca. x 2000.

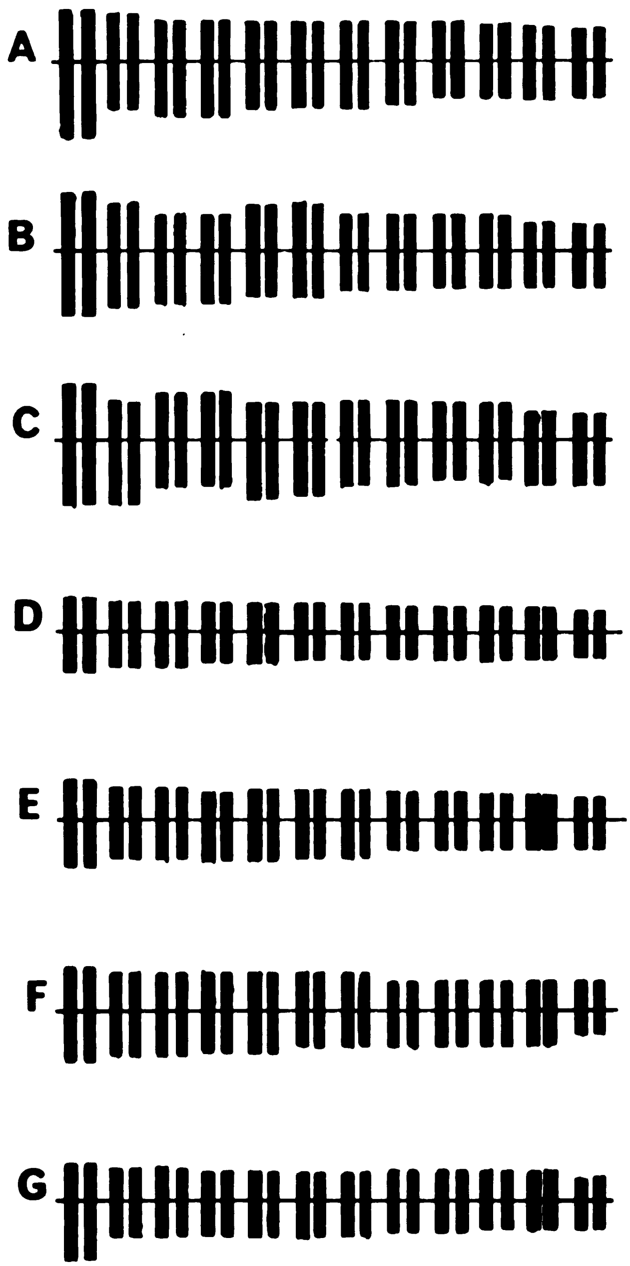

Figure 7. Idiograms of somatic chromosomes of Guardiola. A. *G. rosei*; B. *G. rotundifolia*; C. *G. platyphylla*; D. *G. mexicana*; E. *G. tulocarpus*; F. *G. thompsonii*; G. *G. angustifolia*. All ca. x 4000.

Table 4. --Mean measurements of somatic chromosomes of seven *Guardiola* species.

Species	Chromo-somes	Length in Microns	Short Arm (X 100) / Total Length	Centromere Position
G. rosei	1, 2	4.3	38	Submedian (SM)
	3, 4	3.3	50	Median (M)
	5-8	3.3	40	M
	9-16	3.0	44	M
	17-20	2.7	50	M
	21-24	2.5	47	M
	Total length 73.2			
G. rotundifolia	1, 2	4.3	46	M
	3, 4	3.6	45	M
	5-8	3.3	40	M
	9-12	3.3	50	M
	13-16	2.8	47	M
	17-20	2.7	50	M
	21-24	2.3	42	M
	Total length 73.4			
G. platyphylla	1, 2	4.3	46	M
	3-6	3.7	36	SM
	5-8	3.3	50	M
	9-12	3.3	40	M
	13-16	3.2	47	M
	17-20	2.8	47	M
	21-24	2.7	38	SM
	Total length 77.80			

Table 4. --Continued.

Species	Chromo-somes	Length in Microns	Short Arm (× 100) / Total Length	Centromere Position
G. mexicana	1, 2	2.7	44	M
	3-6	2.3	43	M
	7-10	2.2	46	M
	11-14	2.0	50	M
	15-22	1.8	45	M
	23, 24	1.7	40	M
	Total length	55.4		
G. tulocarpus	1, 2	3.0	44	M
	3-6	2.7	44	M
	7-10	2.5	40	M
	11-14	2.3	43	M
	15-22	2.0	50	M
	23, 24	1.8	45	M
	Total length	55.60		
G. thompsonii	1, 2	3.3	45	M
	3-6	3.0	44	M
	7-10	2.8	47	M
	11-14	2.7	50	M
	15-22	2.3	43	M
	23, 24	1.8	40	M
	Total length	62.60		

Table 4. --Continued.

Species	Chromo-somes	Length in Microns	Short Arm (× 100) / Total Length	Centromere Position
G. angustifolia	1, 2	3.3	40	M
	3-6	2.5	47	M
	7-14	2.3	43	M
	15-18	2.2	46	M
	19-22	2.0	50	M
	23, 24	1.8	45	M
	Total length 55.4			

Among the somatic karyotypes in Guardiola there are readily detected differences in chromosome size and total chromosome length between the broad- and narrow-leaved species. Chromosome length varies from 1.7 to 3.3 microns in the narrow-leaved species and from 2.3 to 4.3 microns in the broad-leaved species (Table 4). The total chromosome length of the broad-leaved species varies from 73.2 to 77.8 microns while that of the narrow-leaved species varies from 49.2 to 62.6 microns. Mean lengths for the two groups are 74.8 and 55.7 microns respectively. In both the broad- and narrow-leaved groups, however, species considered advanced have greater total chromosome length than more primitive ones.

The karyotypes of all Guardiola species examined are rather symmetrical (Figure 7); nearly all chromosomes have median centromeres. (Centromere position nomenclature follows Levan et al., 1965.)

Primitive karyotype characters (Stebbins, 1966) found in Guardiola, i.e. symmetrical karyotypes, median centromeres, and lack of secondary constrictions, suggest a generally primitive karyotype for the genus. However, the small chromosome size, a derived condition (Stebbins, 1966), indicates some karyotype evolution within the genus.

This discussion must be tempered by the possibility that these karyotype differences may not be real. Since the chromosomes were examined in untreated cells, their morphology may have been determined at times prior to maximum shortening and arrest on the metaphase plane, the point at which karyotypes are normally studied. Thus the measurements must be considered approximations. However, consistent chromosome size differences between the broad- and narrow-leaved species appear real and contribute toward that basic subdivision of the genus.

CROSSING STUDIES

Materials and Methods

The plants used in this study (Table 5) were grown from field-collected seeds. The *Guardiola* achene has a very hard seed coat, and this combined with waterproofing properties of the seed coat and inner membranes retard the germination process. To obtain a rapid and high percentage of germination, achenes were placed on damp blotters in petri dishes and maintained in a warm (75 - 80° F), dark chamber for 2 or 3 days. After this time the seed coat and inner membranes were dissected from the embryo proper, and the excised embryo was returned to the incubation chamber. The embryos grew rapidly and after 2 - 3 days the resulting seedlings were large enough to be planted in individual pots in a soil mixture of 6 parts sand: 1 part vermiculite: 3 parts loam. Seedlings were maintained in the growth chamber until the stems were approximately 10 cm high and then transferred to the greenhouse. They were maintained in the greenhouse until buds formed, when they were returned to the laboratory for the experimental procedures.

Table 5.--Individual Guardiola plants used in crossing studies. All were grown from seed. The numbers are Van Faasen collection numbers and the letters refer to individual plants. Locality data are indicated in Table 1.

Taxon	Plants Used
G. angustifolia	1783 A, F, G
G. mexicana	1569 A
	1601 A, B, C, D
	1649 A, B
	1650 A, B, C, D
	1661 A
	1688 A, B, C, D
G. platyphylla	1931 A
	1932 A, B, D
G. rosei	1859 A
	1860 A, B, C, D
	1891 A, B, C
	1906 A, B
G. rotundifolia	1784 A, B, C
G. thompsonii	1727 A, B
	1756 A, B
G. tulocarpus	1759 A, B
	1774 A, B
	1797 A, B, D
	1813 A
	1814 A, B

Guardiola ray florets, with only rare exceptions, are female, the disk florets are functionally male, and the plants were found to be completely self-incompatible. Therefore, emasculation was not necessary prior to hand pollination of the ray florets. Hand pollination was necessary because each head bears only 1 - 5 ray florets, so it was important to be sure that pollination had been accomplished and to be as thrifty as possible in making crosses. At anthesis a disk floret was removed from a head with forceps and then under a dissecting microscope the pollen was applied directly to stigmatic surfaces of the ray florets. This technique made possible the use of several disk florets of a head in different crosses. The heads were tagged and allowed to mature in the growth chamber or in the laboratory if the plants were too large for the growth chambers. Mature heads were harvested, the achenes removed, and germinated according to the procedures outlined above.

Production of a full-sized, apparently mature, fertile achene following hand pollination was considered a successful crossing attempt. Plants grown from seeds of these crosses were compared to parent plants.

Data for the crossing attempts are summarized in Table 6 and illustrated in Figure 8.

As an additional check on fertility of the parent plants, the offspring which did flower, and of some dried specimens, pollen

Table 6. --Summary of crosses attempted in Guardiola.

Seed Parent	Pollen Parent							
	G. angustifolia	G. mexicana	G. platyphylla	G. rosei	G. rotundifolia	G. thompsonii	G. tulocarpus	Successes
G. angustifolia	0:2(2)*	0:2	0	0:2	0:1	0:1	0:1	0:9
G. mexicana	0:1	32:56(10)	5:9	10:15	5:7	15:20	20:27	87:135
G. platyphylla	0	5:7	1:6(3)	5:7	2:3	7:8	4:5	24:36
G. rosei	1:1	3:4	5:8	8:20(5)	3:4	4:5	2:5	26:47
G. rotundifolia	0:1	1:2	1:1	2:2	2:6(3)	0	1:4	7:16
G. thompsonii	1:1	8:8	2:2	6:6	1:2	4:10(5)	6:8	28:37
G. tulocarpus	1:1	13:24	5:7	2:5	4:4	6:10	10:30(11)	41:81
Successes	3:7	62:103	19:33	33:57	17:27	36:54	43:80	213:361

* 0:2(2) is read as no successes in 2 attempts with 2 of the attempts being selfs.

Total successes, all attempts	213:361	59.0%
Successes excluding 39 selfs	213:322	66.1%
Successes of interspecific attempts	156:231	67.5%
Successes of intraspecific attempts excluding selfs	57:91	62.6%

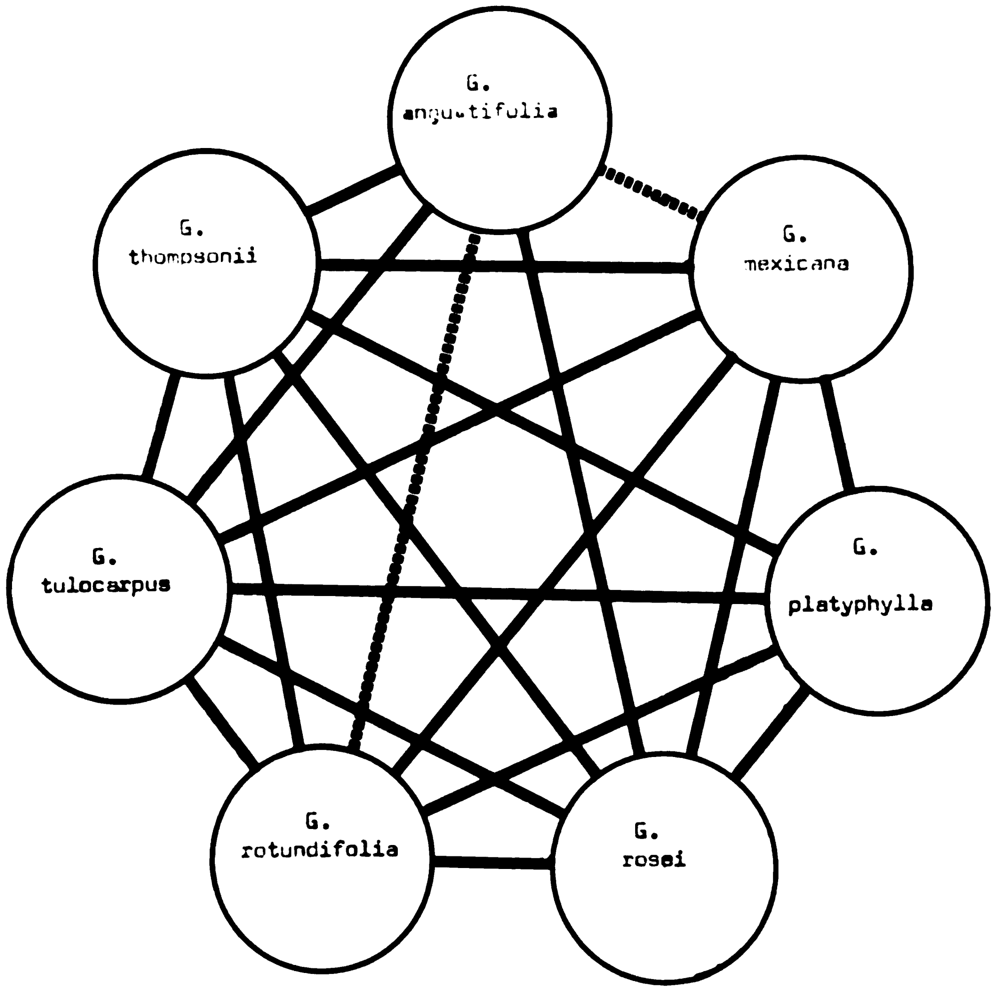

Figure 8. Experimental crosses in Guardiola.
Heavy lines represent successful seed set while broken lines indicate crosses attempted but no seeds set.

stainability with cotton blue in lactophenol was investigated. Pollen stainability among the individual P_1 plants, with two exceptions, viz. 78.6% and 83.7%, varied from 90.5% to 99.3%.

Of the progeny from intraspecific matings only five plants flowered. These had 71.1%, 87.9%, 92.9%, 95.9%, and 98.1% stainable pollen. Four progeny from the interspecific matings flowered and had 95.2%, 97.8%, 97.9%, and 98.0% stainable pollen.

General Observations

Usually the ray florets emerged from the bud a day or two prior to the emergence of the disk florets. However, in many instances, apparently normal disk florets occupied the position of one or more ray florets in the outer ring of flowers and emerged with the ray florets.

The ray floret style with its two stigmatic branches is erect and white when receptive to pollen and will remain thus for about a week if not pollinated. If, however, the ray florets are pollinated with viable, compatible pollen, one can see a yellowing of the style begin to occur in about 6 - 10 hours (or in one case $3\frac{1}{2}$ hours) after pollination. After 24 hours the style and stigma are brown, withered, and withdrawn to the mouth of the tube of the ray corolla. If pollen used for the pollination is either incompatible or no longer viable, the ray stigma remains white and erect. Thus, about 24 hours after pollination I could read the previous day's crosses as to "take" or "no take." During the time I read this reaction to determine if it was more than coincidence, the reading of the reaction was correct in 196 of 232 instances (84.4%), establishing the generalization that the success of a cross can be determined after 24 hours. The majority of the incorrect determinations of crossing success were in cases where seeds were set subsequent to a "no take" reading.

In nature insects pollinate the ray florets with pollen from the disk florets which bloom several days after the ray florets open. The insects may be attracted to the plants by the copious nectar produced by the very large nectaries of the disk florets.

The disk florets are touch-sensitive when they mature. When touched, the style emerges a little from the tube formed by the connate anthers and carries some pollen out with it. At the same time the tip of the floret describes a small circle. Stamen irritability is also reported in <u>Arnica</u> by Vuilleumier (1969) and Small (1915) who state that there are two basic types of stamen irritability. One involves elongation of the style and the second, contraction of the filaments, causes tilting of the floret toward the tactile stimulus.

Hoffman (1894) also noted filament irritability in some Cynareae, especially Centaurea, and in Perezia multifloria Less. and Trixis discolor Gill of the Mutisieae. The mechanism involved in Guardiola, whether elongation of the style or contraction of the filaments, is not known at this time. However, on occasion it was noted that the style of the ray florets also exhibited this movement. Therefore, it seems most likely that stylar elongation, perhaps due to release of tension, is responsible for the pushing out of the pollen, and that the circular movement of the entire disk floret is due to sequential contraction of the filaments. Thus, when an insect lands on a mature disk floret, presumably to obtain nectar, it touches the style, thus initiating the circular movement of the floret, and a little pollen is pushed out and may be rubbed onto the ventral surface of the insect. When the insect then investigates a ray floret it may transfer the pollen to the ray stigma, thus effecting pollination. The disk floret requires about 15-30 minutes to recover from the touch-stimulated movement, and may repeat the process.

Table 6 shows that of 361 total crosses attempted, 213 or 59% were successful; that is, set seed. There were 31 attempts, none of which were successful, to self plants. If these selfing attempts are removed from the total attempts, then 213 of 322 attempts or 66.1% were successful. Successful seed set apparently depended on the condition of the plant at the time of pollination and on the viability of the pollen used. Guardiola pollen appears to be viable, and sticky, for only two or three days. Some crosses were made deliberately using pollen which was powdery and no longer sticky as it is when fresh. No seeds were set under these circumstances, and it is assumed that the pollen retains its viability for a rather short period of time. Some plants would successfully set seed following pollination with pollen from almost any source and then suddenly stop setting seeds for no apparent reason. Light level may have been important in some circumstances, for I had poor success with plants which were too tall to fit into the growth chamber and were maintained under reduced light conditions. Plants of Guardiola angustifolia were especially problematical because when a budding plant was brought into the laboratory from the greenhouse, the buds would abort before flowering.

The time required for maturation of the seeds (from pollination to release of mature seeds) varies considerably; broad- and narrow-leaved species differ (see Table 7). When a broad-leaved plant was the seed parent, seed maturation averaged 23.5 days with a median of 23.5 days, and a range of 20-28 days. When a narrow-leaved plant was the seed parent, seed maturation averaged 19.5 days with a median of 19 days and a range from the remarkably short time of 9 days to 27 days.

Table 7. --Summary of time required for maturation of seeds in Guardiola.

Days to Mature	Broad-leaved Seed Parent			Narrow-leaved Seed Parent		
	Broad-leaved Pollen Parent	Narrow-leaved Pollen Parent	Total	Broad-leaved Pollen Parent	Narrow-leaved Pollen Parent	Total
9			0		1	1
10			0		1	1
11			0		1	1
12			0		0	0
13			0		0	0
14			0		1	1
15			0		2	2
16			0		6	6
17			0	10	5	15
18			0	8	16	24
19			0	2	15	17
20	1		1	6	6	12
21	6		6	6	7	13
22	4	1	5	5	8	13
23	2	3	5	0	1	1
24	4	0	4	5	0	5
25	6	3	9	3	3	6
26	1	2	3	2	0	2
27	0	0	0	0	2	2
28	1	0	1	0	0	0
Mean Days to Mature	23.20	24.22		20.32	18.97	

Mean maturation time for crosses involving two broad-leaved parents was 23.20 days, while that for two narrow-leaved parents was 18.97 days. A t-test comparison of these means indicates that the difference is highly significant at the 5% confidence level. This data supports the contention of evolutionary divergence of those two species groups.

A t-test comparison of the influence of the pollen parent on the mean days required for seed maturation indicated acceptance of the means as the same at the 5% confidence level when a broad-leaved seed parent is involved and at the 2% confidence level when a narrow-leaved seed parent is involved in the cross. This suggests that the source of the pollen used does not significantly alter the mean days required for seed maturation.

Similar comparisons of the influence of the seed parent on the time required for seed maturation indicate highly significant differences at the 5% confidence level for both broad- and narrow-leaved species groups. This suggests a strong seed parent influence on the time required for seed maturation.

Success in establishing hybrid plants in nature depends on seed viability, seedling vitality, and ability of the F_1 plants to reproduce. Viability of seeds set in these experiments was 96.1%. The embryo in apparently fertile seeds which did not germinate was either malformed or absent.

Approximately 75% of the F_1 seedlings survived at least long enough to produce plants of flowering size. Non-survival of the seedlings was due largely to unknown causes, but also contributing were greenhouse pests which destroyed a number of seedlings, and malfunctioning growth chambers, which on two occasions refrigerated to about 35° F, a temperature below the tolerance limits of some of the seedlings.

Very few of the surviving F_1 plants, many of which were nine months old, flowered under greenhouse conditions. Under similar conditions, plants grown from field-collected seeds flowered in 3½ to 5 months. Of the few F_1 plants which did flower, almost all were from seeds produced by intraspecific matings. Mating attempts using these F_1 plants were all unsuccessful. Apparently this type of sterility is important in maintaining the integrity of the species in nature; however, more work must be done with the F_1 plants of *Guardiola* to determine the nature and extent of the hybrid sterility.

Intraspecific Mating Attempts

Seed set occurred in 62.6% of the intraspecific mating attempts (see Table 6). There were successful intraspecific matings within all *Guardiola* species studied except *G. angustifolia* (Table 6) in which the few florets available were all used in interspecific mating attempts. No pattern of successes or failures of intraspecific mating attempts was detected.

Seeds produced from the intraspecific matings were harvested and germinated. The resulting seedlings grew readily to flowering size. As expected, the range of variation of these plants was within the range of variation of the parent species. However, only a few buds were produced by these progeny. Some of the buds were sacrificed in order to examine meiosis, in which pairing appeared normal. The rest of the buds were allowed to flower for use in various mating attempts, none of which were successful.

Interspecific Mating Attempts

Interspecific mating attempts were 67.5% successful (Table 6). This rate of successful seed set is approximately the same as that found in the intraspecific matings.

There were no successful matings involving *G. angustifolia* as the seed parent. However, the 60% success rate when *G. angustifolia* was used as the pollen parent suggests that the problems were physical rather than genetic when *G. angustifolia* was used as the seed parent. Otherwise there was no clear pattern of success or failure.

Seeds resulting from the various interspecific matings were germinated and grew readily to flowering size. The plants varied, but as expected, were vegetatively intermediate between the parental species. Figures 9-14 illustrate typical leaves from parent plants used in the crossing experiments and pictorially describe the leaves of the hybrid plants derived from the crosses. Almost none of these plants set flowers, but in those which did, meiotic pairing appeared normal. A few buds were allowed to flower and all mating attempts using them as either pollen or seed parent failed. While the sample is small, it suggests a fertility barrier in the progeny, a barrier which would prevent reproduction by any hybrid plant which might occur in nature and thus support the integrity of the various species. Because of the small sample, further work is necessary in order to make certain that such a reproductive barrier exists and what may be its nature.

