ORIGIN AND DIVERSITY OF MEXICAN CONVOLVULACEAE

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RESUMEN

Quince géneros y aproximadamente 217 especies de Convolvulaceae se reconocen dentro de la República Mexicana. El grado de diversidad de los elementos primitivos y avanzados que se presentan en la familia es comparable con el de otras zonas tropicales en el mundo, como de África, Sudamérica, Malasia y Australia. Este patrón de distribución sugiere un origen evolutivo relativamente antiguo, posiblemente anterior a la desintegración de Gondwana (ca. 100 MA). El aislamiento de México desde el Paleoceno ha dado origen a muchos taxa endémicos, especialmente a nivel de subgéneros y especies. Sin embargo, hay solamente un género endémico a México y Guatemala, *Itzaea*, el cual es monotípico. La mayoría de los géneros muestran más endemismo al nivel específico en zonas áridas, con la única excepción de *Ipomoea*, el cual muestra más endemismo en regiones tropicales. En virtud de los avances taxonómicos que se han realizado en los últimos años, se presenta una clasificación de las especies de las Convolvulaceae, con datos sobre su distribución. También se presenta una discusión sobre la biología reproductiva, la diversidad morfológica, y la radiación adaptativa dentro de la familia.

Palabras clave: Convolvulaceae, *Ipomoea*, origen, diversidad, endemismo, México.

ABSTRACT

The Convulvaceae represent one of the larger and more diverse families of angiosperms in Mexico. Fifteen genera and about 217 species are known within the political boundaries of the country. Comparable degrees of diversity in both primitive and advanced groups of the family are encountered in other tropical regions of the world, such as South America, Africa, Southeast Asia and Australia, suggesting an evolutionary origin antedating the break-up of Gondwanaland (ca. 100 MA). The family exhibits high levels of endemism at the species and subgeneric levels, though only one genus is endemic to Mexico and Guatemala, *Itzaea*, which is monotypic. Species endemism is highest for *Ipomoea* in tropical zones, while the remainder of the genera exhibit higher rates of species endemism in arid regions. In light of recent advances in the taxonomy of the Convolvulaceae, a revised classification scheme for Mexican morning glories is presented, with data on the known distribution of each species. A discussion on the reproductive biology, morphological diversity and adaptive radiation within the family is presented.

Key words: Convolvulaceae, *Ipomoea*, origin, diversity, endemism, Mexico.

INTRODUCTION

Although the Convolvulaceae do not rank among the ten largest angiosperm families of Mexico (Rzedowski, 1990), they do include some of the country's more ubiquitous and conspicuous floristic elements. Their robust vines bearing large,

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brightly pigmented flowers commoly y cover the Mexican countryside in a mantle of
color, hence their vernacular name, "manto". A widespread presence in the diver-
se vegetation zones of México endows the groups with a wide variety of growth
habits, vegetative specializations, and pollination syndromes that is equalled by few
other angiosperm groups.

By conservative estimates, the Convolvulaceae include about 40 genera and
1400 species worldwide. Fifteen genera are reported from Mexico, comprising a
sixth of the world's known morning glory species (ca. 217 spp.; see Appendix). The
family is allied with the Solanaceae on the basis of alternate leaves, internal
phloem, pentamerous, actinomorphic, gamopetalous flowers, and is generally
distinguished by the presence of one or two styles, capsular fruits, and seed with
nuclear endosperm, plicate cotyledons, and in many groups ergoline alkaloids
(Cronquist, 1981). Generic lines are primarily defined on the basis of gynoecium,
pollen, sepal and stamen characters, generally in this order of relevance. Despite
the apparent parallel reduction of gynoecial features in various lineages within the
family, the characters associated with the pistil are weighted heavily to define
evolutionary trends within the group (Austin, 1973; Choisy, 1845; Hallier, 1893,
Verdcourt, 1963).

For the present discussion, *Cuscuta* (dodder) is excluded from the Convolvula-
ceae and placed in the closely related, sister family, Cuscutaceae (Cronquist, 1981;
Takhtajan, 1980). The close relationship of these two groups has never been
questioned; indeed *Cuscuta* is still often included in the morning glory family with
subfamilial ranking (Austin & Pedraza, 1982; Heywood, 1978). Yet the many
synapomorphies associated with the parasitic species comprising *Cuscuta* (e.g.,
lack or reduction of chlorophyll, internal phloem, cotyledons and leaves, disintegra-
tion of roots after germination, development of haustoria, etc.) place the genus far
into its own taxonomic realm. In addition, the entire gamut of gynoecial traits used
to define generic lines in the Convolvulaceae *sensu stricto* (e.g., styles 1 or 2, free or
fused, stigmas elongate or capitate, etc.) are also presented in dodder lineages.
Thus *Cuscuta* appears to have diverged from its autotrophic sister group at about
the time of the latter's own evolutionary inception.