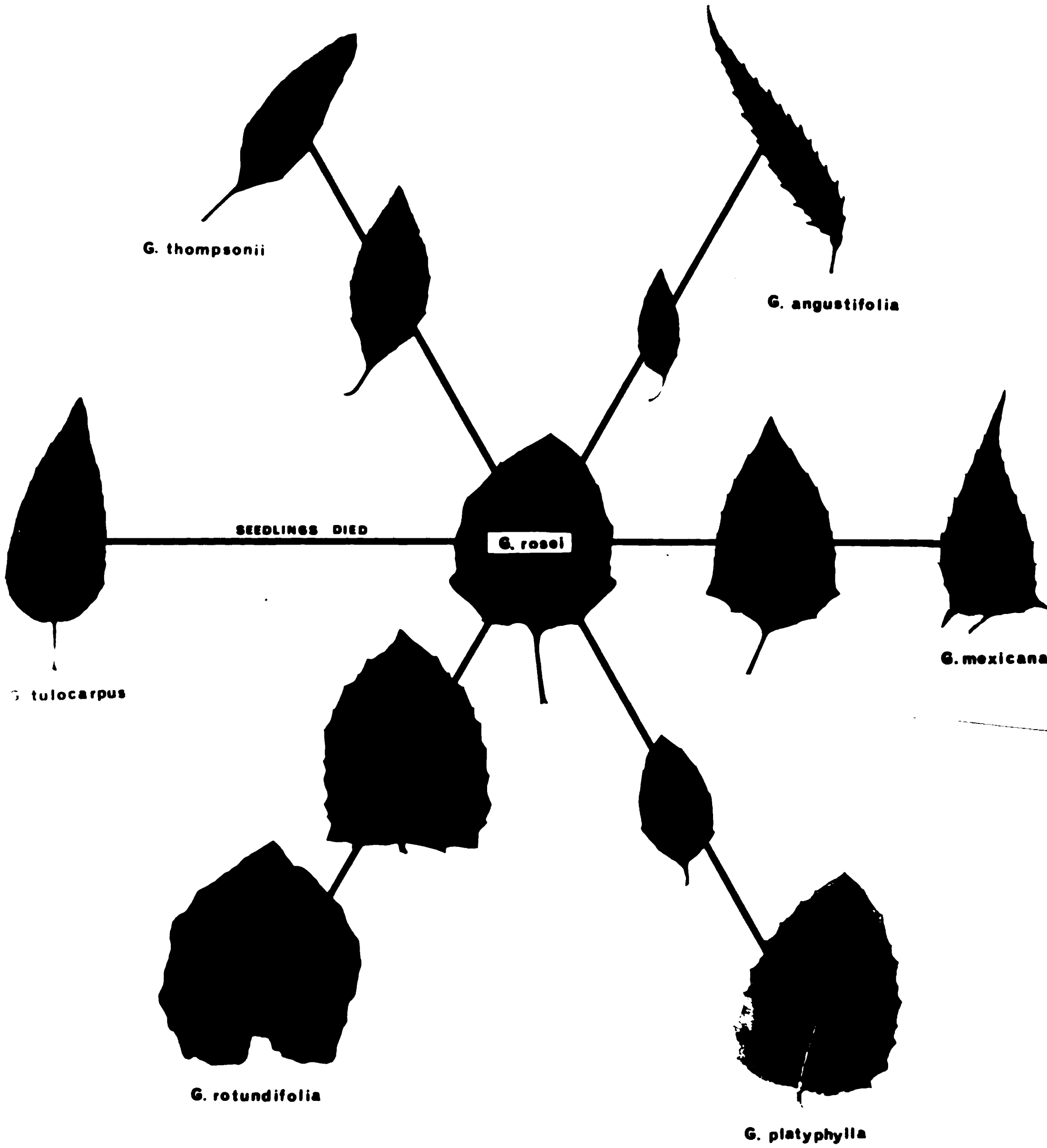

Figure 9. Experimental crosses involving G. rosei as the seed parent. A typical leaf of the seed parent is in the center of the illustration. Typical leaves of the pollen parents are around the periphery. Typical leaves of the F_1s obtained are along the lines.

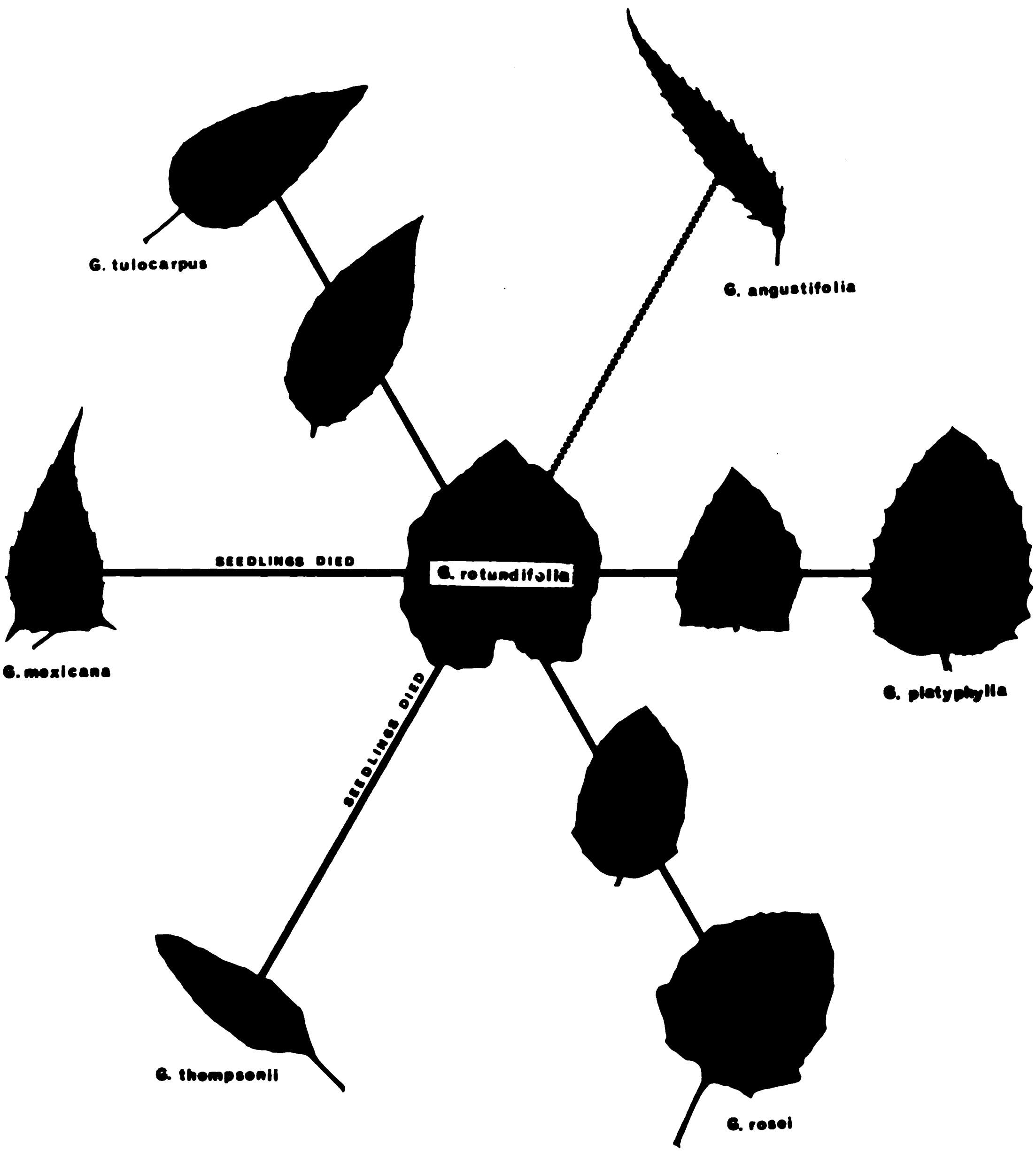

Figure 10. Experimental crosses involving G. rotundifolia as the seed parent. Broken line indicates unsuccessful crossing attempts.

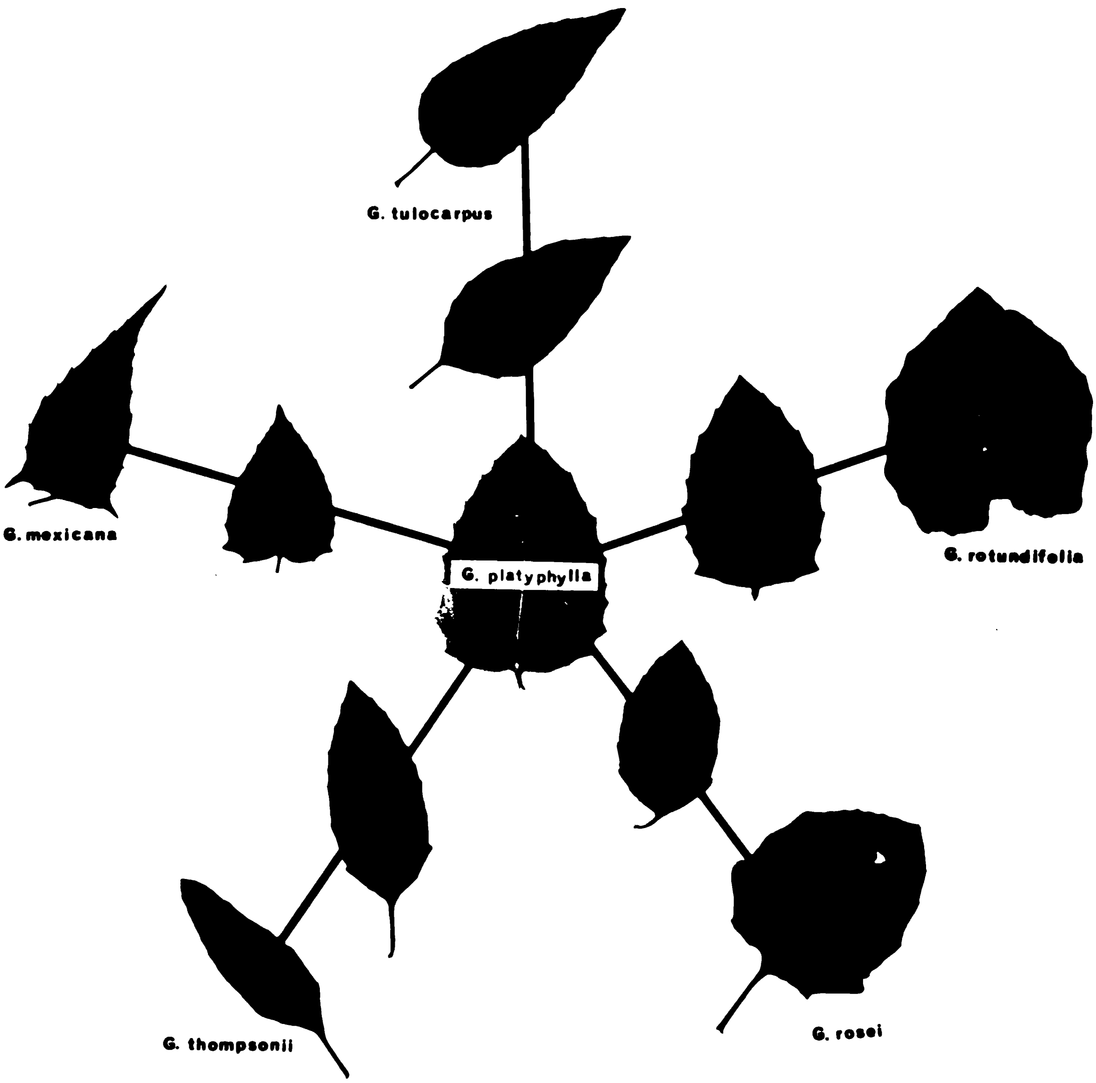

Figure 11. Experimental crosses involving G. platyphylla as the seed parent.

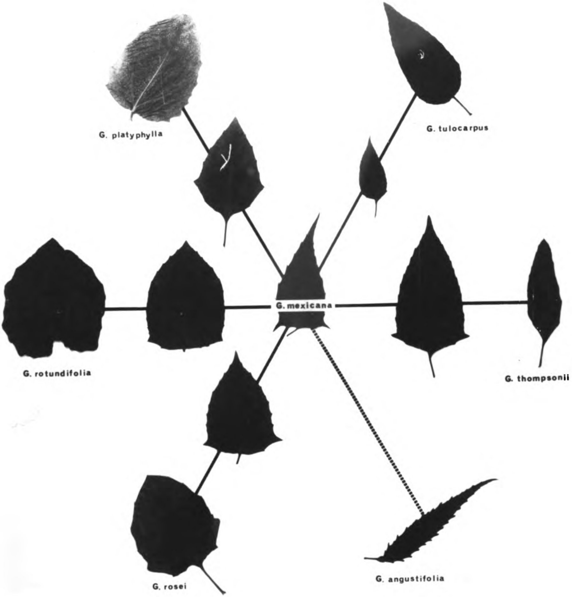

Figure 12. Experimental crosses involving G. *mexicana* as the seed parent. Broken line indicates unsuccessful crossing attempt.

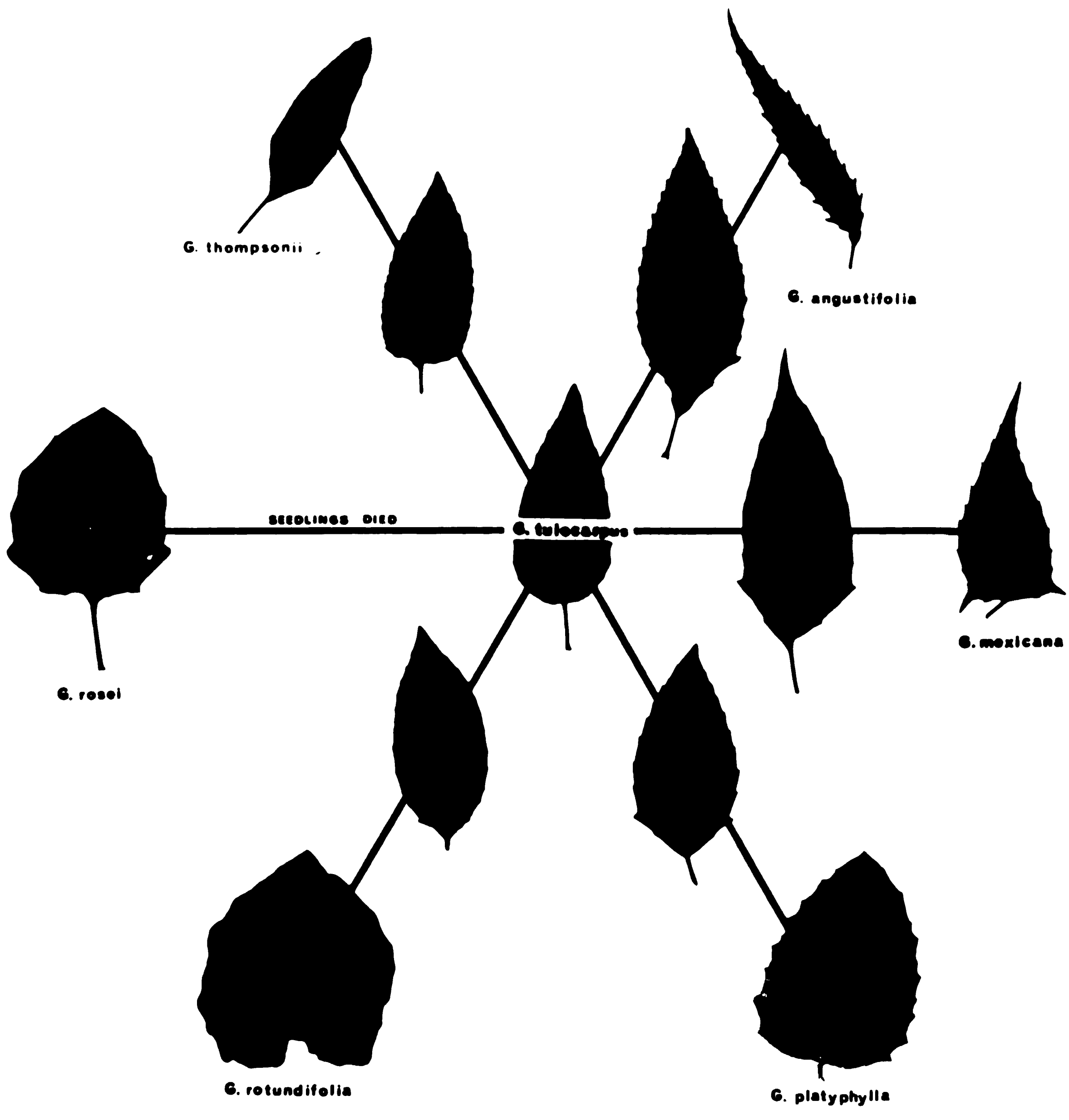

Figure 13. Experimental crosses involving G. tulocarpus as the seed parent.

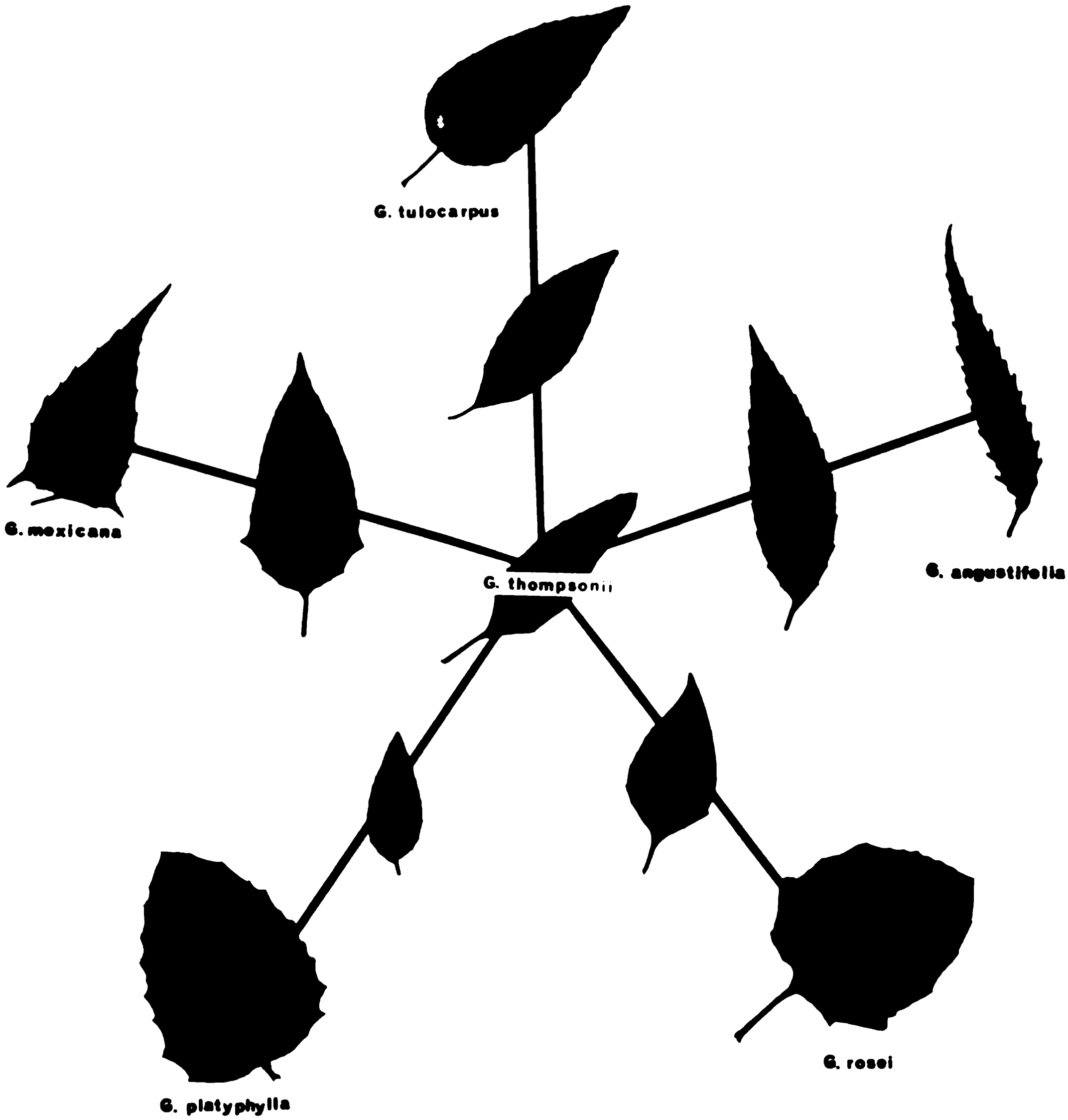

Figure 14. Experimental crosses involving G. thompsonii as the seed parent.

POLLEN STUDIES

Materials and Methods

Heads from dried specimens were softened in warm detergent solution; the anthers were removed from the disk florets and transferred to glacial acetic acid. Fresh materials were collected in glacial acetic acid and the anthers removed. The anthers were broken, the pollen removed from them and washed into a test tube with glacial acetic acid. Pollen grains were acetolyzed, stained, and mounted according to the schedule outlined by Longpre (1970). They were examined at an original magnification of about 1600 diameters.

Pollen

Guardiola pollen grains correspond to the "Helianthus type" pollen grain as it was described by Stix (1960). They were spheroid and tricolporate with transverse equatorial pores in elongate longitudinal furrows. The pollen grain surface is finely granular and bears the evenly spaced long spines typical of Helianthoid pollen. Striae or lacunae were not observed even though they are common in the spine bases of Helianthoid pollen grains (Carlquist, 1957a; Longpre, 1970). No taxonomically useful variations were found in the spines of Guardiola pollen grains although occasional grains have deltoid rather than elongate spines.

Measurements of pollen grains are summarized in Table 8. Pollen grain body diameters, excluding the spines, of individual Guardiola pollen grains vary from 20.3 microns in G. platyphylla to 32.9 microns in G. pappifera. The mean body diameters of Guardiola pollen grains vary from 21.9 microns in G. stenodonta to 28.5 microns in G. pappifera.

Spine length of individual Guardiola pollen grains varies from 3.8 microns in G. tulocarpus to 10.1 microns in G. pappifera. The mean pollen grain spine length in Guardiola varies from 5.1 microns in G. angustifolia to 7.6 microns in G. pappifera.

Tabulation of Guardiola species according to mean pollen grain body diameter provides little information, for although a general trend toward decreasing diameter with advancedness is noted, G. platyphylla, an advanced species, has larger pollen grains than several of the more primitive species. However, when broad-leaved and narrow-leaved species are tabulated separately (Table 9), correlation of decreasing body diameter with evolutionary advancedness is clearly indicated.

Table 8. --Pollen grain measurements in Guardiola. All measurements are in microns.

Species	Collection Number*	Body Diameter (Excluding Spines) Collection Range	Body Diameter Species Range	Body Diameter Collection Mean	Body Diameter Species Mean	Spine Length Collection Range	Spine Length Species Range	Spine Length Collection Mean	Spine Length Species Mean
G. angustifolia	1776	20.3-24.1		21.5		4.4-5.7		5.0	
	1777	20.3-24.1	20.3-22.8	22.2	22.2	4.4-6.3	4.4-6.3	5.3	5.1
	1783	20.9-24.7		22.8		4.4-5.7		4.9	
G. arguta	1822	20.9-26.6		23.4		4.4-6.3		5.4	
	Pringle 678	22.2-25.3	20.9-26.6	23.5	23.8	5.1-6.3	4.4-6.3	5.5	5.4
	Pringle 1281	22.2-25.9		24.5		5.1-6.3		5.4	
G. carinata	Rose 1428	22.8-25.3	22.8-25.3	24.6	24.6	5.1-6.3	5.1-6.3	5.6	5.6
G. mexicana	1688	22.8-25.9		24.7		5.7-7.0		6.3	
	1601	24.1-26.6		25.6		5.7-7.0		6.2	
	1650	21.5-25.3		24.1		4.4-6.3		5.5	
	1661	21.5-24.7		23.1		4.4-6.3		5.2	
	1701	21.5-24.7		22.8		5.1-6.3		5.6	
	1785	21.5-24.7		23.1		4.4-7.0		5.6	
	1649	20.9-24.7	20.9-26.6	22.0	23.3	4.4-6.3	4.4-7.0	5.1	5.5
	1568	21.5-24.7		23.1		4.4-6.3		5.7	
	1569	20.9-23.4		21.8		4.4-5.7		4.9	

Table 8. --Continued.

Species	Collection Number	Body Diameter (Excluding Spines)				Spine Length			
		Collection Range	Species Range	Collection Mean	Species Mean	Collection Range	Species Range	Collection Mean	Species Mean
	Arsene 2737	22.2-24.1		23.2		4.4-5.7		5.4	
	Arsene 5466	22.8-24.1		23.2		4.4-5.7		5.2	
G. odontophylla	Nelson 1683	21.5-24.1	21.5-24.1	22.7	22.7	5.1-6.3	5.1-6.3	5.9	5.9
G. pappifera	Hinton 9533	27.2-32.9		29.5		6.3-7.6		8.1	
	McVaugh 17930	26.6-28.5	26.6-32.9	27.5	28.5	7.0-10.1	6.3-10.1	8.1	7.6
G. platyphylla	1931	20.3-25.9		23.0		5.1-5.7		5.3	
	1932	21.5-24.7	20.3-25.9	23.8	23.6	4.4-6.3	4.4-7.0	5.5	5.7
	1934	21.5-25.9		23.9		5.1-7.0		6.2	
G. rosei	1860	24.1-26.6		25.5		5.1-7.0		6.1	
	1859	24.1-27.2	22.8-27.2	25.9	25.2	5.1-7.0	5.1-7.0	6.3	6.1
	1891	22.8-25.3		23.9		5.1-6.3		5.8	
	1906	24.1-27.2		25.2		2.7-7.0		6.2	

Table 8. --Continued.