The Convolvulaceae have a pantropical distribution, though a few groups have
radiated into temperate latitudes, such as *Convolvulus, Calystegia,* and *Ipomoea.*
Four major centers of diversity for the family are recognized: Mexico, South Ameri-
ca, tropical Africa and Southeast Asia. Because morning glories are mostly vining
heliophytes, they prosper best in open, tropical deciduous forests, where short-sta-
tured neighboring plants provide adequate support for vining growth and allow the
entry of light near ground level. Shaded understories of tropical evergreen forest
generally prohibit the establishment of most Convolvulaceae, excepting a few tall
lianas (e.g., *Ipomoea phillomega, I. reticulata, I. santillanii*), and weedy species that
exploit riparian and disturbed habitats of this vegetation type (e.g., *Ipomoea alba, I.
batatas, Odonellia hirtiflora*).

Origin and distributions. Taking into account continental movements due to
sea-floor spreading, it is a paradox that *Ipomoea,* which is agreed to be one of the
more derived genera of the Convolvulaceae (Austin, 1973; Hallier, 1893), is
almost equally represented on most continents in species numbers, while many

genera with presumed primitive features are endemic to a single continent. *Evolvulus* and *Jacquemontia,* for example, are endemic to the New World and of South American origin (Robertson, 1971; van Ooststroom, 1934), while *Falkia, Cladostigma* and *Hildebrantia* are endemic to Africa (Verdcourt, 1963), and *Polymeria* to Australia (Burbidge, 1963). None of the above genera would be considered more than moderately derived. Raven and Axelrod (1974) questionably contend that the Convolvulaceae ''exhibit no apparently ancient (distribution) patterns, suggesting widespread genera of the family have extended between continents by long-distance dispersal since the Pliocene. However, Cronquist (1981) notes the relatively old age of the Convolvulaceae in relation to other tubiflorous families, based on the presence of fossil pollen from the Eocene. Since seed dispersibility is relatively inefficient for most Convolvulaceae (members of the family generally produce bulky seeds and fruits devoid of any efficient means for long-distance dispersal), their widespread distribution with high degrees of endemism at the generic and species levels on almost every continent affirms a very old origin of the group. Equally relevant are distributions of such genera as *Bonamia,* a relatively primitive member of the Convolvulaceae, which has defined centers of diversity in South America, Africa, Madagascar and Australia (Myint and Ward, 1968). This distribution pattern would suggest a Gondwanan origin for the genus, as does that for the relatively primitive *Calycobolus,* which has a South America-African disjunct distribution (Heine, 1963). *Evolvulus* and *Polymeria* exhibit mostly South American and Australian distributions, respectively (Burbidge, 1963; van Ooststroom, 1934). The distributions of *Calystegia* and *Convolvulus,* with Eurasian and North American centers of diversity, coult not be ruled out as Laurasian in origin, considering their diversity in the northern hemisphere and very poor representation in the southern. *Merremia,* a relatively advanced member of the family, is equally represented in South America, Africa, Mexico and southern Asia, while *Ipomoea* has considerably large and relatively equal representation on most continents. High rates of endemism and species diversity on a worldwide scale for both *Ipomoea* and *Merremia* cannot be easily attributed to an origin on one continent followed by near equal rates of radiation in almost every other continent on earth. Moreover, the high rates of endemism for Mexican morning glories, which cannot be explained by the relatively recent reunion of North and South America ca. 5.7 MA (Raven and Axelrod, 1974), confirm the group's ancient presence in Mexico, a region of North America that separated from Gondwanaland around 100 MA and remained isolated from a European land bridge since the end of the Cretaceous (Cox, 1974; Dietz and Holden, 1970; Smith, Briden and Drewry, 1973).

It can be noted that generic diversity is centered in the southern hemisphere, which suggests a Gondwanan origin for the family. However, it is also possible that the Convolvulaceae were at one time cosmopolitan, but lost ground to temperate elements in the northern hemisphere, as did many tropical genera, when northern hemispheric landmasses became drier and cooler during the Eocene (Axelrod, 1975). Indeed, where tropical climates are present in the northern hemisphere (Mexico and Southeast Asia), morning glory diversity is remarkable. Whatever the case, two distributional trends in the family are clearly observable today: derived genera with pantropical distributions, and primitive genera with

both endemic (at the continental level) and intercontinental distributions. For a family with relatively limited means for transoceanic dispersal, I would suggest that much of the diversification of the Convolvulaceae took place before the palaeocontinents of Gondwanaland and Laurasia became very distant, likely as early as the upper Cretaceous or Paleocene.