Species	Collection Number	Body Diameter (Excluding Spines) Collection Range	Species Range	Collection Mean	Species Mean	Spine Length Collection Range	Species Range	Collection Mean	Species Mean
G. rotundifolia	1784	24.1-27.2		25.5		5.1-6.3		5.7	
	Pringle		24.1-29.1		26.3		5.1-8.2		6.5
	1571	25.3-29.1		27.1		6.3-8.2		7.3	
G. stenodonta	Ortega								
	4986	20.9-22.8	20.9-22.8	21.9	21.9	5.1-5.7	5.1-5.7	5.4	5.4
G. thompsonii	1727	22.2-26.6	22.2-26.6	24.0	24.2	4.4-5.7	4.4-6.3	5.1	5.2
	1756	23.4-25.3		24.4		5.1-6.3		5.3	
G. tulocarpus	1762	22.2-25.9		24.7		5.1-6.3		5.9	
	1757	20.9-22.8		21.9		4.4-5.1		4.8	
	1759	20.9-24.1		22.9		3.8-5.1		4.5	
	1797	21.5-24.7		23.1		5.1-6.3		5.5	
	1813	21.5-24.7		23.0		5.1-6.3		5.6	
	1801	20.3-23.4	20.3-25.9	22.3	22.7	4.4-5.1	3.8-7.0	4.7	5.2
	1795	21.5-25.3		23.4		5.1-6.3		5.9	
	1796	22.2-24.7		23.7		5.1-7.0		5.8	
	1814	20.9-23.4		21.9		4.4-6.3		5.2	
	1774	20.3-22.8		21.6		4.4-6.3		5.2	
	1802	20.3-22.8		21.3		3.8-5.1		4.5	

*Collection numbers are Van Faasen's except where otherwise indicated.

Table 9. --*Guardiola* pollen grain mean body diameters.

Species	Mean Body Diameter (in Microns)
Narrow-leaved Species	
G. stenodonta	21.9
G. angustifolia	22.2
G. tulocarpus	22.7
G. odontophylla	22.7
G. mexicana	23.3
G. arguta	23.8
G. thompsonii	24.2
	Mean 23.0
Broad-leaved Species	
G. platyphylla	23.6
G. carinata	24.6
G. rosei	25.1
G. rotundifolia	26.3
G. pappifera	28.5
	Mean 25.6

A t-test comparison of the mean body diameters of the pollen grains of the broad- *vs.* the narrow-leaved species demonstrates a significant difference at the 5% confidence level. However, an analysis of variance shows no significant differences among the sizes of the pollen grains within either the broad- or narrow-leaved species groups.

The distribution of the mean body diameters of the narrow-leaved (N) and broad-leaved (B) species of *Guardiola* by size from smallest to largest body diameter in the arrangement: N, N, N, N, N, B, N, N, B, B, B, B is statistically significant. According to the Mann-Whitney test, the probability of this arrangement by chance is about 1%. Therefore, additional support for separate lines of evolutionary development within *Guardiola* is assumed.

Discussions of evolutionary relatedness assume that pollen grains of the same and closely related species tend to be alike; if environmental factors are uniform, the degree of similarity is a measure of their closeness of relationship (Wodehouse, 1959). Faegri and Iversen (1964), in reviewing their own work and that of Schoch-Bodmer (1940) and Wagenitz (1955), stress that pollen grains may vary considerably, especially when containing protoplasm, and that variability of pollen grains should not be underrated. Pollen may exhibit a natural range of variation because of gene action or as a result of environmental factors such as nutrition or moisture. Pollen grain body diameter variations within a population, such as that found in Guardiola, are most probably due to gene action, while those variations between populations, especially in wide-ranging species, may be due to either gene action or environmental factors. An impressive example of environmental influence is the size cline in pollen of Pinus echinata, in which there are distinct size differences along the north-south range of that species (Cain and Cain, 1948).

The greatest range of variation of pollen grain diameter in a single collection of Guardiola was 20.9-26.6 microns (G. arguta, Van Faasen 1822). This range of variation includes the means of 11 of the 12 (except G. pappifera) Guardiola species. Thus, Faegri and Iversen's (1964) statement that pollen grains from the same species may exhibit great variations, and transgress into the sphere of variation of pollen of related species, is amply illustrated. This also suggests the need for caution in drawing conclusions concerning the various species based on pollen grain measurements alone.

Nonetheless, this study suggests several conclusions. The evidence supports the grouping of the species in subgenus Guardiola, as can be done readily by gross morphological observations, into two groups of species based on leaf shape. If within a group reduction in pollen grain size occurs along with evolutionary reduction in other floral parts, then advanced species should have smaller pollen grains than primitive species. In Guardiola the narrow-leaved species, in general, have smaller pollen grains than do the broad-leaved species, suggesting their more advanced nature, a conclusion also reached on the basis of other morphological considerations. Within each group, species considered most advanced have the smallest pollen grains, further indicating decrease in size of pollen grains with advancedness.

CHEMICAL STUDIES

Materials and Methods

Six to ten leaves were removed from each collection of dried specimens and were ground to powder with mortar and pestle. Little attempt was made to quantify the material used, although in general the total volume of leaf material taken from each collection was about equal. The powdered leaf was transferred to a four dram vial and extracted in about 2 - 4 ml of acidified alcohol (1 ml concentrated HCl: 100 ml 80% methyl alcohol). The volume of acidified alcohol used was enough to cover the powdered leaf with 1 - 2 mm of extra solution. The leaf material was extracted at 5 degrees C for about 18 hours. The mixture was filtered, and 0.2 ml was spotted on 18 × 22 inch sheets of Whatman No. 1 chromatography paper by 10 applications from a 20 lambda micropipette. The spots were kept as small as possible and ranged from about 15 to 25 mm in diameter.

Replicate two-dimensional chromatograms of each collection were developed in a chromatocab by the descending method. The first dimension ran the length of the paper (with the machine grain of the paper) and was developed for 16 hours in a solvent system of 8 parts N butanol: 2 parts glacial acetic acid: 3 parts distilled water. The developing chromatograms were removed from the chromatocab and dried in a hood. The dried papers were replaced in the chromato-cab and the second dimension was developed for 5 hours in a solvent system of 1 part glacial acetic acid: 5 parts distilled water. The developed chromatograms were removed, dried in a hood, examined under long and short wave ultraviolet light, and the spots were marked and recorded. They were not chemically identified.

A composite chromatogram showing 35 spots for the taxa included in this study is seen in Figure 15. All of the spots seen on the chromatograms are not useful in a taxonomic consideration of *Guardiola*. Some occur infrequently or irregularly, or are faint and their presence is difficult to determine, so they are not considered useful. Only clearly distinct spots are considered in this treatment. Individual chromatograms showing selected useful spots for the taxa included in this study are seen in Figures 16 and 17.

Observations

Guardiola rosei (Chromatogram Figure 16A, based on 3 collections), a primitive broad-leaved species, has a central group

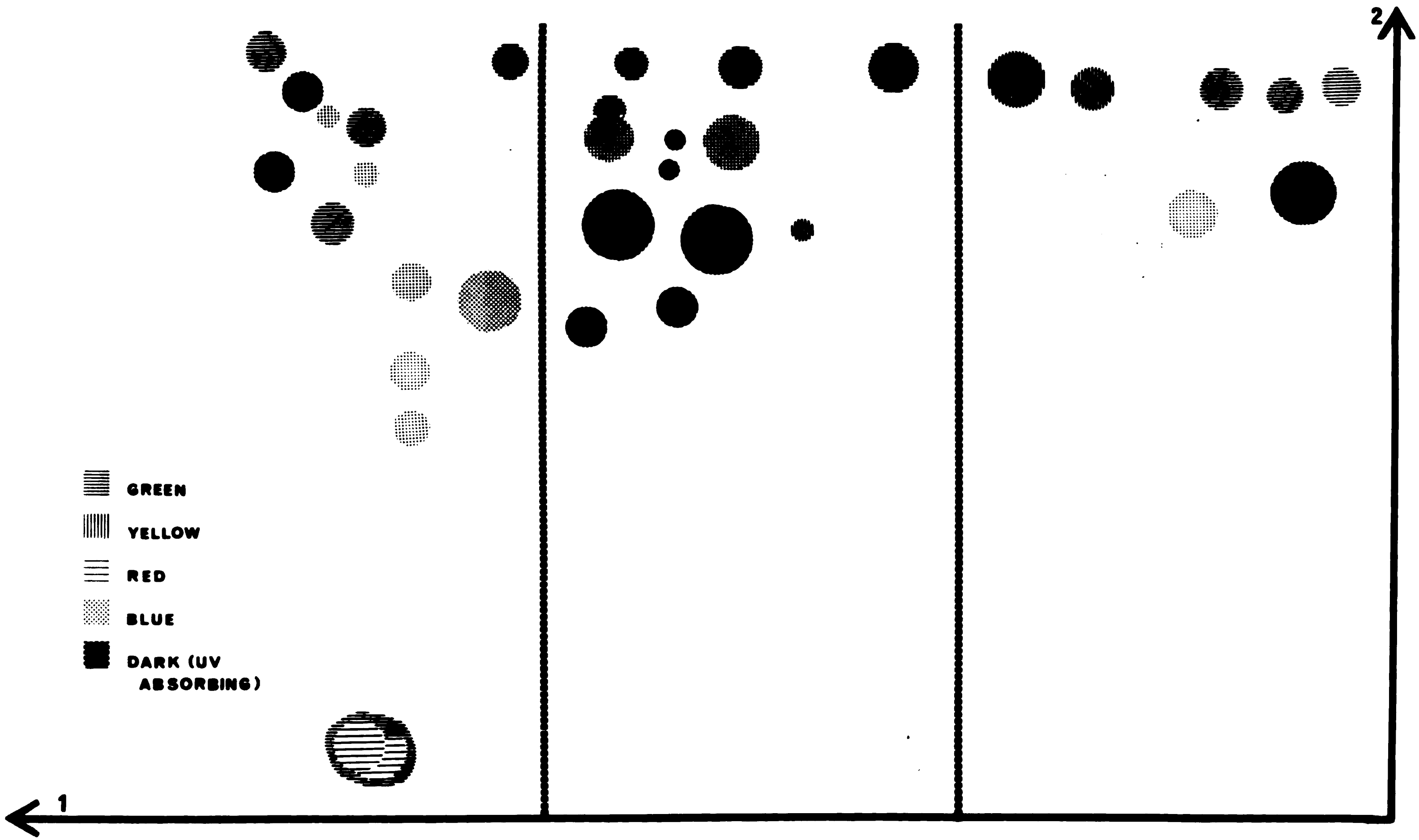

Figure 15. Composite chromatogram of the species of <u>Guardiola</u>. Arrows indicate directions of first and second dimensions of development of the chromatograms.

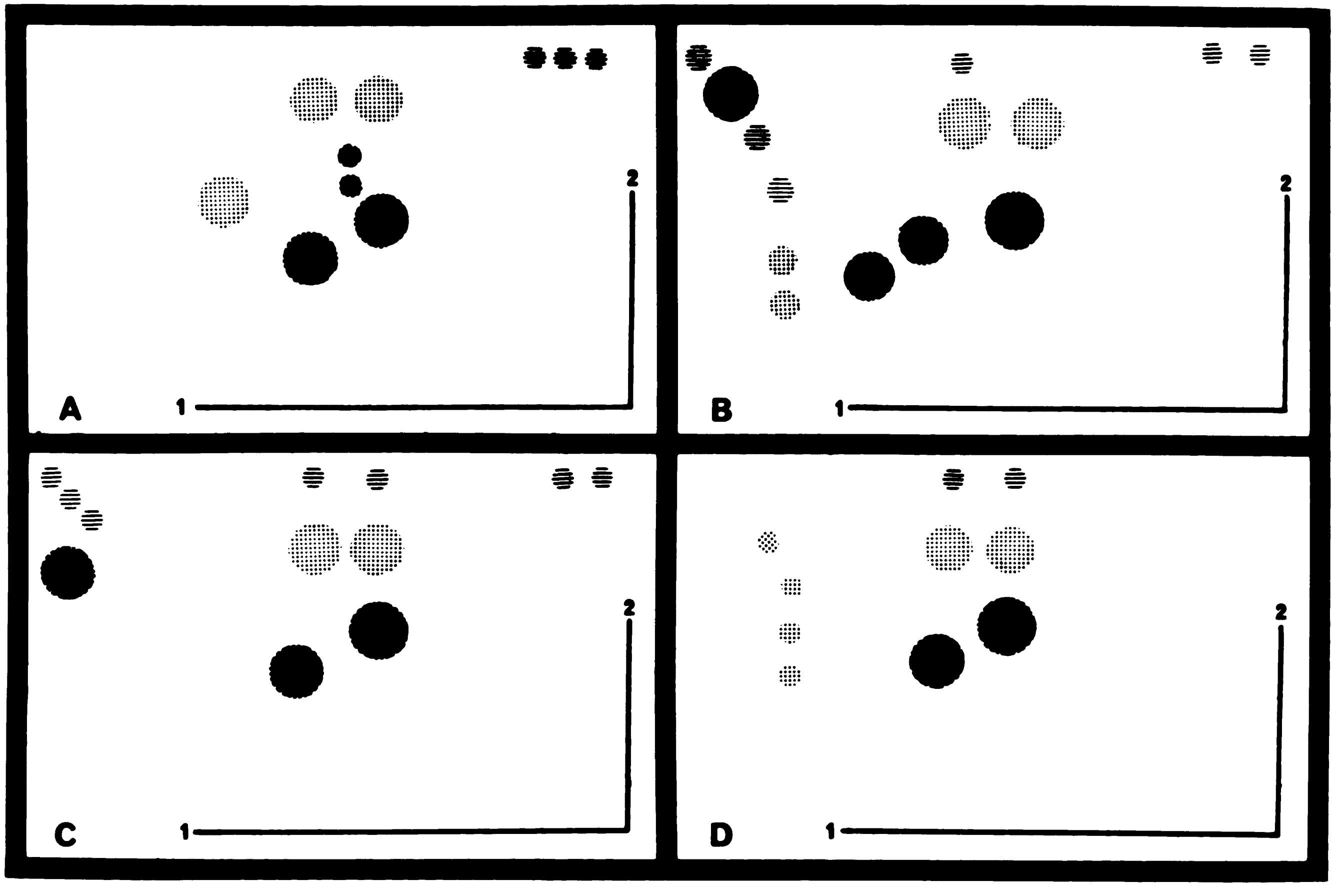

Figure 16. Representative chromatograms of _Guardiola_. I. A. _G. rosei_; B. _G. rotundifolia_; C. _G. platyphylla_; D. _G. mexicana_.

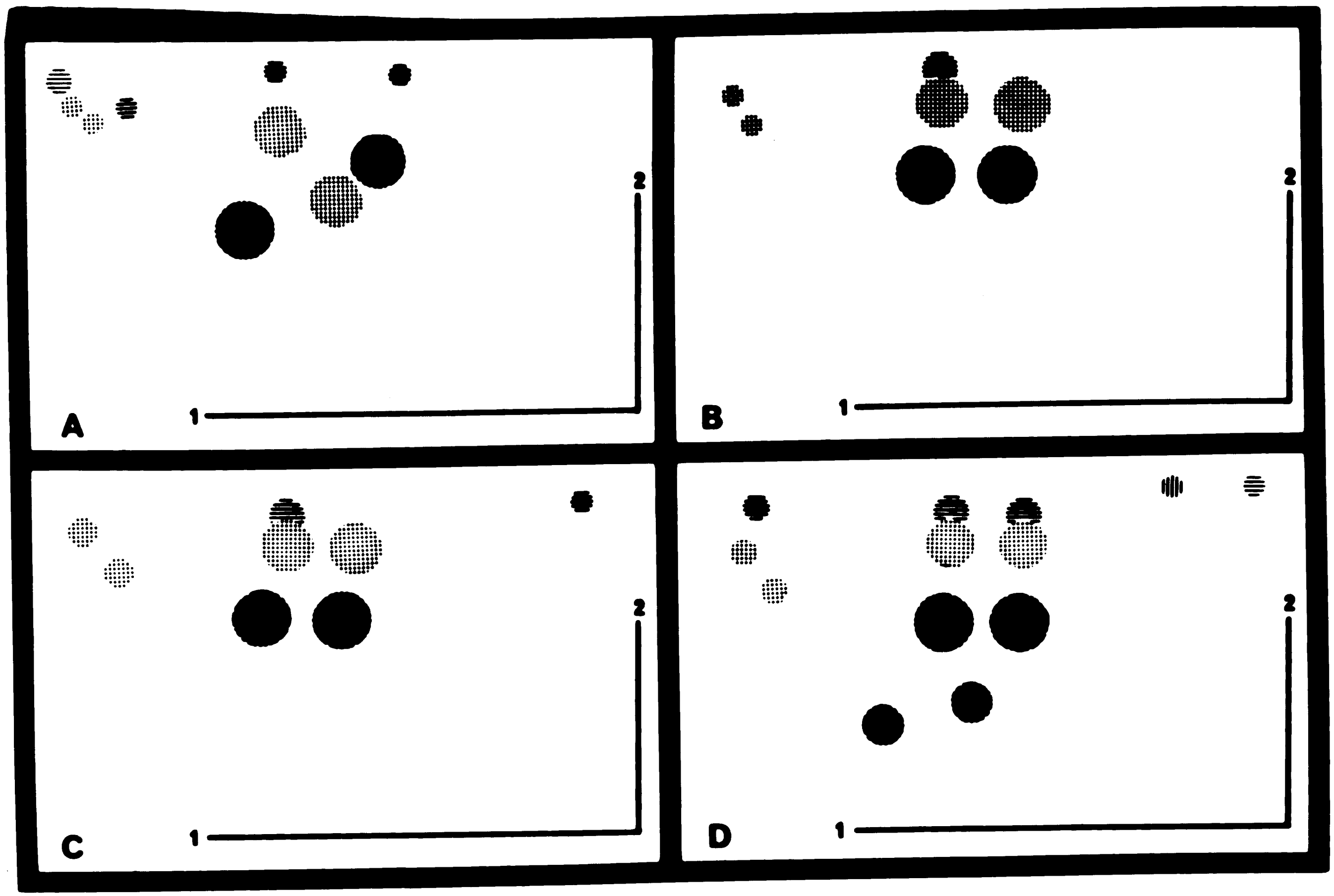

Figure 17. Representative chromatograms of _Guardiola_. II. A. _G. arguta_; B. _G. tulocarpus_; C. _G. thompsonii_; D. _G. angustifolia_.

consisting of two large and two small dark spots below two blue spots. This is distinct from the patterns found in the narrow-leaved species mentioned below. In _G. rosei_ there is a left group consisting of a large blue spot and a right group consisting of three small green spots.

The chromatogram of _G. rotundifolia_ is seen in Figure 16B and is based on one collection. The central group consists of three dark, two blue, and one green spot. The left group is complex and consists of three green, two blue, and one dark spot. The right group consists of two green spots.

The only other species having a dark spot in the left group is _G. platyphylla_, Figure 16C (chromatogram based on 4 collections), an advanced broad-leaved species. Also present in this left group are three green spots. The central group in the _G. platyphylla_ chromatogram consists of two dark, two blue, and two green spots. The right group consists of two green spots.

The representative chromatogram for _Guardiola mexicana_ based on replicated chromatograms of ten collections is seen in Figure 16D. The central group consists of two dark, two blue, and two green spots, all of them distinct. The green spots are always directly above and never touch the blue spots which are above the dark spots. The left group consists of a tier of four blue spots.

Guardiola arguta is morphologically very closely related to G. mexicana, but its chromatogram, Figure 17A, based on one collection, is distinct from that of G. mexicana. The central group of spots consists of two dark, two blue, and two green spots, but the arrangement is slightly different in that one of the blue spots is positioned between the dark spots rather than above the dark spot. The left group of spots consists of two blue and two green and is different from the left group of G. mexicana.

Figure 17B represents the chromatogram of G. tulocarpus, another species which is closely related to G. mexicana. This chromatogram is based on 15 collections. The central group of spots in G. tulocarpus is similar to that of G. mexicana except that the green spot (sometimes two spots are present) always touches the blue spot. The left group consists of two blue spots. While these two species tend to merge morphologically, their chromatograms are distinct and easily separated.

The chromatogram of G. thompsonii, seen in Figure 17C, is based on two collections. The central group is identical to that of G. tulocarpus. The left group consists of one blue and one green spot, and a right group consisting of a green spot is present. These chromatograms are distinct from those of G. tulocarpus.

The chromatogram of G. angustifolia, a species considered advanced, is seen in Figure 17D and is based on three collections.

In this chromatogram the central group consists of four dark spots and two blue spots, each below and touching a green spot. The left group consists of two blue and one green spot, and a right group consisting of one yellow and one green spot is consistently present.

Discussion

The various species of *Guardiola* are identifiable, at least tentatively, from their chromatograms. In fact, it has been possible to construct a key (page 81) to the eight taxa included in this study based on chromatographic data. The chromatograms are sufficiently variable, however, to require the use of considerable caution in making such determinations. The techniques used in this study are gross enough that one cannot determine *Guardiola* species as absolutely as was done in the study of *Asplenium* by Smith and Levin (1963) or of *Artemisia* by Holbo and Mozingo (1965). However, by the position of the green spots of the central group, one can without doubt distinguish between the chromatograms of *G. mexicana* and *G. tulocarpus*. Other species pairs may also be distinguished on other bases. In *Guardiola* chemotaxonomic data can be used with much greater confidence to answer the question, "Is this species x or species y of *Guardiola*?" than "Which species of *Guardiola* is this?" This is due to the variation among and overlap of the chromatograms of the various *Guardiola* species.

Key to Eight *Guardiola* Species Based on Chromatographic Data

1. Green spots absent from central group . . . . *G. rosei*

1. Green spots present in central group 2

    2. Right hand group usually absent 3

    2. Right hand group present 5

3. Central green spot touching blue spot . . . . . *G. tulocarpus*

3. Central green spot distinct from blue spot . . . 4

    4. Left group: tier of 5 blue spots, central group with dark spots below blue spots . . *G. mexicana*

    4. Left group: clump of 2 blue and 2 green spots; central group with 1 blue spot between dark spots . . . . *G. arguta*

5. Central green spot touching blue spot 6

5. Central green spot free from blue spots 7

    6. Central dark spots 4 . . . . *G. angustifolia*

    6. Central dark spots 2 . . . . *G. thompsonii*

7. Left group complex (from corner down--green, dark, green, green, blue, blue) 3 central dark spots . . . . *G. rotundifolia*

7. Left group 3 green above one dark spot 2 central dark spots . . . . *G. platyphylla*

Chromatograms of hybrids demonstrate combined spot patterns of the two parent species. Chromatographic identity of hybrids was conclusively demonstrated in studies by Smith and Levin (1963) in Asplenium, in Vernonia by Hunter (1967), and by the classic studies of Alston and Turner (1962, 1963) in Baptisia. I did not detect any spot patterns in the chromatograms of Guardiola which suggested a hybrid origin for any of the taxa. The laboratory-produced hybrids were not available at the time of this study and therefore were not investigated chromatographically.

Evolutionary relationships among taxa may also be inferred from chromatographic analyses. According to Brehm (1966), however, such conclusions must be tempered because "the presence of similar patterns in two taxa does not necessarily imply either a lack of genetic differences or a close evolutionary relationship between the taxa with common patterns, although these are reasonable deductions, particularly with reference to the genetic regulation of flavenoid production."

Among the narrow-leaved species, G. mexicana, G. arguta, and G. tulocarpus tend to merge morphologically. Experience allows ready separation of G. mexicana and G. tulocarpus with considerable certainty; but G. mexicana and G. arguta are difficult to distinguish on morphological bases. The chromatograms of the three are distinct but suggest a close relationship between G. mexicana and G. arguta with G. tulocarpus more distantly related. Biochemical diversity due to ecological variation occurs and can be identified from chromatograms as seen in Tragopogon (Brehm and Ownbey, 1965), Hymenoxys (Seeligman and Alston, 1967), and Thelesperma (Melchert, 1966). McClure and Alston (1966) report little or no variation in the chromatograms of Spirodela (Lemnaceae) grown under 62 different culture conditions. In direct opposition to the McClure and Alston findings, Ball, Beal and Flecker (1967), in a similar study in Spirodela, report "Variations in environmental conditions produce marked differences in spot patterns." It was not possible within the scope of this study of Guardiola to attribute any variations in spot patterns to ecological variations.

Another narrow-leaved species, G. thompsonii, while morphologically distinct, is chromatographically similar to G. tulocarpus and a close relationship between those two species is suggested.

Guardiola angustifolia, the most advanced of the narrow-leaved species, exhibits a spot pattern with the green spots of the central group above and touching the blue spots. This is seen only in G. tulocarpus, G. thompsonii and G. angustifolia and must indicate an evolutionary relationship among these species.

Among the broad-leaved taxa, G. palmeri and G. rosei are considered, on morphological grounds, to be conspecific. Chromatograms of specimens originally identified as G. palmeri (Van Faasen 1860) were virtually identical to those of G. rosei and this chemotaxonomic evidence is used to confirm conspecificity of the two taxa.

The chromatograms of two other broad-leaved species, G. rotundifolia and G. platyphylla, are both distinct from G. rosei and suggest a closer relationship between these two species than between either and G. rosei, a rather unexpected conclusion.

There appear to be no chromatographic features which allow separation of the genus into broad- and narrow-leaved groups. All species have some spots in common but neither group has a spot pattern unique to it.

Alliance of Guardiola to the Coreopsidinae has been suggested by Gray (1888), Hoffman (1894), and informally to me by Dr. B. L. Turner. In an attempt to evaluate this possible relationship, specimens of several taxa were sent to Dr. T. E. Melchert of the University of Iowa, who chromatographed various parts of them and reported (personal communication):

> I did not find any of the aurones, or chalkones common to the Coreopsidinae . . . we have never found a single species within Bidens, Dahlia, Cosmos, Coreopsis, etc., which did not produce aurones and/or chalkones in their disk florets. This is so even when they do not produce them in all of their tissues.

He further states that, while negative evidence is not conclusive, he sees no reason for the inclusion of *Guardiola* in the Coreopsidinae. Thus, on the basis of chemotaxonomic evidence, we have clarified to some extent the problem of the proper tribal position of *Guardiola*.

EVOLUTION AND PHYTOGEOGRAPHY OF GUARDIOLA

The lack of absolute information concerning evolutionary trends in Guardiola, whether radiating, adaptive, or progressive, makes it necessary to determine advanced or derived and primitive or generalized traits by indirect means. Proceeding on the assumption that forms which are morphologically specialized and/or occupy more xeric sites are derived forms, while those which lack morphological specializations and/or occupy more mesic sites are generalized forms and resemble or are closer to ancestral types than are xeric site forms, we may then infer primitive and advanced traits and evolutionary trends within the genus.

Guardiola mexicana and G. rosei are narrow- and broad-leaved species respectively and exemplify taxa which occupy mesic sites. These two species possess a sparsely branched inflorescence, fewer and larger heads, more ray and disk florets, larger ray and disk corollas, larger pollen grains, petiolate leaves, and the one-marginal vein type of cotyledon petiole vasculature. Guardiola angustifolia among the narrow-leaved species, and G. platyphylla among the broad-leaved species in subgenus Guardiola, are the taxa which occupy sites more xeric than those occupied by any other Guardiola species. Both possess a highly branched inflorescence, numerous small heads, a reduced number of ray and disk florets, reduced size of ray and disk corollas, reduced pollen grain diameter, sessile or subpetiolate leaves, and the two-marginal vein type of cotyledon petiole vasculature. The primary general trend noted is that of reduction in size of heads by incorporating a reduction in number of parts and a reduction in size of parts comprising the head (number and size of ray corollas, number and size of disk corollas, pollen grain diameter) plus an increase in number of heads and degree of branching. In addition, reduction in petiole length is coupled with these traits. These are all common evolutionary trends in the Compositae (Cronquist, 1955) and in this treatment are considered derived traits in Guardiola. However, Stebbins (1967) cites numerous examples of adaptive reversals of these trends in other taxa.

The correlation of these evolutionary trends common among the Compositae with an increase in number of marginal veins per cotyledon petiole is a curious one. It may reflect merely a change in point of divergence of the branches of the marginal veins from the base of the cotyledon blade to the stem below the point of attachment of the cotyledon petiole to the stem. If this is the situation, it may be an early stage in the reduction of the total vascular tissue of the cotyledon rather than proliferation by addition of conducting tissue.

Thus, from the basic assumption that in Guardiola habitat specialization indicates a derived form, and further assuming a combination of progressive and adaptive evolution as the major trends in the genus, it is possible to compile a list (Table 10) of advanced (specialized) and primitive (generalized) characters within the genus. In addition, since these trends are found in both the broad-leaved and the narrow-leaved species groups of subgenus Guardiola, their credibility is strengthened.

Further, if the two groups of species are compared in regard to the traits being considered in this discussion, it is noted that the broad-leaved species possess more primitive characters than the narrow-leaved species group. This in addition to the fact of reduction of leaf width suggests that in general the narrow-leaved species are advanced over the broad-leaved species.

Little or no genetic isolation is apparent among the species of Guardiola and hybrids are synthesized readily in the laboratory. There is a possibility that reproductive barriers may exist in the F_1 plants, however, thereby establishing some genetic isolation. The apparent low level of genetic isolation coupled with extensive

Table 10. --Primitive and advanced characters in Guardiola.

	Primitive characters	Advanced characters
1.	Plant perennial	Plant annual
2.	Habitat preference mesic	Habitat preference xeric
3.	Leaf blade broad	Leaf blade narrow
4.	Leaves petiolate	Leaves sessile
5.	Inflorescence simple	Inflorescence much branched
6.	Phyllaries not keeled	Phyllaries keeled
7.	Heads few (less than 50)	Heads many
8.	Heads large (longer than 9 mm)	Heads small
9.	Ray florets 3-5 per head	Ray florets 1-2 per head
10.	Disk florets more than 15 per head	Disk florets fewer than 15 per head
11.	Floral parts large (ray corolla longer than 10 mm, disk corolla longer than 10 mm)	Floral parts small
12.	Pollen grains large (body diameter more than 23 microns)	Pollen grains small
13.	Pappus present	Pappus absent
14.	Marginal cotyledon vein 1	Marginal cotyledon veins 2

spatial isolation might suggest relatively young species. Grant (1963) suggests that spatial isolation is usual and perhaps is an essential condition for development of reproductive isolation. Guardiola may be in the process of evolving reproductive isolation among the species.

Guardiola is a genus of very compact distribution and is essentially endemic to western Mexico and southeastern Arizona. Several factors have probably been involved in production and maintenance of this distribution.

Self incompatibility may be at least a partial explanation for the limited range of the genus. Because two propagules must be imported into an area to originate a sexually reproducing population in that area, a deterrent to wide distribution of the species is thereby provided. A single propagule may produce a single plant, but without a second plant of the species to establish a breeding population, the species range will not be expanded, except for the duration of the life of that original single plant (Baker, 1955).

Guardiola achenes are relatively large, lack any apparent modification for wind dispersal, drop to the ground as the phyllaries and outer pales reflex when the fruiting head matures, and possess what might be described as protective coloration in that they are mostly mottled shades of brown, making them difficult to see when on the ground. These traits do not facilitate, and in fact, appear to be evolutionary adaptations against wide dispersal of the achenes. Wind and animals seem to be precluded as primary dispersal factors. Rather there is a tendency for establishment of new plants in the immediate vicinity of the parents, an obvious advantage to any obligate outcrosser.

The above-mentioned achenial traits in conjunction with the obligate outcrossing nature of the reproductive system of *Guardiola* may operate to significantly retard expansion of the range of the taxa and thus in part would account for the limited distribution of the genus.

Guardiola achenes possess a hard, mechanically resistant seed coat. They are waterproof, so they float. The achenes are produced and shed during the rainy season; and the plants are found in disturbed, often eroding habitats. These facts suggest the intriguing possibility that running water, one of the least evolutionary complex escape mechanisms (Janzen, 1969), could be an agent of seed dispersal. It is a likely one, at least in a downslope direction, and is the probable explanation for some of the low elevation coastal populations.

Neither wind nor water, however, probably account for two populations of *G. tulocarpus* (one on the Tres Marias Islands and the other near Ciudad Victoria, Tamaulipas) which occur some distance outside of the range of the other populations of that species. The Tres Marias Islands lie along the west coast flyway in Mexico, and long distance dispersal by birds is probably the most likely explanation of the presence of Guardiola on those islands. Birds and/or humans may have been accidental long-distance dispersal vectors to account for the Tamaulipas population.

Guardiola is distributed almost exclusively in the Sierra Madre Occidental and the Sierra Madre del Sur. It occurs primarily in disturbed habitats between 1500 and 2000 meters elevation in areas dominated by oak-pine forests, the characteristic vegetation of the mountains of western Mexico from about 800 to 2800 meters elevation (Rzedowski and McVaugh, 1966). In general these are areas where the mean annual temperature at 1600 meters is about 20° C; where the average rainfall is about 750-1000 mm, about 90% of which falls from May through October; and where there is some frost in the winter (Rzedowski and McVaugh, 1966). While Guardiola occurs primarily in oak-pine transition areas, its distribution seems to correlate better with the natural region of pine forests of the western cordillera as outlined by Leopold (1950), Dice (1943), and Sanders (1921) than with the oak forest vegetation type.

Few Mexican genera of comparable size possess a distribution as restricted as that of Guardiola, although some genera contain one or several species with a distribution similar to that of *Guardiola* (e.g. *Hymenothrix* [Turner, 1962], *Cleome* [Iltis, 1959], *Bursera* [McVaugh and Rzedowski, 1965], and *Polansia* [Iltis, 1958]). The genus does not exhibit the pattern of many montane genera in Mexico which have a U- or Y-shaped distribution in the mountainous regions of eastern, western, and southern Mexico (e.g. *Astranthium* [DeJong, 1965], *Phoradendron* [Wiens, 1964], *Arceuthobium* [Hawksworth and Wiens, 1965], and others [see Hemsley, 1879-1888]).

Few collections of *Guardiola* have been made in areas south of the Rio Balsas depression. The Rio Balsas forms a great natural barrier to plant migrations, in which and south of which is found considerable tropical vegetation (Leopold, 1950; Goldman and Moore, 1946), a vegetation type with which *Guardiola* is not generally associated.

Evolutionary divergence of *Guardiola*, which is probably rather recent, and its present geographic distribution may be explained, at least in part, by the postulate of Martin (1958) that climatic conditions during the Pleistocene caused a 4000-5000 foot downward depression of vegetation zones. This would remove valley barriers from a group such as *Guardiola*, which is now most common at about 1500 to 2000 meters elevation, and allow mixing of gene pools at the lower elevations. One could then postulate a few ancestral taxa occupying greater areas of distribution in the foothills. As the Pleistocene closed and the climate became warmer and drier, the vegetation, including the Guardiola taxa, may have migrated back up the mountainsides to present elevations. During or subsequent to migration, speciation occurred and the present general distribution and evolutionary divergence were obtained.

The evolutionary history of Guardiola, since it appears to have a fairly close relationship to a vegetation type (viz. pine forests and oak-pine transition), must, as McVaugh and Rzedowski (1965) state is the case for Bursera, be closely related to the evolutionary history of that vegetation type. Dressler (1954) and especially Sharp (1953) point out that invasion of Mexico by temperate floras must be relatively recent, for there was little continuous area with sufficient elevation to support temperate vegetation in Mexico prior to Miocene uplift of the Sierra Madre Occidental and Pliocene elevation of the Sierra Madre Oriental and the Sierra Madre del Sur. Evolution of temperate floras in Mexico may, then, be even more recent if Sharp (1953) is correct that "the present temperate element of the flora of Mexico must have come from the north during the late Pliocene and Pleistocene," and if the plants of this flora formed the ancestral stock for evolution of the present temperate flora.

The above considerations suggest two alternative origins for *Guardiola*. It could be an old genus derived from the temperate flora which migrated into Mexico from the north, and as populations in the Sierra Madre Occidental became isolated, the species diverged to the level at which we recognize them today. Pleistocene influences would probably be minimal on the evolution of such a genus. Or, more likely, *Guardiola* could be a recently derived genus having originated in Mexico and prior to the Pleistocene had only a few widely distributed species. Pleistocene and post-Pleistocene events may have encouraged rapid evolutionary development of the genus and produced the present level of evolution and distribution. The result is a genus distant from other genera but containing species which appear to be closely related.

The compact distribution and apparent lack of closely related genera seem to demand a Mexican origin and center of dispersal for the genus, making it part of that considerable portion, 21% according to Miranda and Sharp (1950), of the temperate Mexican flora endemic to that country. Other authors: Hemsley (1879-1888), Rzedowski (1962, 1964), and Beaman and Andresen (1966) also discuss the sizable endemic element of the Mexican flora. Although *Guardiola* is essentially endemic to Mexico, its relationships in the Heliantheae appear to be with southern rather than northern elements of the Mexican flora.

Using the above considerations, sequences of speciation may be postulated. A perennial, broad-leaved form probably similar to _G. rosei_ or _G. pappifera_ in general appearance, and with a pappus, occurred most likely in the southern part of the Sierra Madre Occidental, in the general area where the borders of the states of Durango, Nayarit, Jalisco, and Zacatecas meet. This hypothetical ancestral taxon produced two main evolutionary branches. In one, now expressed as _Guardiola_ subgenus _Rzedowskia_, evolutionary development led primarily to the annual habit and vegetative accommodations to that habit. Few modifications, other than decrease in size of the lamina of the ray florets, occurred in the heads of plants in this evolutionary line, and the taxon presently recognized as _G. pappifera_ evolved.

The second evolutionary branch, now recognized as _Guardiola_ subgenus _Guardiola_, retained the perennial habit and evolutionary changes occurred in vegetative parts, number and size of floral parts, and achenial characters. All taxa in this subgenus are now epappose.

Further postulating evolutionary sequences in subgenus _Guardiola_, a broad-leaved form, similar to _G. rosei_, was probably the basal form of subgenus _Guardiola_ which was derived from the common ancestral type described above. This taxon, distributed in the southern part of the Sierra Madre Occidental, gave rise to an advanced type, a narrow-leaved form resembling *Guardiola mexicana*. The narrow-leaved form became widely distributed in the southern part of the Sierra Madre Occidental and the northern part of the Sierra Madre del Sur. These two types, broad-leaved, and narrow-leaved, provided the material from which the present species evolved.

In the broad-leaved group evolution led toward *G. rosei*, the most primitive of the broad-leaved species, and then to *G. platyphylla*, the most advanced species of that group. Specialized side branches from near *G. rosei* led to *G. carinata* and *G. rotundifolia*.

One can postulate that widespread populations of the narrow-leaved form were separated into eastern and western populations by either orogeny or downslope migrations due to Pleistocene depression of the vegetation. Migration, especially upslope migration which would isolate populations, could have influenced speciation. As the varying populations were isolated, responses of individuals of a population to the various factors both causing and resulting from the isolation, could result in the evolution of new taxa by adaptive radiation. The Pacific slopes of the Sierra Madre Occidental contain innumerable variations of habitat. Local endemism, suggesting considerable adaptive radiation associated with ecological and geographical factors, is conspicuous (McVaugh and Rzedowski, 1965).

One postulates, then, that the Pacific slope populations of the early narrow-leaved form of Guardiola were subjected to the above-mentioned evolutionary influences and evolved more rapidly than those populations on the eastern or inland slopes of the Sierra Madre Occidental. The more rapidly evolving western complex led to *G. tulocarpus* and then to *G. angustifolia* with specialized side branches from near *G. tulocarpus* to *G. thompsonii* and *G. stenodonta*. The inland complex was probably wide-ranging on the eastern slopes of the Sierra Madre Occidental and the northern portion of the Sierra Madre del Sur during the Pleistocene. Warming and drying at the close of the Pleistocene may have then separated the two ends of the population by eliminating the geographically intermediate populations. The southern portion led to *G. mexicana* and the northern complex led to *G. arguta* and *G. odontophylla*.

Figure 18 illustrates the presumed evolutionary relationships of the species of Guardiola as they are discussed above. The evolutionary tree is prepared according to the quantitative methods outlined by Kluge and Farris (1969), Farris (1970), and Farris, Kluge and Eckardt (1970). Table 11, which was used in the

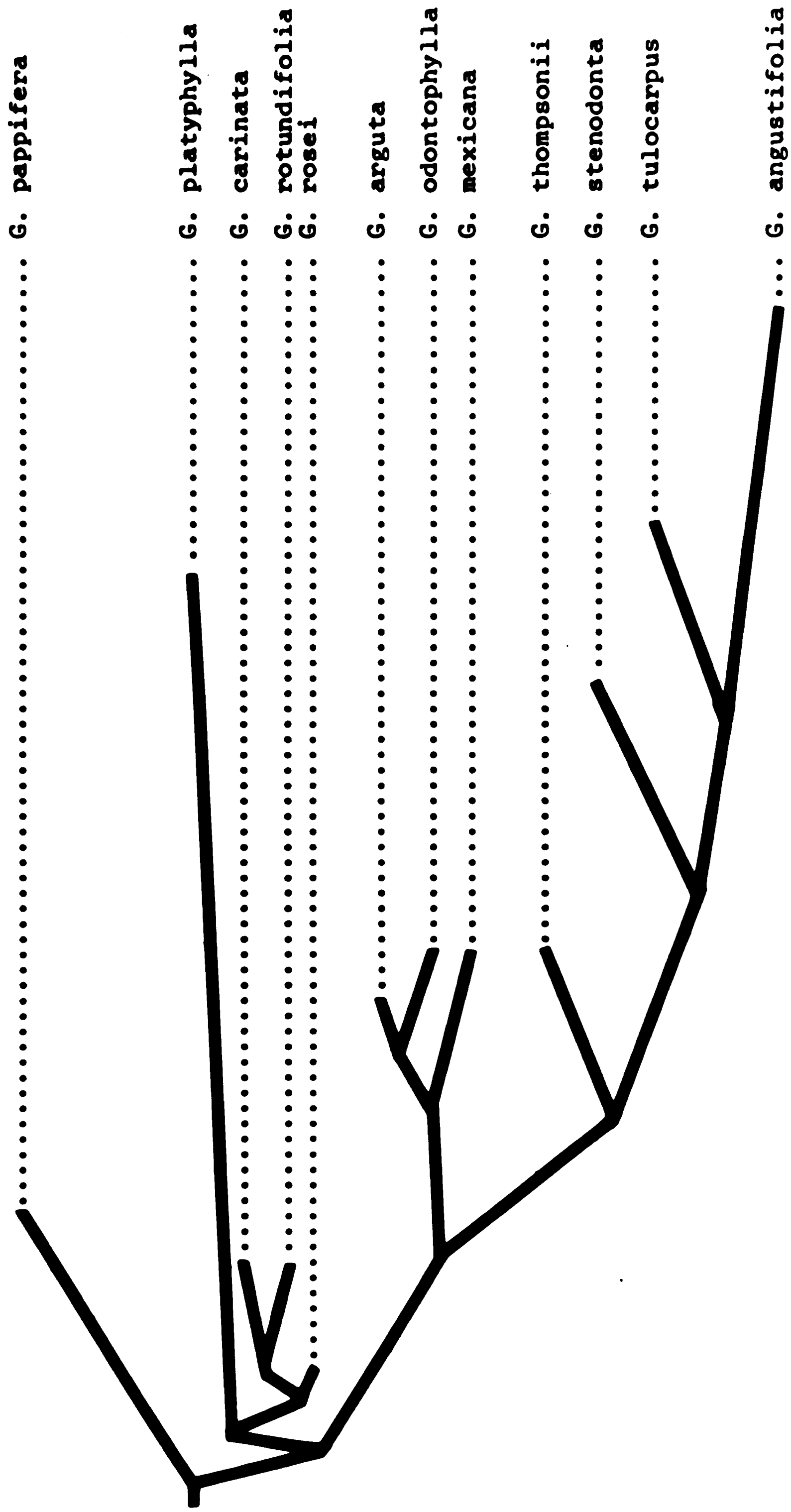

Figure 18. Presumed evolutionary relationships of the species of Guardiola.

Table 11. --Coded character states in Guardiola. Traits are in sequence from Table 10, with the deletion of the last item (marginal vein number) due to lack of data. The primitive state is indicated by 0, the derived state by 1, and a few intermediate states by $\frac{1}{2}$.

Species	Coded Character States												
	1	2	3	4	5	6	7	8	9	10	11	12	13
G. pappifera	1	0	0	0	0	0	0	0	0	1	$\frac{1}{2}$	0	0
G. rosei	0	0	0	0	0	0	0	0	0	0	0	0	1
G. rotundifolia	0	0	0	1	0	0	0	0	0	0	0	0	1
G. carinata	0	0	0	0	0	1	0	0	0	0	0	0	1
G. platyphylla	0	1	0	1	1	0	1	1	1	1	$\frac{1}{2}$	0	1
G. arguta	0	0	1	0	0	0	0	0	1	1	$\frac{1}{2}$	0	1
G. odontophylla	0	0	1	0	0	0	$\frac{1}{2}$	0	1	1	$\frac{1}{2}$	0	1
G. mexicana	0	0	1	0	0	0	0	0	1	1	1	0	1
G. thompsonii	0	0	1	0	0	0	0	0	1	1	1	0	1
G. stenodonta	0	0	1	0	1	0	1	1	0	1	$\frac{1}{2}$	1	1
G. tulocarpus	0	0	1	0	1	0	1	1	1	1	1	1	1
G. angustifolia	0	1	1	1	1	0	1	1	1	1	1	1	1

preparation of Figure 18, illustrates from Table 10 the character states of these traits in the various species.

GENERIC RELATIONSHIPS AND TAXONOMIC POSITION

The characters which clearly place Guardiola in the tribe Heliantheae according to the current arrangement and understanding of the Compositae include their heterogamous heads with ligulate (radiate), fertile, female marginal florets; functionally male (bisexual but with a vestigial ovary), 5-lobed, actinomorphic disk florets with bifurcate Helianthoid styles. In addition, the heads are paleaceous, the anther bases rounded, and the phyllary margins are not scarious. The combination of heterogamous head, Helianthoid style, and anthers with rounded bases eliminates most of the tribes as possible places for inclusion of Guardiola. The non-scarious phyllary margins eliminate the Anthemideae, and the Helenieae are eliminated by the paleaceous receptacle.

Within the tribe Heliantheae, the sterile disk florets mark the genus as a member of the Melampodinae. The genus seems to stand by itself without any closely related genera apparent.

There is some indication of relationships with members of the subtribe Verbesininae. Rumfordia and Jaegeria have green anthers and Wedelia has dark-colored anthers. It must be noted, however, that green or dark-colored anthers are found in diverse genera of the Compositae. Achenial characters of Guardiola resemble those of Rumfordia, Jaegeria, and Wedelia. A reduced number of veins in the ray florets and spherical buds suggest a possible relationship with Tetragonotheca. In addition to the above-mentioned characters which Guardiola shares with Wedelia, the two have in common a general growth habit and leaf form, a reduced number of veins in the ray corollas, and achenial mottling.

Stamen irritability may suggest connections with the Mutiseae through Perezia and Trixis, the Cynareae through Cynara and Centaurea, and the Senecioneae through Arnica, all of which possess irritable stamens. This character is perhaps more common than suspected, but observations of living plants are inadequate. These, however, are probably cases of parallel or convergent evolution rather than indications of phylogenetic relatedness.

TAXONOMIC CONCEPTS

I have recognized, on morphological grounds, two subgenera of Guardiola. Subgenus Guardiola consists of a rather homogeneous group of 11 perennial, epappose species, while subgenus Rzedowskia consists of a single annual, pappose species. Considering other similarities between the subgenera, the degree of relationship between them, and the apparent lack of other closely related genera, neither of these major differences, presence or absence of a pappus, or perennial vs. annual habit, either individually or collectively are considered strong enough evidence to merit erection of a segregate genus to accommodate *G. pappifera*.

Within subgenus Guardiola I have recognized as species those taxa which are morphologically distinct and which are geographically isolated from each other. The apparent lack of genetic barriers to synthesis of F_1 hybrids in Guardiola under controlled conditions precludes the use of genetic isolation as a criterion for delimiting species. Further, the general lack of qualitative differences among the heads of various taxa introduces additional taxonomic difficulties. Therefore, the criteria most valuable in delimiting the species are: morphological distinctness in nature and when growing under common conditions in the greenhouse or growth chambers, geographic isolation, quantitative differences in the heads, and the nature of the inflorescence.

Leaf characters, especially blade size and shape, and petiole length are the most valuable characters in considerations of morphological distinctness. Size of heads and numbers of flowers per head, as well as the degree of branching of the inflorescence, are also useful characters in species delimitation. Further studies may reveal genetic barriers in the F_1 hybrids, but these studies have not yet been conducted. Some of the common taxa are phenotypically plastic and tend to merge morphologically, but the majority of specimens of these species are readily distinguished. With few exceptions the taxa recognized as species have limited, well-defined distributions.

TAXONOMY OF GUARDIOLA

Guardiola Humb. & Bonpl. Pl. Aeq. 1. p. 144. t. 41. 1808. Tulocarpus Hook. & Arn. Bot. Beech. Voy. p. 298. t. 63. 1838.

Plants perennial, except the slender tap-rooted annual G. pappifera, stems annual, branching from the stout, tap-rooted, woody perennial caudex, erect, ascending, branched, terete, striate or not, succulent above to lignescent below, sparsely pilose to glaucous, green to reddish purple, 3-25 dm high; leaves opposite, petiolate to subsessile, blade narrowly linear-lanceolate to broadly cordate, 3-nerved from base, sparsely pilose to glaucous, succulent to firm or coriaceous, apices acute or apiculate, bases cordate to truncate or cuneate, margins from nearly entire to serrate or dentate, hastate teeth or lobes present or absent; heads few to more than 500 per main stem branch, rarely borne singly, usually in subumbellate clusters of 3-20 or occasionally more; involucre uniseriate, narrowly cylindrical to urcinate to nearly spherical, 6-16 mm high, 2-6 mm wide to 12 mm wide in G. pappifera, phyllaries 3, imbricate, canaliculate to strongly concave at base, equal, linear-ovate to ovate, apices acute, margin entire, glabrous, 7-15 lined, green to reddish purple; receptable paleaceous, slightly convex, 0.5-1.5 mm wide, pales persistent, scarious, glabrous, entire, linear-lanceolate to ovate, apices acute; ray florets 1-8, pistillate, fertile, white, glabrous, 4-12 mm long, usually 3-toothed at apex but sometimes deeply lobed, style branches white, recurved; disk florets 3-25, white, functionally male, crateriform, 8-15 mm long, 5-lobed, apices acute, style bifurcate, branches appressed and seldom exserted more than 1-2 mm from anther tube, nectary 0.5-1.5 mm high around base of style, anthers green, 1.5-3 mm long, touch-sensitive at anthesis, appendages ovate-deltoid, rounded at base, filaments densely pilose; achenes narrowly linear to obovoid to obconic, slightly compressed to terete, 4-8 mm long, 1.5-2.5 mm wide, pappus lacking except in G. pappifera which has pappus of squamellate scales, sparsely pubescent, lined or not, light brown to gray or dark gray, uniformly colored or mottled, callose on lower abaxial surface opposite point of attachment. Type species (originally the only species) Guardiola mexicana Humb. & Bonpl.

KEY TO THE SPECIES OF GUARDIOLA

A. Plants annual from slender taproot; stems herbaceous and often decumbent; buds spherical; achenes 4-angled, obconical, with small callus at base; pappus of 5 squamellate scales. Subgenus *Rzedowskia*, one species . . . . . . 1. *G. pappifera*

AA. Plants perennial from a woody caudex; stems lignescent, erect; buds cylindrical to urcinate; achenes oblong, slightly flattened, with large callus at base; epappose. Subgenus *Guardiola* . . . . B

B. Leaf blade broad, cordate to orbicular, length: width ratio less than 1.75 C

C. Phyllaries carinate . . . . 3. *G. carinata*

CC. Phyllaries dorsally convex but not carinate . . . . . . D

D. Involucre nearly cylindrical (2-3 mm in diameter); inflorescence diffusely branched; heads numerous, usually several hundred per main stem, few flowered (2-3 ray and 8-10 disk florets); leaves usually with sharp-toothed margin, sessile or subsessile . . . . 5. *G. platyphylla*

DD. Involucre urceolate (4-7 mm in diameter); inflorescence sparsely branched, heads fewer than 40 per main stem; 3-5 ray and 15-25 disk florets present; leaf teeth, if present, not sharp pointed; leaves sessile or petiolate . . . . . E

E. Leaves clearly petiolate, petiole 5-10 mm long; blade cordate to deltoid, hastate lobed . . . . 2. _G. rosei_

EE. Leaves sessile or apparently so (petiole may be as long as 2 mm); blade orbicular to ovate, not hastate lobed . . . . 4. _G. rotundifolia_

BB. Leaf blade narrow, linear-lanceolate to ovate; length: width ratio greater than 2.0 . . . . F

F. Hastate lobe usually present; inflorescence few-branched, heads usually few in number (mostly fewer than 50 per main stem branch), involucre mostly 1.5-2.5 times as tall as wide . . . . G

G. Leaf blade length: width ratio greater than 5, hastate lobe long and slender (5-14 mm long × 1-2 mm wide at base); known only from Sinaloa . . . . 11. _G. stenodonta_

GG. Leaf blade length: width ratio less than 5; hastate lobe deltoid rather than elongated . . . . H

H. Margin of leaf blade coarsely dentate, teeth to 1.5 mm long along most of margin; involucre about 11-13 mm long; leaf blade length: width ratio greater than 3.2; known only from northeastern Durango . . . . 8. _G. odontophylla_

HH. Margin of leaf blade serrate to entire above hastate lobe, few teeth more than 0.5 mm long, involucre less than 12 mm long (the involucre of _G. arguta_ may occasionally reach 12-13 mm long); leaf blade length: width ratio less than 3.0 I

I. Involucre mostly 7-9 mm × 4-5 mm; leaf blade length: width ratio less than 2.5; leaf usually less than 5 cm long; peduncle pubescence extending onto base of involucre; southern species occurring mostly from Jalisco to Morelos . . . . 6. _G. mexicana_

II. Involucre mostly 10-12 mm × 4-5 mm; leaf blade length: width ratio greater than 2.5, leaf usually more than 6 cm long, peduncle pubescence not extending onto base of involucre; northern species occurring mostly in Chihuahua and adjacent Durango . . . . . 7. G. arguta

FF. Hastate lobe absent (occasionally a tooth may be present at widest point of blade); inflorescence usually diffusely branched, heads numerous (mostly more than 50 per main stem branch), involucre mostly 2.5-3.5 times as high as wide . . . . J

J. Leaf blade long and slender, length: width ratio greater than 6; heads very numerous and slender (ca. 7 mm tall, 1.5-2 mm wide); inflorescence very diffusely branched . . . . . 12. G. angustifolia

JJ. Leaf blade not long and slender, length: width ratio less than 4; heads fewer and not so slender; inflorescence less branched . . . . . K

K. Involucre mostly 8-10 mm tall, (2-) 3-4 mm wide, urcinate; leaf blade coriaceous, length: width ratio about 3.7, margins nearly entire with scattered teeth . . . . 10. G. thompsonii

KK. Involucre 6-8 mm tall, 2-3 mm wide, cylindrical to somewhat urcinate; leaf blade not coriaceous, length: width ratio about 2.5, margins serrate . . . . 9. G. tulocarpus

GUARDIOLA HUMB. & BONPL. SUBGENUS RZEDOWSKIA VAN FAASEN, SUBG. NOV.

Plantas annuae cum radices palaribus gracilibus; caulis decumbens ad erectus; folia petiolata, laminae latae, tenues; capitula pauca portata singulatim vel in turmae 2-3; involucrum latum sphaericum 12-16 mm altae, 7-12 mm latae; paleae glabrae vel cum trichomae adscendens; flores radii 6-8, lamina fere circularis c. 1 mm latus, corolla non deciduus; flores disci 10-15; achenia obconica, 4-angulata, 9-10 mm longae, c. 2 mm latae, pappus constatus e 5 squamis, cum callo parvo oppositus in affixu; achenium puberulus cum paucus longus trichomae. Typus: Guardiola pappifera P. G. Wilson.

Plants annual with a slender taproot; stems decumbent to erect, leaves petiolate, blades broad, thin; heads few, borne singly or in groups of 2 or 3, involucre broadly spherical, 12-16 mm high, 7-12 mm wide; pales glabrous or usually with upward pointing trichomes; ray florets 6-8, lamina nearly circular, about 1 mm in diameter, corolla remaining attached to achene; disk florets 10-15; achenes obconic, weakly 4-angled above and strongly so at base, 9-10 mm long, about 2 mm wide, pappus of 5 squamellate scales about 2 mm high, with a small callus on lower abaxial surface opposite point of attachment, achenial pubescence of a few longer trichomes among numerous very small ones. Type species: Guardiola pappifera P. G. Wilson.

I have the privilege of naming this subgenus in honor of Dr. Jerzy Rzedowski, a leading student of the flora of Mexico, who provided invaluable assistance to my work in Mexico.

1. Guardiola pappifera P. G. Wilson

Guardiola pappifera Wilson. Kew Bull. 13: 162-163. 1958. Type: MEXICO. GUERRERO: District of Mina; Paruncio, 320 m. "Woods." 28 September 1936, Hinton 9533 (not 9333) (K, sheets I & II, holotype, MSC photo 687 sheets I & II; MICH, NY, UC, US isotypes).

Plants annual from a short slender taproot with relatively few branch roots; stems 0.5-1 m high, bushy, branches opposite, green to reddish purple; leaves petiolate, the petiole 1-5 cm long, often pilose in the axils, blades broadly ovate to cordate, 4-8.5 cm long, 2-6.5 cm wide, average leaf blade length: width ratio 1.61, blade 3-nerved from base, apices rostrate, bases truncate to obtuse, margins widely serrate, a hastate tooth usually present, deltoid, to 4 mm long; peduncles 2-3 (-5) cm long, glabrous or sparsely pubescent, heads few to about 25 per main stem branch, urcinate, 14-18 mm high, 7-12 mm wide; receptacle flat or slightly convex, 1-2 mm wide; involucre 12-16 mm high, 7-12 mm wide, broadly urcinate to nearly spherical; phyllaries 12-16 mm high, 5-7 mm wide, apices acute, tips somewhat recurved, margins entire, about 20-striate, green or greenish purple; pales persistent, 12-15 mm long, 2.5-3.5 mm wide, lanceolate, scarious, 4-8 lined, glabrous or with upward pointing trichomes on inner surface, entire, apices acute; ray florets 6-8, 6-9 mm long, tube 5-8 mm long, ligule elliptical to rotund, ca. 1 mm long and 0.7-0.9 mm wide, with 3 apical teeth; disk florets 10-15, 12-15 mm long, tube 10-13 mm long, limb ca. 2 mm high, lobes 1.5 mm high, apices acute; anthers 1.5-2 mm long, appendages ovate-deltoid; disk floret ovary 2.5-3 mm long, less than 0.5 mm wide, aborted, epappose; ray floret achenes obconic, weakly 4-angled above and strongly so at base, 9-10 mm long, pappus about 2 mm high, the fruit proper 7-8 mm high, striate, pilose at base with a few scattered pilose trichomes above, the longer trichomes among numerous, very small trichomes less than 0.1 mm long, which cover the entire dark brown to gray achene surface (Plate 1).

ECOLOGY AND DISTRIBUTION. In sparse woodlands; known from the type locality in Guerrero and one locality in Michoacan

Plate 1. --Holotype of Guardiola pappifera P. G. Wilson.


HERBARIUM of GEO. B. HINTON
No.
Family
Name
Determined by
Locality
District , Mexico.
Collected by date
Vernac. Name
Habitat
Description
687 Sheet I
K

Plate 1.

where it is reported from among rocks in a sparsely wooded arroyo (Figure 19).

SPECIMENS EXAMINED. MEXICO. GUERRERO: Woods, to 1 m, half procumbent, Paruncio, 320 m, Dist. Mina, Hinton 9533 (MSC photo 687 of K holotype, MICH, NY, UC, US). MICHOACAN: Old lava flows 4 mi NW Apatzingan, 300 m, among rocks in sparse woodland of *Cordia*, *Amphipterygium*, *Apoplanesia*, weedy in arroyo, McVaugh 19730 (MICH).

This species, the only one in *Guardiola* subgenus *Rzedowskia*, is readily distinguished from the other species of *Guardiola* on the basis of its annual habit, its pappus of five squamellate scales, and the length and shape of the achene. Annual taproots of *G. pappifera* are seldom more than 2 mm thick or a few inches long while caudices of subgenus *Guardiola* are woody and up to 6 cm in diameter with a taproot up to 2.8 cm in diameter.

Achenes of *G. pappifera* differ also in that they, in addition to possession of a pappus, retain the ray corolla at maturity and are obconic, slender, and four-angled in cross section. Pubescence on the achenes of *G. pappifera* consists of a few long trichomes among many very short ones while in the other species of *Guardiola* the achenial pubescence consists of only long trichomes. In addition the basal callus of the achenes of *G. pappifera* is smaller than that in

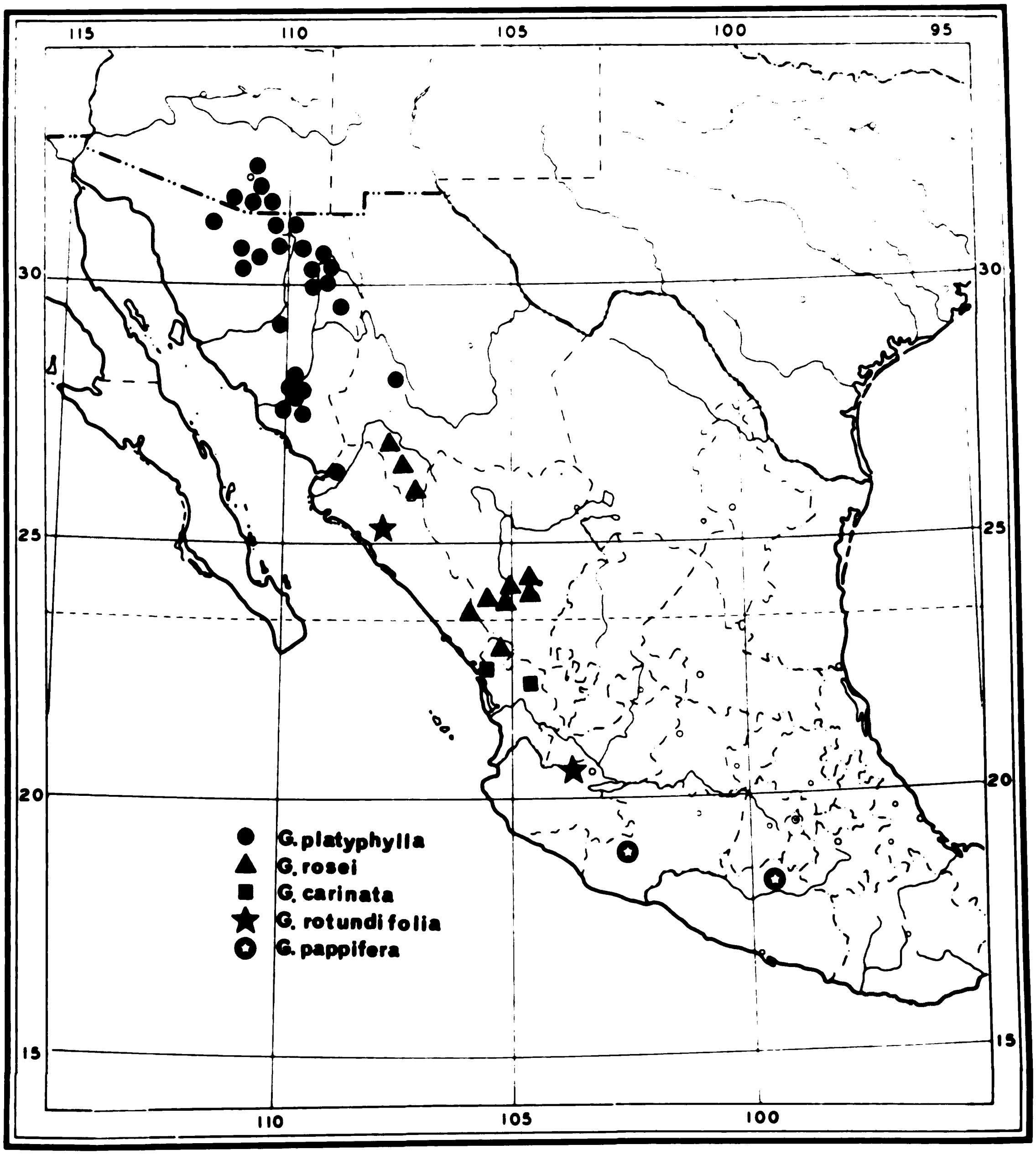

Figure 19. Distribution of G. platyphylla, G. rosei, G. carinata, G. rotundifolia, and G. pappifera.

other species of *Guardiola*. Plate 2 illustrates achenial differences between the two subgenera.

There is a typographical error in the citation (Wilson, 1958) of the type specimen of *Guardiola pappifera*. The holotype is cited as *Hinton 9333*, but a photograph of the type at Kew, as well as duplicate specimens with the same label data, all bear a *Hinton 9533* collection number.

Plate 2. Achenes of Guardiola.
A. G. mexicana, B. G. tulocarpus, C. G. thompsonii, D. G. arguta, E. G. angustifolia, F. G. rotundifolia, G. G. rosei, H. G. platyphylla, I. G. [illegible]. (All ca. x 17.)

GUARDIOLA HUMB. & BONPL.

SUBGENUS *GUARDIOLA*

Plants perennial, annual stems erect, ascending, succulent above to lignescent below, branching from a stout, tap-rooted, woody perennial caudex; heads few to many, involucre cylindrical to urcinate, 6-13 mm high, 2-6 mm wide; pales glabrous; ray florets 1-5, lamina elongate, corolla deciduous; disk florets 3-25; achenes oblong, slightly flattened, mostly 4-6 mm long, 1.5-2.5 mm wide, epappose, with large callus on lower abaxial surface opposite point of attachment, achenial pubescence of all long trichomes. Type species: *Guardiola mexicana* Humb. & Bonpl.

2. Guardiola rosei Robins.

Guardiola rosei Robins. Bull. Torrey Bot. Club 26:233. 1899. *Type*: MEXICO. NAYARIT: Between Sta. Gertrudis and Sta. Teresa, August 8, 1897, *Rose 2078* (GH, holotype!, US, isotype).

Guardiola palmeri Robins. Proc. Amer. Acad. 43:38. 1907. Type: MEXICO. DURANGO: Outer circle of mesas, Otinapa; 2450 m. July 25-August 5, 1906, Palmer 377 (GH, holotype!, F, MO, NY, UC, US, isotypes).

Stems 3-6 dm high, striate, green to purple, glabrous to glaucous below, occasionally pubescent in leaf axils and on inflorescence branches; leaves petiolate, petiole (2-) 5-8 (-10) mm long, blade cordate-ovate, thick to coriaceous, (1-) 2-4.5 cm long, (1-) 2.0-4.5 cm wide, average blade length: width ratio 1.02, apices apiculate to nearly rounded, bases cordate to truncate, margin dentate, hastate tooth or lobe 2-10 mm long, surface glabrous to glaucous; peduncles 5-10 mm long, sparsely pilose; heads 6-25 per main stem branch, urcinate, 13-16 mm high, 8-12 mm wide, borne in clusters of 3-4 heads on branch termini; receptacle slightly convex, 0.5-1.5 mm wide; involucre (7-) 9-12 mm high, 5-6 mm broad, phyllaries ovate, (7-) 9-12 mm high, 4-7 mm wide, apices acute, 10-15 striate, green to reddish purple; pales ovate, 5-7 mm high, 1-2 mm wide, apices acute; ray florets 3-5, 8-12 mm long, tube (3-) 5-8 mm long, ligule 3-5 mm long, 1-2 (-3) mm wide, obovate, 3-toothed at apex; disk florets 15-20, 11-17 mm long, tube 8-13 mm long, limb 3-4 mm long, lobes 1.5-2 mm high, apices acute;

anthers 2-3 mm long; achenes obovoid to linear-obovoid, slightly compressed, 4.5-7 mm long, 2-3 mm wide, pubescent over entire length, striate or not, light brown to gray or dark gray, uniformly colored or mottled; chromosome number _n_ = 12 (Plate 3).

ECOLOGY AND DISTRIBUTION. In disburbed areas, often in crevices on rock outcrops, mostly between 1800-2200 m elevation. Flowering from June to November. Distributed in the Sierra Madre Occidental in Durango and extending just into Sinaloa, Chihuahua, and Nayarit (Figure 19).

SPECIMENS EXAMINED. MEXICO. CHIHUAHUA: At base of Mt. Mohinora 60 mi S Guadalupe y Calvo, 7500-8500 ft, Nelson _4806_ (GH, US). DURANGO: Rocky hillside, 13 mi E El Salto, 8050 ft, _Breedlove 14326_ (MICH); moist edge of pasture along Highway 40, E of Hacienda Coyotes, Km 1024-1025, 8000 ft, _DeJong 1381_ (MSC); limestone outcrop 14 mi W C. Durango on Highway, 2000-2200 m, _Maysilles 7008_ (MICH); tributary arroyo to Rio del Presidio, 5 mi N of railroad at Coyotes, 2400-2500 m, _Maysilles 7186_ (MICH); wooded canyon 26 mi N Coyotes at Quebrado de San Juan, 2700 m, _Maysilles 7198_ (MICH); oak-pine forest, San Luis 51 mi NW Coyotes, 2600 m, _Maysilles 7233_ (MICH); north slopes of Cerro Huehueto south of Huachicheles, 75 mi W of C. Durango, 2900-3150 m, _Maysilles_

Plate 3. Holotype of Guardiola rosei Robins.

7294 (MICH); Barranca Rio Jaral, 15 mi NW Coyotes, 2100 m, McVaugh 21710 (MICH, NY); dry soil, Sianori, 800 m, Ortega 5.276 (GH, US); at Otinapa, Palmer 377 in 1906 (GH, holotype of *G. palmeri*; MO, NY, UC, US); rocky andesite banks, Rio Chico, on RR W of Durango, Pennell 18240 (NY); face of rocky cut, 1 m W of Llano Grande, Mex. 40 Km 1042-1043, Van Faasen 1859 (MSC); roadside cuts and woods, pine-oak transition, Mex. 40 Km 1024-1025, Van Faasen 1891 (MSC); rocky cut 20 mi E Llano Grande, Mex. 40 Km 1019, Van Faasen 1906 (MSC); open oak-pine woods, 5.5 mi E El Salto, about 55 mi SW C. Durango, Waterfall & Wallis 13624 (US). NAYARIT: Between Santa Gertrudis and Santa Teresa, Rose 2078 (GH, holotype, US). SINALOA: Arroyo de la Labor, San Ignacio, 360 m, Montes & Salazar 304 (US); San Juan, Ortega 4022 (US); Balboa, Ortega 5015 (US).

Guardiola rosei has clearly petiolate leaves and a few large heads with unkeeled phyllaries, characters which readily separate it from the other broad-leaved species. Those specimens which Robinson (1907) described as *G. palmeri* have no major differences from *G. rosei*, though they are somewhat depauperate plants. Among other specimens which have been identified as *G. palmeri* are small, weak-stemmed plants which appear distinct because of size and leaf-shape differences. Weak-stemmed plants appeared among specimens I grew from seed obtained from plants of _G. rosei_. On the basis of morphological and chemotaxonomic evidence, _G. rosei_ and _G. palmeri_ appear conspecific.

Guardiola rosei possesses nearly all of the primitive characters listed in Table 10, page 89, and appears to be the most primitive species in subgenus _Guardiola_. It presumably resembles the ancestral type more than does any other species in that subgenus.

3. Guardiola carinata Robins.

Guardiola carinata Robins. Bull. Torrey Bot. Club. 26: 233. 1899. _Type_: MEXICO. NAYARIT: At Acaponeta, June 23, 1897, _Rose 1428_ (US, holotype!).

Stems 4-8 dm high, glaucous, green; leaves petiolate, petiole 10-18 mm long, young leaves with finely ciliate petioles, blades broadly ovate to subcordate, 2.5-4.3 cm long, 1.6-3.2 cm broad, average leaf blade length: width ratio 1.48, blade coriaceous, apices apiculate, bases cordate to truncate, margins nearly entire to slightly serrate, hastate lobe 3-5 mm long, blade glabrous; peduncles 7-9 mm long, glabrous or sparsely pilose; heads 4-7 (-50) per main stem branch, urcinate, 15-20 mm long, 8-11 mm wide, borne in subumbellate clusters on branch termini; receptacle convex, 1-2 mm wide; involucre 10-13 mm high, 5-8 mm wide, phyllaries 3, carinate, ovate, 10-13 mm high, 3-5 mm wide, 10-15 striate, green; pales ovate, entire, 6-7 mm long, 1-3 mm wide, apices acute; ray florets 4-5, 10-11 mm long, tube 7-8 mm long, ligule about 3 mm long, 2 mm wide, broadly ovate; disk florets 20-25, 14-15 mm long, tube 10-11 mm long, limb 4 mm long, lobes 2 mm high, apices acute; anthers 2-2.5 mm long; achenes narrowly ovate, 5-6 mm long, 1.5 mm wide, tan or dark brown to gray, uniformly colored or mottled, villous over entire surface (Plate 4).

ECOLOGY AND DISTRIBUTION. Known only from along the river at Acaponeta, Nayarit and from an indeterminate location in the Sierra de Nayarit in Jalisco (Figure 19). Flowering from April to June. Although little data are given with any of the three localities, the river banks at Acaponeta are of reddish clay and the elevation is about 40 meters.

SPECIMENS EXAMINED. MEXICO. JALISCO: Sierra de Nayarit (Territoire Huichol), Diguet (MICH, NY); NAYARIT: At Acaponeta, June 23, 1897, Rose 1428 (US, holotype); along river, vicinity of Acaponeta, April 11, 1910, Rose, Standley & Russell 14277 (NY, US).

Plate 4. Holotype of Guardiola carinata Robins.

The specific epithet of this taxon is derived from the keeled phyllaries which clearly mark it as distinct from the other broad-leaved species. It also possesses a rather long petiole (10-18 mm), nearly entire leaf margins, and a hastate lobe, a combination of characters consistently present in *G. carinata* but not in the other broad-leaved species.

Guardiola carinata is known from just three collections from the vicinity of Acaponeta, Nayarit, the last one made in 1910. Since 1910 the village of Acaponeta has extended to and along the river and *G. carinata* may no longer exist there. In one and one-half days of searching we did not find it, and a number of local residents to whom we showed photographs of the plant claimed to have never seen it.

4. *Guardiola rotundifolia* Robins.

Guardiola rotundifolia Robins. Proc. Amer. Acad. 29: 317. 1894. *Type*: MEXICO. JALISCO: Hills near Tequila, Oct. 15, 1893, *Pringle 4571* (GH, holotype!, ENCB, F, 2 sheets, MO, MSC, UC, US, 2 sheets, isotypes).

Stems 4-8 (-12) dm tall, striate, glabrous to glaucous throughout, green to purplish; leaves subsessile, petiole 1-2 (-3) mm long, blade ovate to rotund, 3-9 cm long, 2-7 cm wide, average blade length: width ratio 1.21, apices apiculate, bases cordate, margins widely serrate to dentate, hastate tooth 2-3 mm long, blade coriaceous, glaucous; peduncles 6-11 mm long, glabrous; heads few to 50 per main stem branch, urcinate, 13-18 mm high 10-16 mm wide, borne in clusters of 3-4 on branch termini; receptacle slightly convex, 0.5-1.5 mm wide; involucre 8-12 mm high, 5-7 mm wide, phyllaries ovate, 8-12 mm long, 5-8 mm broad, apices acute, 10-15 striate, green; pales ovate to lanceolate, 4-6 mm long, 1-3 mm wide, apices acute; ray florets 4-5, 9-14 mm long, tube 5-7 mm long, ligule 4-7 mm long, 1-2 mm broad, linear-oblong, usually 3-toothed at apex; disk florets about 25, 11-15 mm long, tube 8-11 mm long, limb 3-4 mm long, lobes 1.5-2 mm high, apices acute; anthers 2-2.5 mm long; achenes linear-ovoid, slightly compressed, 5-6 mm long, 2 mm wide, sparsely pilose over entire surface, striate or not, light brown to gray or dark gray, uniformly colored or mottled; chromosome number $\underline{n} = 12$ (Plate 5).

ECOLOGY AND DISTRIBUTION. In disturbed habitats, steep clayey or grassy banks. Known only from two locations in Sinaloa, at about 100 m elevation, and one location near Tequila, Jalisco, at about 1600 m elevation (Figure 19). Flowering from August to October.

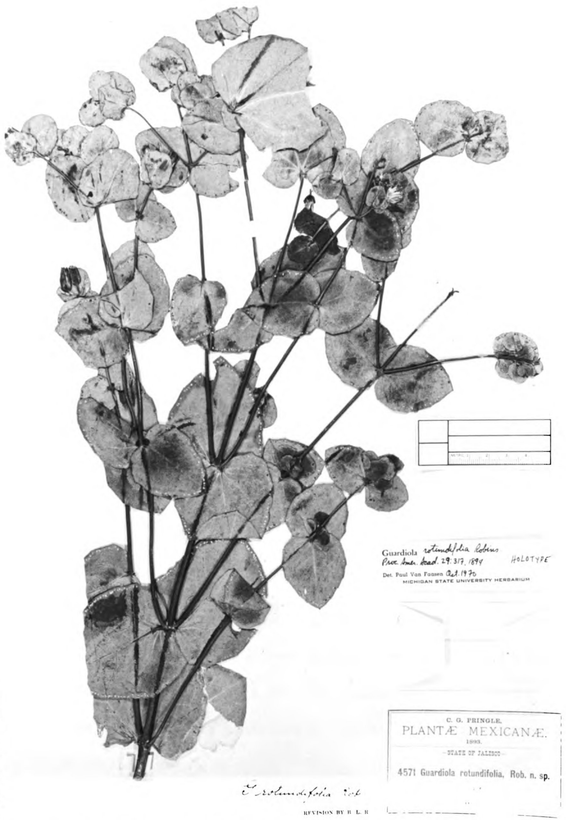

Plate 5. Holotype of Guardiola rotundifolia Robins.

SPECIMENS EXAMINED. MEXICO. JALISCO: Hills near Tequila, Pringle 4571 (ENCB, F, 2 sheets; GH, holotype; MO, MSC, UC, US, 2 sheets); rocky hillside, 4 mi NW Tequila, Mexico Route 14, Km 741, Van Faasen 1784 (MSC). SINALOA: Vicinity of Culiacan, Brandegee (UC); Cerrenos de Balboa, Ortega 1054 (ENCB).

Leaf shape, the subsessile condition, head size, number of heads, and number of florets per head set the species apart from the other broad-leaved taxa. It is very distinct in Jalisco but the Sinaloa collections tend toward *G. platyphylla* in head characters.

5. Guardiola platyphylla A. Gray

Guardiola platyphylla A. Gray. Pl. Wright. II: 91. 1852. Type: MEXICO. SONORA: Hillsides along desiccated streams between Babocomori and Santa Cruz, September 1851-1852, C. Wright 1236 bis (GH 4 sheets, holotype! & 3 isotypes, MO, UC).

Stems 4-7 dm high, striate, glabrous to glaucous throughout, green to reddish purple; leaves subsessile, the petiole 1-2 mm long, the blade broadly ovate to cordate, coriaceous, 1.9-6.2 cm long, 1.2-4.2 cm wide, average blade length: width ratio 1.25, apices apiculate, bases truncate to cuneate, margins serrate to dentate, teeth usually sharp pointed, hastate lobe or large deltoid tooth usually present, to 1.7 mm long, both blade surfaces glabrous, often glaucous; peduncles 1-4 mm long, glabrous; heads (20-) 50-150 (-200) per main stem branch, 12-14 mm high, 5-8 mm wide, borne in subumbellate clusters at branch termini; the receptacle slightly convex, about 0.5 mm wide; involucre 8-10 mm high, 2-3 mm wide, cylindrical to slightly urcinate, phyllaries ovate, 8-10 mm high, 3-5 mm wide, 10-15 striate, green to reddish purple; pales ovate, 4-5 mm high, 1-2.5 mm wide; ray florets 2-3, 9-12 mm long, tube 4-7 mm long, ligule 3-5 mm long, 1.5-2 mm wide, oblanceolate to obovate, usually with 3 teeth at apex; disk florets about 10, 10-14 mm long, tube 8-11 mm long, limb 2-4 mm high, lobes 1.5-2 mm long; anthers 2-2.5 mm long; achenes narrowly obovoid, slightly compressed, 4.5-7 mm long, 1.5-2 mm wide, sparsely pilose over entire surface, striate or not, light tan to dark brown or gray, uniformly colored or mottled; chromosome number $\underline{n}$ = 12 (Plate 6).

ECOLOGY AND DISTRIBUTION. In disturbed areas with mostly dry to mesic soils, in dry, sandy arroyo bottoms, in rocky cuts, along streams, on rocky hillsides, mostly between 1500 and 2000 meters elevation. Distributed primarily in southeastern

Plate 6. Holotype of Guardiola platyphylla A. ay

Arizona to southern Sonora (Figure 19). Flowering specimens collected during all months.

REPRESENTATIVE SPECIMENS. MEXICO. CHIHUAHUA: Canyon, near stream, Guasaremos, Rio Mayo, Gentry 2364 (ARIZ, F, GH, MO, US); SW Chihuahua, Palmer 35 in 1885 (GH, MICH, MO, NY, US). DURANGO: Alluvial canyon bottom, Sierra Tres Picos, 3500 ft, Gentry 5330 (ARIZ, DS, MICH, NY). SONORA: Dry, rocky slopes, Canyon Saucito, Dist. Alamos, Gentry 695M (ARIZ, DS, MICH); canyon, San Bernardo, Rio Mayo, Gentry 1251 (F, GH, MO); Los Pinitos, 6000 ft, Hartman 124 (F, GH, UC); rocky arroyo floors, El Rio Bonito about La Nopalera, Muller 3636 (GH, MICH, UC); Alamos, Palmer 280 in 1890 (F, GH, 2 sheets, MICH, 2 sheets, NY, US); canyon, vicinity of Alamos, Rose, Standley & Russell 12989 (F, MO, NY, US); Canyon de Bavispe, White 3022 (ARIZ, MICH); Canyon de los Otates, White 3533 (GH, MICH); El Rancho de la Nocha, 25 mi west of La Angostura, 4300 ft, White 3906 (GH, MICH); rocky soil in adjoining canyons along Rio Magdalena, Whitehead M33 (ARIZ); SW side of Sierra Batuc, between Matape and Batuc, 8 mi from Matape, 3300 ft, Wiggins & Rollins 426 (ARIZ, DS, GH, MICH, MO, NY); hillsides between Babocomori and Santa Cruz, Wright 1236 bis (GH, 4 sheets, holotype & 3 isotypes,

MO, UC). UNITED STATES. ARIZONA: COCHISE CO. Rocky draws, Montezuma Canyon, Huachuca Mts, Goodding 289-60 (ARIZ); Huachuca Mts, Lemmon (F, NY, US); grassy oak hillside one mi W of E gate to Coronado National Monument, Van Faasen 1934 (MSC). PIMA CO. Rocky slope, Manning Trail 4900 ft, Ricon Mts, Blumer 3606 (F); creek bank, Molino Canyon, 1300 m, 17 mi NE Tucson, Brass 14245 (GH, MO, NY); ledges of Marista Canyon, Baboquivari Mts, Clark 12608 (GH); Soldier Trail, 4200 ft, Frost 474 (ARIZ, DS, UC); Fresnal Canyon, Baboquivari Mts, Gilman 86 (ARIZ, NY); along stream course in Mountain Spring Canyon, W of Rincon Peak, 4000 ft, Gould 3026 (ARIZ, DS, F, GH, MO, NY, UC, US); The Basin, Santa Catalina Mts, Harris C16277 (US); Sabino Canyon, 3000 ft, M. R. Jones in 1903 (DS, 2 sheets, US, 3 sheets); wash of El Rioulta, south of Santa Catalina Mts, Lemmon 213 (GH, UC); Fresnal, Papago Reservation, Loomis 888 (US); Baboquivari Canyon, Thackery & Leding 1117 (ARIZ); dry wash, Bear Canyon, Van Faasen 1931 (MSC); dry stream bed, Sabino Canyon, Van Faasen 1932 (MSC). SANTA CRUZ CO. Grassland near Patagonia, Anderson & Buzan 69 (ARIZ); near road fork south of Pena Blanca Creek, Atascosa Mts, Barr 61-277A (TEX); Atasca Mts, Darrow in 1937 (ARIZ, GH, UC); roadside, 1 mi from Ruby, 4500 ft, Kearney & Peebles 13789 (ARIZ, NY, US); rocky hillside 12 mi west of Nogales on Arizona 289 to

Ruby, Van Faasen 1933 (MSC); among rocks in open, Bear Valley, Ruby, Whitehead 1720 (ARIZ).

Guardiola platyphylla is the most advanced of the broad-leaved species and is readily distinguished from the other broad-leaved taxa. It has more and smaller heads with fewer ray and disk florets borne in a more profusely branched inflorescence than any other broad-leaved species. The leaves are subsessile, more coriaceous and with more, sharper, and larger teeth than in G. rosei. There may be some possibility of confusing it with an extremely profusely-flowered specimen of G. rotundifolia, but leaf and head characters are distinctive, heads are smaller and with fewer florets, and the leaves lack hastate lobes and have more and sharper pointed teeth than in G. rotundifolia.

6. Guardiola mexicana Humb. & Bonpl.

Guardiola mexicana Humb. & Bonpl. Pl. Aeq. 1: 144, t. 41. 1808. Type: MEXICO. MICHOACAN: Between Ario de Rosales and Volcan Jorullo, Humboldt & Bonpland (P, holotype; MSC photo 2790).

Guardiola atriplicifolia A. Gray. Pl. Wright. 1: 111. 1850. Type: MEXICO. MICHOACAN: Morelia, 7000 feet, Galeotti 2418 (GH, holotype!; MSC photo 694 of isotype in K).

Stem 5-9 dm high, green to purplish, striate or not, glabrous to glaucous below and pilose in leaf axils, peduncles and often on inflorescence branches; leaves petiolate, petioles 3-23 mm long, blade ovate to lanceolate-ovate, 2.2-11.2 cm long, 0.7-4.0 cm wide, average leaf blade length: width ratio 2.26, apices acute, base obtuse or truncate, hastate lobes deltoid to subulate, 0.2-1.4 cm long, blade margins mostly serrate with teeth spreading, occasionally with scattered pilose trichomes on lower surface of blade and on petiole; peduncles 4-11 mm long, pilose with pubescence extending onto base of involucre; heads 5- more than 200 per main stem branch, urceolate, 11-15 mm high, 7-10 mm wide, inflorescence subumbellate; receptacle slightly convex, 0.5-1.5 mm wide; involucre (6-) 7-9 (-10) mm high, 3-6 mm wide, phyllaries 3, imbricate, broadly ovate to cuneiform, 6-7 mm long, 3-4 mm wide, apices acute, tips usually recurved, green to purplish, 10-15 striate; pales elliptic-lanceolate, acuminate, 2-5 mm long, 0.5-1.5 mm wide; ray florets 2-3 (-5), tube 3-6.5 mm long, ligule 2.5-4 mm long, 1.5-2 mm wide, 3-5 toothed; disk florets 10-15 (-25), tube 6-10 mm long, limb 3-4 mm high, lobes 1.5-2 mm long; anthers 2-2.5 mm long; achenes slightly laterally compressed, obovoidal, 4-7 mm long, 1.5-2.5 mm wide, villous above, variegated dark brown or gray above to beige below, sometimes striate; chromosome number $\underline{n} = 12$ (Plate 7).

ECOLOGY AND DISTRIBUTION. In disturbed habitats in clay to sandy soil or in cracks in faces of rocky cuts and outcrops at elevations of 1500-2000 meters. Distributed from Nayarit to Morelos (Figure 20). Flowering from May to December.

REPRESENTATIVE SPECIMENS. GUANAJUATO: Rocky hills, 3000-4000 ft, Silao, Purpus 466 (MO, RSA, UC, US). GUERRERO: Barranca, Dist. Mina, Parates, 800 m, Hinton 9200 (MICH, 2 sheets, NY, UC, US); grassy hillside, 2 mi N Taxco, 5500 ft, Hitchcock & Stanford 7057 (DS, F, GH, MO, NY, RSA, UC, US); loose granitic cliff, 3 mi N Taxco, Paxson, Westlund & Barkley (17M) 886 (F, TEX); 2 km N Taxco sobra la carretera a Amazuzac, Rzedowski 21484 (ENCB, MICH, TEX); steep clayey roadcut 20 mi NE Taxco, Km 153 of Mexico 95, Van Faasen 1568 (MSC). HIDALGO: Sierra de Pachuca, 10,000 ft, Pringle 9884 (MICH). JALISCO: Open pine woods, 6100 ft, 19 mi W Ayutla and 60 mi NW Autlan, Cronquist 9807 (MICH, MO, MSC, NY, TEX, US); open rocky ravine in oak zone, 1650 m, 14 m SW

Plate 7. --Holotype of Guardiola mexicana Humb. & Bonpl.

Plate 7.

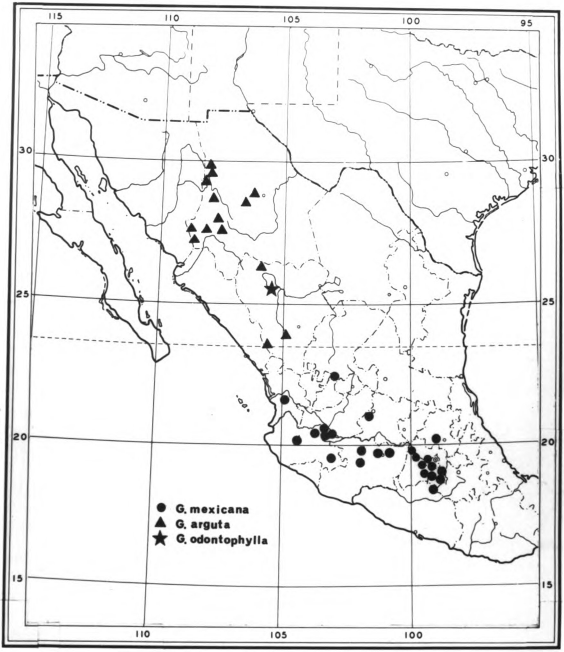

Figure 20. Distribution of G. mexicana, G. arguta, and G. odontophylla.

Ayulta, McVaugh 22008 (MICH, NY); near Guadalajara, Pringle 3484 (GH, MICH, MO, US); plains near Guadalajara, 5000 ft, Pringle 9916 (F, GH, MICH, MO, NY, US); La Primavera, 30 km al oeste de Guadalajara, 1700 m, Rzedowski 20271 (ENCB); rocky hill, 4 mi NW Tequila, Km 741 of Mexico 15, Van Faasen 1785 (MSC). STATE OF MEXICO: Volcan, 1400 m, Temascaltepec, Hinton 990 (US); rocky meadow, Telpintla, 1840 m, Temascaltepec, Hinton 1138 (GH, MO, US); Barranca, Ixtapan, Hinton 7497 (F, GH, MICH, NY, US); along stone fence, San Lucas, Temascaltepec, Hinton 7509 (US); margins of oak woods, cercania de Valle de Bravo, 1800 m, Matuda 28865 (NY); 5 km al NNW de Tejupilco, 1700 m, Rzedowski 20660 (ENCB, MSC); laderas de cañon 8 km W de Ixtapan de la Sal sobre la carretera a Zacualpan, Rzedowski 21832 (ENCB); vertical rocky road-cut, 45 mi W of Toluca on road to Valle de Bravo, near Juantepec, Van Faasen 1601 (MSC). MICHOÁCAN: Vicinity of Morelia, 2000 m, Arsene 5466 (DS, F, GH, MO, NY, 2 sheets, UC, US, 2 sheets); base of forested hill, Zitacuaro bosque, Hinton 11995 (MICH, 2 sheets, NY, UC, US); between Ario de Rosales and Volcan Jorullo, Humboldt & Bonpland (MSC photo 2790); steep south-facing Quercus woodland, 2300 m, 16 km ESE Zacapu, Iltis et al. 454 (MICH, TEX, WISC); hills about Patzcuaro, Pringle 4167 (F, GH, ENCB, MICH, 2 sheets, MO, 2 sheets, MSC, NY, UC, 2 sheets, US); steep, red, clayey bank

10 mi E Morelia, Km 291-292 of Mexico 15, Van Faasen 1649 (MSC); steep rocky hillside 3 km SE Zacapu, Van Faasen 1661 (MSC); rocky cut, 9 m S of Carapan on road to Uruapan, Van Faasen 1701 (MSC). MORELOS: Barrancas near Cuernavaca, 5000 ft, Pringle 6184 (ENCB, F, GH, MICH, 2 sheets, MO, MSC, NY, UC, US); orilla de camino, 2 km S Amacuzac, cerca de los limites con el estado de Guerrero, 1100 m, Rzedowski 23509 (MSC). ZACATECAS: On the Sierra de los Morones near Plateado, Rose 2737 (GH, US).

This is a common and rather variable species distributed mainly in the states of Guerrero, Jalisco, Mexico, Michoacan, and Morelos. It is phenotypically plastic and apparently rather sensitive to precipitation when the dry season dormancy is broken by the rain. An early rain followed by a dry spell before the onset of the regular rains of the rainy season may initiate growth of one or two branches from the caudex before the rest of the branches appear. The leaves on these early branches will usually be smaller, thicker, more coriaceous and the blade length: width ratio will be greater than on the later branches. Difficulties in specific determination may result from not considering this phenotypic plasticity by attempting to apply a too rigid specific circumscription for this taxon.

Guardiola mexicana, *G. odontophylla*, and *G. arguta* are closely related. *Guardiola mexicana* is distinguished from *G. arguta* on the basis of a number of technical characters. The involucre of *G. mexicana* is usually 7-9 mm high while that in *G. arguta* is 9-13 mm high. The leaf of *G. mexicana* is usually shorter than that of *G. arguta* (usually less than 5 cm vs. usually more than 6 cm long) and the mean leaf length: width ratio is smaller in *G. mexicana* (2.26) than in *G. arguta* (2.83). Seedlings and young plants of *G. arguta* are more succulent, more pubescent, greener, and more branched than those of *G. mexicana*. Peduncle pubescence extends onto the base of the involucre in *G. mexicana* while in *G. arguta* it does not extend to the juncture of the peduncle and the base of the involucre. Leaf margin teeth, although variable, are usually spreading in *G. mexicana* but curved toward the leaf apex in *G. arguta*. Chromatograms of the two are similar but separable. *Guardiola mexicana* is a southern taxon distributed primarily in Jalisco, Mexico, Michoacan, and Morelos, while *G. arguta* is a northern species distributed primarily in Chihuahua and Durango.

Guardiola mexicana is distinguished from *G. odontophylla* on the basis of a much shorter involucre, 7-9 mm vs. 11-13 mm; the mean leaf blade length: width ratio in *G. odontophylla* is 3.31; the leaf margin teeth are longer in *G. odontophylla*. In addition *G. mexicana* is a widespread southern species while *G. odontophylla* is known only from NE Durango.

There is also a fairly close relationship and some morphological convergence of G. mexicana and G. tulocarpus, another common and phenotypically plastic species. Several characters distinguish the latter two species, and I never had trouble distinguishing the two in the field. Leaf shapes of the two taxa are similar; the average blade length: width ratio is 2.26 for G. mexicana and 2.38 for G. tulocarpus. However, the leaf of G. mexicana has a hastate lobe while this lobe is usually lacking or is present as a tooth rather than a lobe in G. tulocarpus. Guardiola mexicana has larger and fewer heads with more ray and disk flowers, and is less branched than is G. tulocarpus. The peduncular pubescence extends up onto the involucre in G. mexicana, but, with the exception of a few extremely pubescent individuals, does not do so in G. tulocarpus. Distributions of the two taxa also differ in that G. mexicana occurs mostly on the eastern slopes of the Sierra Madre Occidental in the states of Jalisco, Mexico, Michoacan, and Morelos, and the northern slopes of the Sierra Madre del Sur in Guerrero, while G. tulocarpus occurs mostly on the western slopes of the mountains in Jalisco, Michoacan and Nayarit. Although rather variable, the achenes of G. mexicana are a little longer (4-7 mm) than those of G. tulocarpus (4.5-5 mm long) and are on the average less slender.

7. Guardiola arguta (A. Gray) Robins.

Guardiola tulocarpus var. arguta A. Gray. Proc. Amer. Acad. 21:387. 1886. Guardiola arguta (A. Gray) Robins. Bull. Torrey Bot. Club 26: 234. 1899. Type: MEXICO. CHIHUAHUA: rocky hills near the town of Chihuahua, August 6, 1885, Pringle 678 (GH, holotype!; F, MICH, 2 sheets, NY, RSA, US, isotypes).

Stems 5-10 dm high, erect, sometimes striate, glabrous below to sparsely pilose above, green to reddish purple; leaves petiolate, petiole 4-15 mm long, often pilose; leaf blades broadly ovate to lanceolate-ovate, 3-9 cm long, 1-3.6 cm wide, average leaf length: width ratio 2.83, blades fleshy, apices acute, bases (subcordate) truncate to obtuse, margins serrate to dentate, teeth usually curved toward apex, hastate lobe 4-12 mm long, upper surface glabrous, lower surface glabrous to pilose; peduncles 7-15 mm long, villous, pubescence not extending to juncture of peduncle and base of head; heads 10-50 per main stem branch, urcinate, 12-16 mm high, 6-10 mm wide, in subumbellate clusters at branch termini; receptacle convex, 1-1.5 mm wide; involucre 9-13 mm high, 3-6 mm wide, phyllaries 3, imbricate, convex, equal, ovate, 9-13 mm long, 4-7 mm wide, apices acute, margin entire, 10-15 striate, green; pales ovate, 5-8 mm high, 1-2.5 mm wide; ray florets (1-) 2-3, 9.5-14 mm long, tube (5-) 6-7 (-11) mm long, ligule 3-5 (-7) mm long, 2-3 mm wide, usually 3-toothed at apex; disk florets 10-15 (-25), 12-14 mm long, tube 9-11 mm long, limb 2-3 mm high, the lobes 1.5-2 mm long, anthers 2-3 mm long; achenes narrowly ovoid, slightly compressed, 5-7 mm long, 2-3 mm wide, sparsely pilose, striate or not, beige to dark brown to gray, mottled or uniformly colored; chromosome number $\underline{n}$ = 12 (Plate 8).

ECOLOGY AND DISTRIBUTION. In disturbed areas, rocky hills and cuts, in clayey loam soil at 1800-2500 meters elevation. Distributed in the Sierra Madre Occidental from central Chihuahua to southern Durango (Figure 20). Flowering from July through October.

SPECIMENS EXAMINED. MEXICO. CHIHUAHUA: Canyon, Sierra des (sic) Pappas, Gentry 626M (DS, MICH, US); Loreto, Rio Mayo, Gentry 2565 (ARIZ, F, GH, MO, UC, US); Sandiago (sic) Canyon, 6400 ft, Sierra Madre Mts., M. E. Jones (NY, RSA, 2 sheets); Mojarachic, Knobloch (MSC); pass between Yepomera and Madero, 90 mi NW Chihuahua, Kruckeberg (MICH); Rio Gavalan, 7 mi SW Pacheco, 600 ft, Leopold 138 (UC); Chihuichupa, LeSueur 962 (ARIZ, F, GH, MO, TEX, UC); rocky arroyo banks, Cañon Huahuatan 10 mi SW Madera, Muller 3431

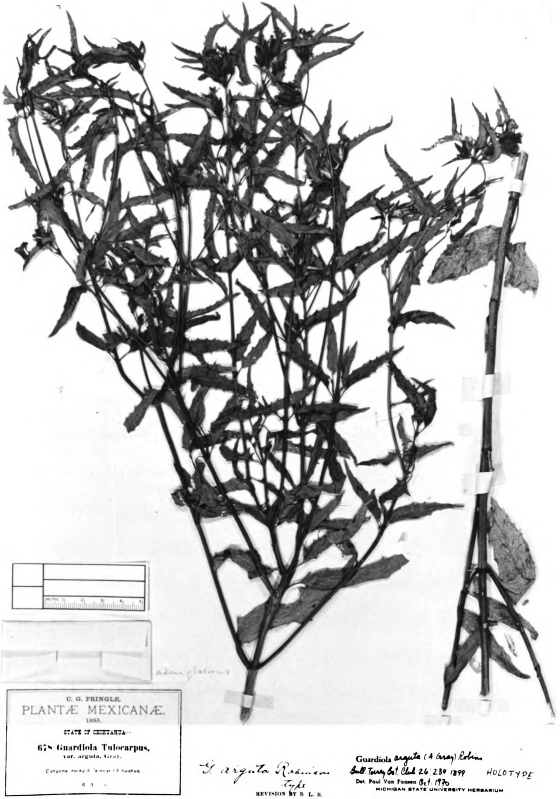

Plate 8. Holotype of Guardiola arguta (A.Gray)Robins.

(MICH, UC); in Sierra Madre near Colonia Juarez, Nelson 6003 (GH, US); stony pineland, 2150-2200 m, Pennell 19238 (MICH, NY); rocky hills near Chihuahua, Pringle 678 (F, GH, holotype, MICH, 2 sheets, NY, RSA, US); foothills of Sierra Madre, Pringle 1281 (F, GH, MICH, NY, 2 sheets, US); near Picochic, Dist. of Guerrero, 7100 ft, Shreve 8036 (ARIZ, F, GH, MICH, US); near Colonia Garcia in the Sierra Madres, 7500 ft, Townsend & Barber 180 (F, GH, MICH, MO, NY, RSA, UC, US). DURANGO: 10.6 mi East of Concordia, Breedlove 4265 (DS, MICH); rangeland, along dry wash, Casuitillo, Evans 10 (NY); rocky arroyo, 1900 m Zarca Mesa, near Torreon de las Canas, Gentry 8645 (GH, MICH, UC, US); vicinity of Rancho Los Angeles 50-54 mi WSW El Salto near Sinaloa border along Durango-Mazatlan Road, McVaugh 11572 (MICH, US); steep ravines along Mazatlan-Durango road, 3-15 km from Sinaloa border, 1950-2200 m, McVaugh 23598 (ENCB, MICH); steep roadfill, km 1142 of Mexico 40 (Mazatlan-Durango road) on Espinoza del Diablo, Van Faasen 1822 (MSC); mountainside, 46 mi SW of El Salto, Waterfall 12720 (MICH). SINALOA: Rocky roadside, 4-8 mi W of El Palmito on Durango-Mazatlan road, Oatman & Rowlett (TEX, WISC).

Guardiola arguta appears to be very closely related to *G. mexicana* and *G. odontophylla*. It is readily separated from

G. odontophylla by the nature of the dentition of the leaf, the latter species having much larger teeth than found in G. arguta. Guardiola odontophylla is an isolated species and is found only in eastern Durango while G. arguta is widely distributed in Sonora, western Chihuahua and northern Durango.

Separation of this species from G. mexicana has been discussed previously under G. mexicana.

8. Guardiola odontophylla Robins.

Guardiola odontophylla Robins. Bull. Torrey Bot. Club. 26:234. 1899. Type: MEXICO. DURANGO: Between Ramos and Inde, August 11-14, 1898. Nelson 4683 (GH, holotype!, US, isotype).

Stems 4-10 dm high, terete, striate, glabrous to glaucous except in leaf axils and on lesser inflorescence branches; leaves petiolate, the petiole 6-10 mm long, the blade lanceolate, 4.5-5.3 cm long, 1.4-1.7 cm wide, the average leaf length: width ratio 3.31, apices acute, bases truncate, margins coarsely and somewhat doubly dentate, teeth barely incurved, hastate lobe to 1.5 cm long, blade glabrous; peduncles 3-4 mm long, sparsely pilose to velutinous, pubescence not extending onto base of involucre; heads about 5 per main stem branch, urcinate, 14-18 mm high, 8-12 mm wide, borne in subumbellate clusters on branch termini; receptacle slightly convex, 0.5-1.5 mm wide; involucre 12 mm long, 4 mm wide, phyllaries ovate, (10-) 11-13 mm long, 6 mm wide, apices acute, not recurved, 10-15 striate, green to reddish purple; pales ovate, 6-7 mm long, 1-3 mm wide; ray florets 2-3, 10 mm long, tube 6 cm long, ligule 4 mm long, 1.5 mm wide, obovate, usually 3-toothed at apex; disk florets 7-10, 12 mm long, tube 10 mm long, limb 2 mm high, lobes 1.5 mm high; anthers 2 mm long; achenes linear-ovoid, slightly compressed, 6-7 mm long, 2 mm wide, sparsely pilose over entire surface, striate, light tan mottled with dark spots (Plate 9).

ECOLOGY AND DISTRIBUTION. Known only from the type specimen collected in August in the Sierra Madre Occidental of northeastern Durango between Ramos and Inde (Figure 20).

The relationships between this species and the closely related species *G. mexicana* and *G. arguta* have been discussed under *G. mexicana*. Because it is morphologically more similar to *G. arguta* than to *G. mexicana*, and because of its northern distribution, it is probably more closely related to *G. arguta* than to *G. mexicana*.

The species is distinctive and identified immediately on the basis of leaf dentition, the teeth being much larger in *G. odontophylla*

Plate 9. --Holotype of Guardiola odontophylla Robins.

[illegible]

Between [illegible] and [illegible].

Plate 9.

than in either G. mexicana or G. arguta. In addition, the involucre is longer, and the leaf blade length: width ratio is larger.

9. Guardiola tulocarpus A. Gray

Guardiola tulocarpus A. Gray. Pl. Wright. 1:111. 1850. Tulocarpus mexicana Hook. & Arn. Bot Beechey's Voy.:299. 1838. Type: MEXICO. NAYARIT: Zopelote, Nayarit, Lay & Collie (K, 2 sheets; holotype, MSC photo 685; isotype, MSC photo 684).

Guardiola tulocarpus subsp. pubescens Blake. Contr. U. S. Natl. Herb. 22: 587-661. 1924a. Type: MEXICO. SINALOA: Arroyo del Espinal, San Ignacio, Sinaloa, 1922, Ortega 4593 (US, holotype!).

Stems 4-10 dm high, striate, glabrous below, sparsely pilose in leaf axils and often on inflorescence branches, green to reddish purple; leaves petiolate, the petioles 0.4-5.5 cm long, often pubescent at base, blade broadly ovate to ovate-lanceolate, 2.4-14 cm long, 0.8-4.8 cm wide, average leaf length: width ratio 2.38, apices acute, bases truncate to cuneate, margins serrate to widely serrate, occasionally with a hastate tooth to 2 mm long, both surfaces of blade usually glabrous, occasionally sparsely pilose; peduncles

5-10 mm long, upwardly velutinous but pubescence not extending onto the base of the involucre except in very pubescent individuals; heads 50 to more than 500 per main stem branch, cylindrical to urcinate, 8-12 mm high, 6-10 mm wide, borne in subumbellate clusters; receptacle slightly convex, 0.5-1 mm wide; involucre (5-) 6-8 (-9) mm long, 2-3 mm wide, phyllaries ovate, 5-9 mm long, 3-4 mm wide, apices acute, 10-15 striate, green to reddish purple; pales linear-lanceolate, 3-4 mm long, 1-2 mm wide; ray florets (1-) 2-3, 5-10 mm long, tube (3-) 4-5 (-6) mm long, ligule 3-5 mm long, 1-1.5 mm wide, linear to obovate, usually 3-toothed at apex; disk florets 10-15, 8-11 mm long, tube 5-8 mm long, limb 2-3 mm long, lobes 1.5-2 mm long, apices acute; anthers 2 mm long; achenes obovoid, slightly compressed, 4-5.5 mm long; 1.5-2 mm wide, upwardly villous, striate or not, gray to dark brown, solid colored or mottled; chromosome number $\underline{n} = 12$ (Plate 10).

ECOLOGY AND DISTRIBUTION. In disturbed habitats, cracks in rocky cuts, clayey or loam banks, and eroding hillsides, at mostly 1500-2000 meters elevation. Flowering specimens collected in all months. Distributed from Nayarit to Oaxaca in the Sierra Madre Occidental and in Tamaulipas in the Sierra Madre Oriental (Figure 21).

Plate 10. --Holotype of Guardiola tulocarpus A. Gray.

Plate 10.

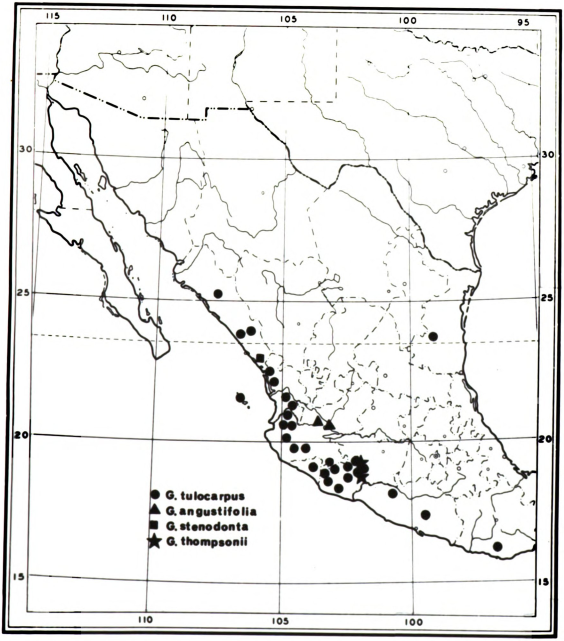

Figure 21. Distribution of G. tulocarpus, G. thompsonii, G. stenodonta, and G. angustifolia.

REPRESENTATIVE SPECIMENS. MEXICO. COLIMA: Colima, Palmer 1198 in 1891 (GH, NY, UC, US). GUERRERO: Pass, 8 mi S Chilpancingo, 4200 ft, Cronquist 9710 (MICH, NY); Arroyo, Parotas, Mina, 800 m, Hinton 9407 (MICH, NY, UC, US). JALISCO: South-facing foothills of Sierra Manantlan, about 40 km SE Autlan, McVaugh 23231 (ENCB, MICH); Quimixto on river border near coast, 5 m, Mexia 1183 (DS, F, GH, 2 sheets, MICH, MO, NY, UC, US); steep slopes, trail from Real Alto to San Sebastian, Mexia 1635 (DS, F, GH, MICH, MO, NY, UC, US); hills above Etzatlan, Pringle 11536 (ARIZ, MICH, MO, US); canyon near Tuxpan, Purpus 487 (MO, RSA, UC, US); ladera metamorfica, 20 km al SE Autlan, 1700 m, Rzedowski 14535 (ENCB, MICH, TEX); vertical rocky cut, 1 km S Tecalitlan, Mex. 10 Km 135, Van Faasen 1759 (MSC); steep rocky cut, 8 mi SW Autlan, Mex. 80, Km 1044, 4000 ft, Van Faasen 1774 (MSC); open roadside, 10 mi E Tequila, Mex. 15 Km 73, Van Faasen 1782 (MSC); rocky hillside, 44 mi NW Tequila, Mex. 15, Km 769, Van Faasen 1795 (MSC). MICHOACAN: Alrededores de San Jose Purua, Gonzales Quintero 1709 (ENCB); dry hills, Coalcoman 1100 m, Hinton 12326 (MICH, 2 sheets, NY, UC, 2 sheets); roadsides NW Aguiletle, 6-7 km S. Aserradero Dos Aguas, 2000 m, McVaugh 22680 (ENCB, MICH); Volcan de Jorullo, Nelson 6942 (GH, NY, US); ladera basaltica, 3 km al S de Tocambaro sobre el camino a Pedernales, 1500 m, Rzedowski 23719 (ENCB); bare spots in field and along stream, 4 mi S Los Reyes, Van Faasen 1757 (MSC). NAYARIT: Flats north of village of Jalisco, Ferris 5859 (DS, GH, US); near Tepic, Lay & Collie (K: type photos: MICH Negative No. 684, MSC photos 684, 685); Tepic, Jones 23338 (MO, NY, RSA, UC); Zopelote, Tepic, Lamb 580 (DS, F, GH, MO, MSC, NY, US); Tepic, Palmer 1902 in 1892 (ARIZ, F, GH, MICH, NY, UC, US); Volcan Ceboruco, 1500-1700 m, Parray 3402 (ENCB); roadside 1 km N El Cuatante, 100 m, Rzedowski 17877 (DS, ENCB, MICH, TEX); rocky cut 1 mi W village of Santa Isabella, Mex. 15 Km 851-852, Van Faasen 1797 (MSC); steep rocky hillside 3 mi N Tepic along Mex. 15, Van Faasen 1805 (MSC). SINALOA: Arroyo margin 8 mi N Badiraguato, Gentry 5786 (ARIZ, DS, F, MICH, MO, NY, UC); Arroyo de Espinal, San Ignacio, Ortega 301 (US, holotype of G. tulocarpus subsp. pubescens). TAMAULIPAS: Limestone mountainsides, on Juamave Road, 13 mi SW C. Victoria, 1000 m, McVaugh 10525 (GH, ENCB, MICH, TEX, US); Victoria, mountainside, Runyon 810 (US); mountainside La Jolla Ranch, 900 m, Runyon 1001 (US).

Guardiola tulocarpus is a common and widely distributed narrow-leaved species. The identification difficulties caused by phenotypic plasticity and sensitivity of the plants to environmental factors, especially precipitation, as discussed for _G. mexicana_, are as applicable to _G. tulocarpus_. Therefore, a broad circumscription is required for the species.

There are two isolated populations of _G. tulocarpus_, one near Ciudad Victoria in Tamaulipas and one on Maria Madre of the Tres Marias Islands. The Ciudad Victoria population is about 350 air miles from Zacapu, Michoacan, the nearest known population of _G. tulocarpus_, and about 250 air miles north of the nearest known _Guardiola_ population, _G. mexicana_ near Pachuca, Hidalgo. It is the only known population from the Sierra Madre Oriental, Pachuca being at the eastern end of the transvolcanic belt. This population is clearly _G. tulocarpus_, although the heads are slightly larger and fewer in number than in typical _G. tulocarpus_.

The Tres Marias Islands are about 70 miles off the coast of Nayarit. The specimen from there is probably an aberrant branch from a typical plant and might have been recognized as a separate species had I not collected a similar aberrant branch from an otherwise normal plant of _G. tulocarpus_ in Nayarit. The Tres Marias Islands are along the route migratory birds travel each year in their northward spring migration. Birds are the most probable long distance transport vector in accounting for the presence of _G. tulocarpus_ on the Tres Marias Islands. The reason for _G. tulocarpus_ in the vicinity of Ciudad Victoria in Tamaulipas is less obvious but birds might also be the transport vector in this case. Man is also a possible vector, since Ciudad Victoria lies on the Pan American Highway and considerable vehicular traffic passes through this area.

Characters useful in distinguishing *G. tulocarpus* from *G. mexicana*, *G. arguta*, and *G. odontophylla* are discussed above. Leaf shape, especially the long, slender hastate lobes present in *G. stenodonta*, separates it from that species. *Guardiola thompsonii* has fewer and larger heads, a less branched inflorescence, taller involucre, and much thicker and more coriaceous leaves than found in *G. tulocarpus*, and these two species are distinguished on these bases. *Guardiola tulocarpus* is readily separated from *G. angustifolia* on the basis of leaf shape, petiole length, branching of the inflorescence, and head size.

Guardiola tulocarpus subsp. *pubescens* Blake is not retained as a taxon because all specimens of *G. tulocarpus* are pubescent to some extent; there is a lack of correlation of geographical distribution and pubescence. The extremely pubescent individuals or populations are scattered and appear to me to be merely pubescent variants which do not merit taxonomic recognition.

10. Guardiola thompsonii Van Faasen, sp. nov.

Type: MEXICO. MICHOACAN: Steep clayey-loam, rocky roadcut in oak-pine forest, 12 mi south of Uruapan, Km 90-91 along Mexico route 37, July 26, 1967, Van Faasen 1727 (MSC, holotype!).

Caules 6-10 dm alti, striati, glabri usque glauci praeter axillas foliorum et pedunculos interdum pilosos, viridipurpurei usque purpurei; folis petiolata, petiolus 5-16 mm longus, lamina lanceolata crassa, succulenta usque firma et coriacea, 3-11.8 cm longa, 0.9-3.5 cm lata, ratio longitudis: latitudis laminae folii 2.58, apices acuti, bases cuneati, margines late serati usque fere integri, plerumque destituta lobos hastatos vel dentes, glabra; pedunculi 5-10 mm longi, glabri usque parce pilosi; capitula 15-20 per ramum caulis principali, cylindrica usque urcinata, 11-15 mm alta, 7-10 mm lata, portata fasciculis subumbellatis constatis e 3-12 capitulis in terminis ramorum; receptaculum leviter convexum, 0.5-1.0 mm latum; involucrum 8-10 mm altum, 3-4 mm latum, phyllaria ovata, 8-10 mm longa, 3-5 mm lata, apices acuti, 10-15 striati, viridipurpurei usque rubropurpurei; paleae ovatae, 4-6 mm altae, 2-3 mm latae; flores radii 2-3, 6-8 mm longae, tubus 3-4 mm longus, ligula 3-4 mm longa, 1-1.5 mm lata, oblonga, plerumque tridens apice; flores disci 10-15, 8-10 mm longi, tubus 5-6 mm longus, limbus 3-4 mm longus, lobi 1.5-2 mm alti, apices acuti; antherae 2 mm longae; achenia ovoidea, leviter compressa, 5-6 mm longa, 2-2.5 mm lata, parce pilosa per totam longitudinem, striata, brunnea diluta usque cana, uniformiter colorata vel maculata; numerus chromosomatum $\underline{n}$ = 12 (Plate 11).

Stems 6-10 dm high, striate, glabrous to glaucous except sometimes pilose in leaf axils and on peduncles, greenish purple to purple; leaves petiolate, petiole 5-16 mm long, blade lanceolate, thick, succulent to firm and coriaceous, 3-11.8 cm long, 0.9-3.5 cm side, average leaf blade length: width ratio 2.58, apices acute, bases cuneate, margins widely serrate to nearly entire, usually lacking hastate lobes or teeth, glabrous; peduncles 5-10 mm long, glabrous to sparsely pilose; heads 15-50 per main stem branch, cylindrical to urcinate, 11-15 mm high, 7-10 mm wide, borne in subumbellate clusters of 3-12 heads on branch termini; receptacle slightly convex, 0.5-1.0 mm wide; involucre 8-10 mm high, 3-4 mm wide, phyllaries ovate, 8-10 mm long, 3-5 mm wide, apices acute, 10-15 striate, greenish purple to reddish purple; pales ovate, 4-6 mm long, 2-3 mm wide; ray florets 2-3, 6-8 mm long, tube 3-4 mm long, ligule 3-4 mm long, 1-1.5 mm wide, oblong, usually 3-toothed at apex; disk florets 10-15, 8-10 mm long, tube 5-6 mm

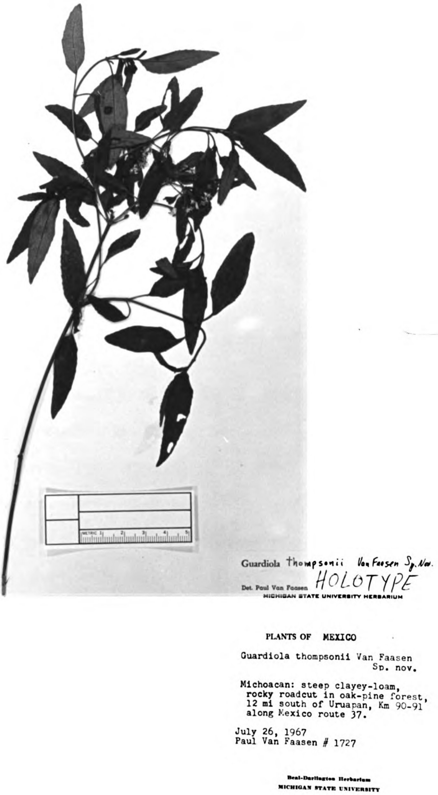

Plate 11. Holotype of Guardiola thompsonii Van Faasen

long, limb 3-4 mm long, lobes 1.5-2 mm high, apices acute; anthers 2 mm long; achenes ovoid, slightly compressed, 5-6 mm long, 2-2.5 mm wide, sparsely pilose over entire length, striate, light brown to gray, uniformly colored or mottled; chromosome number *n* = 12 (Plate 11).

ECOLOGY AND DISTRIBUTION. In disturbed areas, eroding clayey-loam banks in oak-pine woods or in cracks in rock outcrops in the open at 1500-1700 meters elevation. Flowering in July and August. Distributed in Michoacan (Figure 21).

SPECIMENS EXAMINED. MEXICO. MICHOACAN: Steep clayey-loam, rocky roadcut in oak-pine forest, 12 mi S Uruapan, Km 90-91 along Mexico route 37, July 26, 1967, *Van Faasen 1727* (MSC, holotype); sides of vertical rocky road cut, Km 106 along Mexico route 37, just south of barranca, about 22 miles S of Uruapan, July 27, 1967, *Van Faasen 1756* (MSC).

Guardiola thompsonii is named in honor of Oscar E. Thompson, my first botany professor, who introduced me to field biology.

This species is of limited distribution in Michoacan and is most closely related to G. tulocarpus. It is distinguished from the latter on the basis of its fewer and larger heads, purple-colored stem, and more lanceolate leaf with only slightly toothed leaf margin. The leaves are much thicker and more coriaceous than are those of G. tulocarpus. Head size and numbers may relate it to G. mexicana, though morphologically it is closer to G. tulocarpus than to G. mexicana. Although distinct from both species on morphological bases, there is some question from the chemotaxonomic studies of a possible hybrid origin with G. tulocarpus and G. mexicana as parent species. However, none of the hybrids of those two species, as synthesized in the laboratory, were morphologically similar to G. thompsonii.

11. Guardiola stenodonta Blake

Guardiola stenodonta Blake. Proc. Biol. Soc. Wash. 37: 56. 1924. Type: MEXICO. SINALOA: Balboa, Sinaloa, January, 1923, Ortega 4986 (US, holotype!).

Stems 4-10 dm high, striate, glabrous to glaucous except sparsely pilose on the peduncles; leaves petiolate, petiole 1-1.5 cm long, blade linear-lanceolate, 5-8.5 cm long, 1.2-1.5 cm wide, average leaf blade length: width ratio 6.83, apices acute, bases cuneate to truncate, margins serrate, hastate lobe 0.5-1.4 cm long, 1-2 mm wide at base, blade glabrous; peduncles 6-9 mm long, sparsely pilose; heads about 75 per main stem branch, urcinate, 1.1-1.2 cm tall, 8-9 mm wide, borne in clusters of 3 to 4 on branch termini; receptacle slightly convex, 0.5-1.0 mm wide; involucre 7-8 mm high, 3.5-5 mm wide, phyllaries ovate, 7-8 mm long, 4-5 mm wide, apices acute, 10-15 striate, green; pales ovate, 4-5 mm high, 1-2 mm wide; ray florets 3-4, 10 mm long, tube 5 mm long, ligule 5 mm long, 2 mm wide, obovate, 3-toothed at apex; disk florets 10-15, 13 mm long, tube 9 mm long, limb 4 mm long, lobes 1.5 mm high, apices acute; anthers 2 mm long; achenes linear obovoid, slightly compressed, 4-5 mm long, 2-2.2 mm wide, sparsely pilose over entire length, striate, dark gray mottled with light spots (Plate 12).

ECOLOGY AND DISTRIBUTION. Known only from the type specimen collected at Balboa, Sinaloa, and without ecological data (Figure 21). Flowering in January.

This species has a very distinctive leaf shape and on this basis is readily distinguished from other narrow-leaved species. The leaf blade is slightly constricted just above the hastate lobes

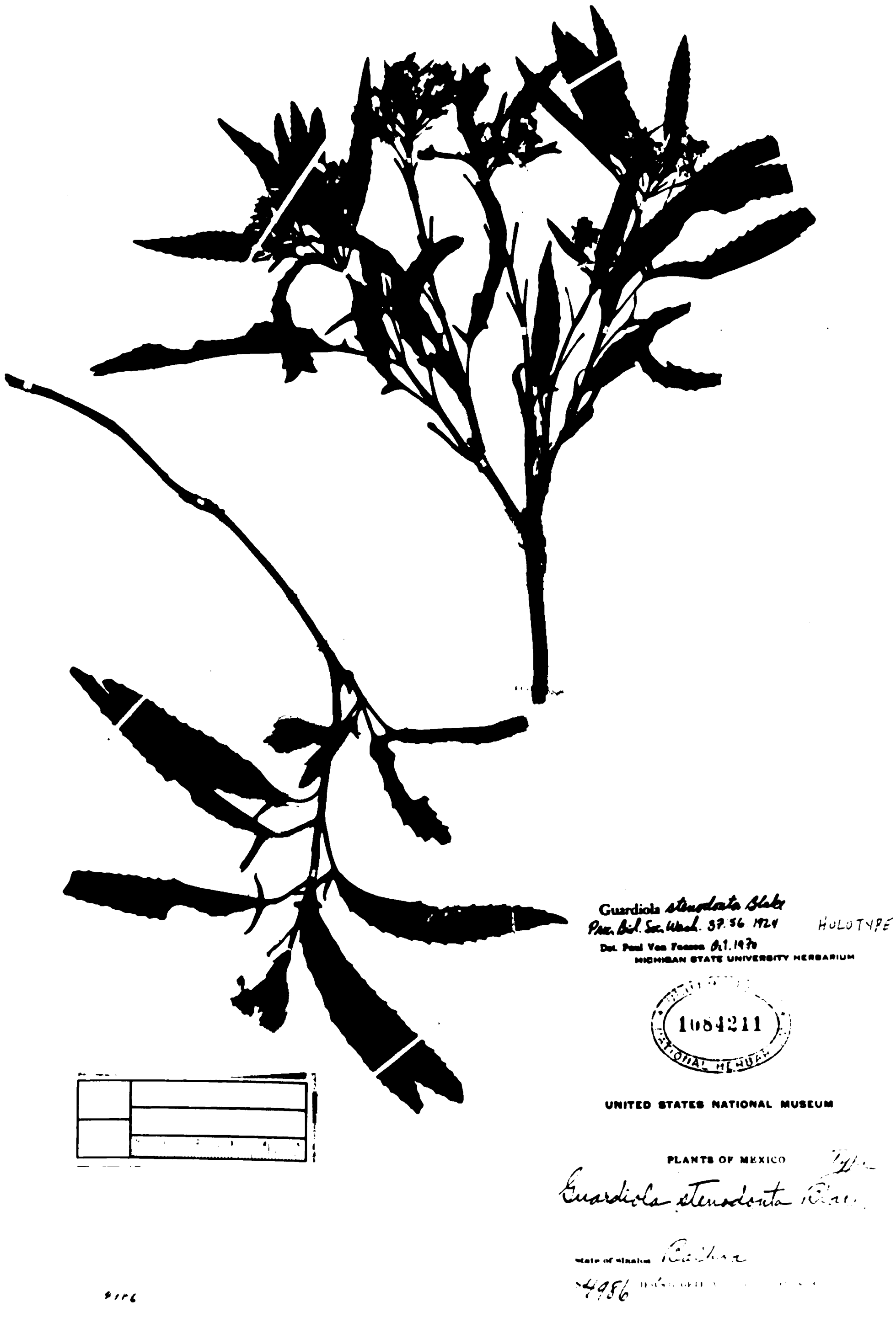

Plate 12. Holotype of Guardiola stenodonta Blake

which are very long and slender. The morphological features of this plant suggest a relationship with G. tulocarpus.

12. Guardiola angustifolia (A. Gray) Robins.

Guardiola tulocarpus var. angustifolia A. Gray in S. Wats. Proc. Amer. Acad. 22: 423. 1887. Guardiola angustifolia (A. Gray) Robins. Bull. Torrey Bot. Club. 26: 235. 1899. Type: MEXICO. JALISCO: Ravines near Tequila, Palmer 360 in 1886 (GH, holotype! ; MO, US isotypes).

Stems 12-25 dm high, erect, sometimes striate, glabrous, sparsely pilose in leaf axils, glabrous below to glaucous above, green to reddish purple, caudex to 3.5 cm in diameter; leaves petiolate, petiole 3-12 mm long; blades linear-lanceolate (2-) 5-10 (-12) cm long and (6-) 8-15 (-22) mm wide, average leaf length: width ratio 8.90, blades subsucculent to coriaceous, apices acute, bases cuneate, margins serrate to serrate-dentate often with curved teeth, occasional hastate teeth to 4 mm long, sparsely pilose to glabrous below; peduncles 2-8 mm long with scattered villous pubescence; heads 80 to more than 500 per main stem branch, narrowly cylindrical, 10-15 mm long, 5-7 mm wide, borne in subumbellate clusters in a diffusely branched paniculate inflorescence; receptacle 0.5-1 mm wide; pales linear-lanceolate; involucre 7 mm

high, 1.5-2 mm in diameter, phyllaries linear-ovate, 7 mm long, 2-3 mm wide, 7-12 striate, green to reddish purple; ray florets mostly 1 per head, 5.5-7 mm long, tube 3-5 mm long, ligule 2-3 mm long, 1 mm wide; disk florets 3-4, 9-10 mm long, the tube 6-7.5 mm long, the limb 3-4 mm long, corolla lobes 1.5-2 mm high, anthers 2 mm long; achenes narrowly obovoid, slightly compressed, 4.5-6 mm long, 1.5-2 mm wide at widest point, villous upward, striate or not, beige to brown to gray mottled or solid colored; chromosome number $\underline{n}$ = 12 (Plate 13).

ECOLOGY AND DISTRIBUTION. In dry, disturbed areas with clayey-loam or rocky soils at 1200-1800 meters elevation. Flowering from July through December. Known only from Jalisco (Figure 21).

SPECIMENS EXAMINED. MEXICO. JALISCO: Barranca of Rio Grande de Santiago, 5 mi NE Guadalajara, Cronquist 9816 (MICH, NY, TEX); La Barranca, Guadalajara, M. E. Jones 27774 (DS, MICH, MO, NY, RSA, 2 sheets, UC, US); steep rocky hills 2 mi NW Tequila, 1200 m, McVaugh 18636 (MICH); ravines near Tequila, Palmer 360 in 1886 (GH holotype, MO, US); hillsides near Guadalajara, Pringle 1737

Plate 13. Holotype of Guardiola angustifolia (A.Gray)Robins.

(F, GH, MICH, NY, 2 sheets, RSA, UC, US); hills near Guadalajara, Pringle 2752 (F, ENCB, MO, MSC, UC); plains near Guadalajara, 5000 ft, Pringle 9915 (F, GH, MO, NY, US); slopes of the barranca of Guadalajara, 4500 ft, Pringle 11535 (F, MICH, US); near Tequila, Rose & Hough 4747 (GH, MICH, US); Carretera a Saltillo al Norte de Guadalajara, 1500 m, Villareal de Puga 397 (ENCB); La Barranca, 5 mi NE Guadalajara, Van Faasen 1776 (MSC); slopes and road cuts, 10 mi N Guadalajara, Van Faasen 1777 (MSC); open roadsides, 2 km NW Tequila, Van Faasen 1783 (MSC).

This is a very distinctive species, and I have seen no specimens which could be confused easily with any other taxa. The plants are tall and diffusely branched with many small heads and very narrow leaves. It is the most advanced of the narrow-leaved species, and is adapted to xeric conditions. Above the barranca of Guadalajara *G. angustifolia* grows to be about 8 feet tall and occurs only among the large erect *Opuntia* plants there. Elsewhere *G. angustifolia* grows in the open, so the relationship with the cacti seems to be a serendipitous one affording both shading and mechanical protection to the *Guardiola* plants. Shading allows young plants to become established more readily. The area above the barranca is popular with both picnickers and cows, and the cacti cause both to keep their distance, thereby preventing trampling of the plants. Grazing is not a problem, for the herbage of Guardiola is rank-smelling and nowhere in Mexico did I note any grazing damage to it.

Morphological evidence suggests a close relationship of G. angustifolia with G. tulocarpus, which may be ancestral to it; at least the two species may share a common ancestry. Biochemical evidence also suggests a close relationship with G. thompsonii. The narrow leaves, diffuse branching, numerous heads, small head size, and xeric adaptation distinguish it from those species and clearly mark it as an advanced species.

SPECIES EXCLUDED FROM *GUARDIOLA*

Guardiola diehlii M. E. Jones. Contr. Western Bot. 12: 48. 1908 = *Flaveria campestris* J. R. Johnston (Blake, 1945).

LITERATURE CITED

LITERATURE CITED

Alston, R. E., and B. L. Turner. 1962. New techniques in the analysis of complex natural hybridization. Proc. Nat. Acad. Sci. (U.S.) 48: 130-137.

__________, and B. L. Turner. 1963. Natural hybridization among four species of Baptisia (Leguminosae). Amer. Jour. Bot. 50: 159-173.

Anderson, L. C. 1964. Studies on Petradoria (Compositae): Anatomy, Cytology, Taxonomy. Trans. Kansas Acad. Sci. 66: 632-684.

Baker, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9: 347-349.

Ball, G. A., E. O. Beal, and E. A. Flecker. 1967. Variation of chromatographic spot patterns of two species of clonal plants grown under controlled environmental conditions. Brittonia 19: 273-279.

Beaman, J. H., and J. W. Andresen. 1966. The vegetation, floristics, and phytogeography of the summit of Cerro Potosi, Mexico. Amer. Midl. Nat. 75: 1-33.

Blake, S. F. 1924a. New American Asteraceae. Contr. U.S. Nat. Herb. 22: 587-661.

__________. 1924b. Eight New Asteraceae from Mexico, Guatemala, and Hispaniola. Proc. Biol. Soc. Wash. 37: 55-62.

__________. 1945. Asteraceae described from Mexico and the southwestern United States by M. E. Jones, 1908-1935. Contr. U.S. Nat. Herb. 29: 117-137.

Brehm, B. E. 1966. Taxonomic implications of variation in chromatographic pattern components. Brittonia 18: 194-202.

__________, and M. Ownbey. 1965. Variation in chromatographic patterns in the Tragopogon dubius-praetensis-porrifolius complex (Compositae). Amer. Jour. Bot. 52: 811-819.

Cain, S. A., and D. E. Cain. 1948. Size frequency characteristics of Pinus echinata. Bot. Gaz. 110: 325.

Carlquist, S. 1957a. The genus Fitchia (Compositae). Univ. Calif. Publ. Bot. 29: 1-144.

__________. 1957b. Anatomy of Guayana Mutisieae. Mem. N. Y. Bot. Gard. 9: 441-476.

__________. 1962. Comparative plant anatomy. Holt, Rinehart and Winston. N.Y. 146 pp.

Cronquist, A. 1955. Phylogeny and taxonomy of the Compositae. Amer. Midl. Nat. 53: 478-511.

DeJong, D. C. D. 1965. A systematic study of the genus Astranthium (Compositae-Astereae). Publ. Mus. Michigan State Univ. Biol. Ser. 2: 429-528.

Dice, L. R. 1943. The biotic provinces of North America. U. Mich. Press. Ann Arbor. 78 pp.

Dressler, R. L. 1954. Some floristic relationships between Mexico and the United States. Rhodora 56: 81-96.

Faegri, K., and J. Iversen. 1964. Textbook of Pollen Analysis. Hafner Publ. Co. N.Y. 237 pp.

Farris, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19: 83-92.

__________, A. G. Kluge, and M. J. Eckardt. 1970. A numerical approach to phylogenetic systematics. Syst. Zool. 19: 172-191.

Gentry, H. S. 1942. Rio Mayo Plants. Carnegie Inst. Wash. Publ. No. 527. 328 pp.

Goldman, E. A., and R. T. Moore, 1946. The biotic provinces of Mexico. Jour. Mammalogy 26: 347-360.

Grant, V. 1963. The origin of adaptation. Columbia U. Press. N.Y. 606 pp.

Gray, A. 1850. Plantae Wrightinae Trans-Neo-Mexicanae. Part I. Smithsonian Contr. Knowledge 3: 1-146.

__________. 1952. Plantae Wrightinae Trans-Neo-Mexicanae. Part II. Smithsonian Contr. Knowledge 5: 1-119.

__________. 1886. Contributions to American botany. 2. Sertum Chihuahuaense. Proc. Amer. Acad. 21: 378-409.

__________. 1888. Synoptical flora of North America. Smithsonian Misc. Coll. v. 31.

Hawksworth, F. G., and D. Wiens. 1965. Arceuthobium in Mexico. Brittonia 17: 213-238.

Hemsley, W. B. 1879-1888. Botany, in: Goodwin, F. D., and O. Salvin, Biologia Centrali-Americana. R. H. Porter. London. 5 vol.

Hoffmann, O. 1894. Compositae in: Engler and Prantl, Die Natürlichen Pflanzenfamilien. 4: 217.

Holbo, H. R., and H. N. Mozingo. 1965. The chromatographic characterization of Artemisia, Section Tridentatae. Amer. Jour. Bot. 52: 970-978.

Hooker, W. J., and G. A. W. Arnott. 1838. The Botany of Captain Beechey's Voyage. Reprinted 1965. J. Cramer, Weinheim. 485 pp. & 91 plates (dist. Stechert-Hafner, N.Y.).

Humboldt, F. A., and A. Bonpland. 1808. Pl. Aequin. 1: 143-146. t. 41.

Hunter, G. E. 1967. Chromatographic documentation of inter-specific hybridization in Vernonia: Compositae. Amer. Jour. Bot. 54: 473-477.

Iltis, H. H. 1958. Studies in the Capparidaceae IV. Polansia Raf. Brittonia 10: 33-58.

__________. 1959. Studies in the Capparidaceae VI. Cleome sect. Physostemon. Brittonia 11: 123-162.

Janzen, D. H. 1969. Seed-eaters versus seed size, number, toxicity, and dispersal. Evolution 23: 1-27.

Jones, M. E. 1908. Contr. Western Botany 12: 48.

Kluge, A. G., and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1-32.

Koch, M. F. 1930a. Studies in the anatomy and morphology of the Composite flower I. The Corolla. Amer. Jour. Bot. 17: 938-954.

__________. 1930b. Studies in the anatomy and morphology of the Composite flower II. The corollas of the Heliantheae and Mutisieae. Amer. Jour. Bot. 17: 995-1012.

Lee, E. 1914. Observations on the seedling anatomy of certain sympetalae. II Compositae. Ann. Bot. 28 (10): 303-329.

Leopold, A. S. 1950. Vegetation zones of Mexico. Ecology 31: 507-518.

Levan, A., K. Fredger, and A. S. Sandberg. 1965. Nomenclature for centromeric position on chromosomes. Hereditas 52: 201-220.

Longpre, E. K. 1970. Systematics of the genera Sabazia, Selloa, and Tricarpha (Compositae). Publ. Mus. Michigan State Univ. Biol. Ser. 4: 283-384.

Martin, P. 1958. Pleistocene ecology and biogeography of North America. In: Hubbs, C. L. Zoogeography. Amer. Assoc. Adv. Sci. 51: 375-420.

McClure, J. W., and R. E. Alston. 1966. A chemotaxonomic study of Lemnaceae. Amer. Jour. Bot. 53: 849-860.

McVaugh, R., and J. Rzedowski. 1965. Synopsis of the genus Bursera L. in western Mexico, with notes on the material of Bursera collected by Sessé and Mociño. Kew Bulletin 18: 317-382.

Melchert, T. E. 1966. Chemo-demes of diploid and tetraploid Thelesperma simplicifolium (Heliantheae, Coreopsidinae). Amer. Jour. Bot. 53: 1015-1020.

Miranda, F., and A. J. Sharp. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology 31: 313-333.

Phillips, W. S. 1937. Seedling anatomy of Cynara scolymus. Bot. Gaz. 98: 711-724.

Robinson, B. L. 1894. Descriptions of new and hitherto imperfectly known plants contained in C. G. Pringle's Mexican collections of 1892 and 1893. Proc. Amer. Acad. 29: 314-325.

__________. 1899. Revision of the genus Guardiola. Bull. Torrey Bot. Club 26: 232-235.

__________. 1907. New or otherwise noteworthy spermatophytes chiefly from Mexico. Proc. Amer. Acad. 43: 21-48.

Rzedowski, J. 1962. Contribuciones a la fitogeografia floristica e historica de Mexico I. Algunas consideraciones acerca del elemento endemico en la flora Mexicana. Bol. Soc. Bot. Mex. 27: 52-65.

__________. 1964. Relaciones geograficas y posibles origenes de la flora de Mexico. Bol. Soc. Bot. Mex. 29: 121-177.

__________, and R. McVaugh. 1966. La vegetacion de Nueva Galicia. Contr. U. Mich. Herb. 9: 1-123.

Sanders, E. M. 1921. The natural regions of Mexico. Geogr. Rev. 11: 212-242.

Schoch-Bodmer, H. 1940. Influence of nutrition upon pollen grains in Lythrum salicaria. Jour. Genetics 40: 393.

Seeligmann, P., and R. E. Alston. 1967. Complex variation and the taxonomy of Hynenoxys scaposa (Compositae). Brittonia 19: 205-211.

Sharp, A. J. 1953. Notes on the flora of Mexico: world distribution of the woody dicotyledonous families and the origin of the modern vegetation. Jour. Ecol. 41: 374-380.

Shinners, L. H. 1946. Revision of the genus Chaetopappa DC. Wrightia 1: 63-81.

Siler, M. B. 1931. The transition from root to stem in Helianthus annuus L. and Arctium minus Bernh. Amer. Midl. Nat. 12: 425-487.

Small, J. 1915. The pollen-presentation mechanism in the Compositae. Ann. Bot. 29: 457-470.

Smith, D. M., and D. A. Levin. 1963. A chromatographic study of reticulate evolution in the Appalachian Asplenium complex. Amer. Jour. Bot. 50: 952-958.

Stebbins, G. L. 1966. Chromosomal variation and evolution. Science 1952: 1463-1469.

__________. 1967. Adaptive radiation and trends of evolution in higher plants. In Dobzhansky, Th. et al. Evolutionary Biology Vol. I: 104-142. Appleton-Century-Crofts. N.Y.

Stix, E. 1960. Pollenmorphologische Untersuchungen an Compositen. Grana Palynologica 2: 41-104.

Thomas, E. N. 1907. A theory of the double leaf-trace founded on seedling structure. New Phytologist 6: 77-91.

Turner, B. L. 1962. Taxonomy of Hymenothrix (Helenieae, Compositae). Brittonia 14: 101-120.

__________. 1966. Taxonomy of Oxypappus (Compositae). Sida 2: 431-433.

Van Faasen, P. 1963. Cytaxonomic studies in Michigan Asters. Mich. Bot. 2: 17-27.

Vuilleumier, B. S. 1969. The genera of Senecioneae in the southeastern United States. Jour. Arnold Arb. 50: 104-123.

Wagenitz, G. 1955. Über die Änderung der Pollengrösse von Getreiden durch verschiedene Ernährungsbedingungen. Ber. Beritschen Bot. Ges. 58: 297.

Watson, S. 1887. Contributions to American botany. XXI. Proc. Amer. Acad. 22: 396-481.

White, S. S. 1948. The vegetation and flora of the region of the Rio de Bavispe in northeastern Sonora, Mexico. Lloydia 11: 229-302.

Wiens, D. 1964. Revision of the acataphyllous species of Phoradendron. Brittonia 16: 11-54.

Wilson, P. G. 1958. Contributions to the flora of tropical America. LXII. Plantae Hintonianae XII. Kew Bull. 13: 155-170.

Wodehouse, R. P. 1959. Pollen Grains. Hafner Publ. Co. N.Y. 574 pp.

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