About one third of the morning glory genera of Mexico are New World endemics, including *Evolvulus, Itzaea, Jacquemontia, Maripa,* and *Odonellia.* Only one of these is restricted to Mexico and Central America, *Itzaea,* a monotypic group with close relations to *Bonamia* (Austin, 1971b). The remaining five genera are likely of South American origin. *Evolvulus* consists of ca. 100 species, but is represented by only 12 species in Mexico, half of which are widely distributed weeds throughout the New World (van Ooststroom, 1934). *Jacquemontia,* as well, is comprised of ca. 100 species, but only 19 are found in Mexico, including the weedier elements of the genus (e.g., *J. nodiflora, J. pentantha, J. tamnifolia, J. ovalifolia,* etc.; Robertson, 1971). *Maripa* includes about 19 species, most of which are restricted to the Amazon basin (Austin, 1973), with one species *(M. nicaraguensis)* extending into Chiapas. *Odonellia* is a small genus probably of South American origin. Thus the remergence of North and South America about 5.7 MA (Raven and Axelrod, 1974) apparently resulted in a significant northward migration of several genera from South America. The degree of floristic interchange, however, does not appear to be reciprocal; morning glory genera of northern hemispheric origin, including *Calystegia, Convolvulus, Itzaea,* and *Stylisma,* have a limited presence in South America.

The remaining genera of Mexico have transoceanic distributions: *Aniseia, Bonamia, Calycobolus, Cressa, Calystegia, Convolvulus, Dichondra, Ipomoea, Merremia, Operculina. Dichondra* and *Aniseia* are small genera of obscure New World origin (see Appendix), each including one or two Old World species that probably represent descendents of relatively recent waifs. *Calycobolus,* a genus of American-African distribution (Heine, 1963), is represented by a single species *(C. nutans)* in Mexico (Austin, 1971a). The two species of *Cressa* in Mexico are amphitropical disjuncts, inhabiting saline or gypseous soils in North and South America. Their relatives in the Old World are few and occupy similar habitats. The two most widespread genera of the Convolvulaceae, *Ipomoea* and *Merremia* (ca. 275 and 27 New World species, respectively), generally include sections restricted to either South or North America. For example, the species most closely related to *Merremia tuberosa* are endemic to Mexico and Central America (McDonald, 1987a), while the weedy *M. aturensis* is likely the sole northern migrant of a group whose origin is in South America (e.g., sect. *Halliera* O'Donell; O'Donell, 1941).

The tremendous size and diversity of New World *Ipomoea* (ca. 300 spp.) provide the largest source of information concerning the origin of morning glory diversity in Mexico. Of the major subgeneric and sectional groupings of *Ipomoea* in Mexico, few share more than a few representatives in South America (and vice versa). Over 80% of the *Ipomoea* sections and series present in Mexico are either endemic to the country, or at least of Mexican origin. Examples of these include sections *Arborescentes, Calonyction, Exogonium, Quamoclit, Microsepalae, Setosae, Tyrianthinae* and series *Ipomoea,* and *Heterophyllae* (see Appendix). Only about 15% of the 144 native *Ipomoea,* species native to Mexico extend into South

America. About half of these members are tropical, autogamous weeds, and probably represent recent migrants from Mexico that extended through Central America into South America within the last 5.7 MA.

Two groups have likely extended into Mexico from South America: series *Anisomeres* and the Microsticta group (sensu McPherson, 1979). These groups account for only about 4% of the Mexican *Ipomoea* species. A portion of the species in the "Species Inquirendae" group (Appendix) may also be of South American origin, but these too comprise a modest number of taxa. The series *Mirandinae* represents the only group with a Caribbean center of diversity. All five species recognized in Mexico are endemic and closely related to the approximately 20 species of the West Indies (Austin, 1977; House, 1908). Interestingly, two groups of *Ipomoea*, series *Ipomoea* and *Heterophyllae*, have only a few weedy species in South America, but are well represented by distinct species in tropical East Africa and Mexico. The only group of obscure origin, whether from the New or from the Old World, comprises the ocean-dispersed members of *Ipomoea*, section *Erpipomoea* (e.g., *I. imperata*, *I. pres-caprae*, *I. violacea*).

Given the tropical affinities of the Convolvulaceae, it is not surprising that the temperate regions to the north of Mexico have had little influence on Mexico's morning glory flora. With the exception of a few Californian endemics that barely extend across the northern border of Baja California Norte, only two species of *Convolvulus* and one of *Calystegia* range into Mexico. These two genera have evolved moderate species numbers in the United States (ca. 10 and 20, respectively). *Stylisma* (perhaps best considered a section of *Bonamia*), an endemic element of the southeastern United States coastal plains, is wholly absent from Mexico. Only about three of the 34 *Ipomoea* species present in the United States are absent from Mexico, and these United States endemics clearly pertain to groups of Mexican origin.

Species Endemism. In general, two floristically unique centers of diversity for the Convolvulaceae are found in Mexico; one is in the tropical, seasonally arid regions of southwestern Mexico, the other is along the humid, coastal plain of eastern Mexico (Fig. 1). Species that occur in the eastern center tend to be widespread in distribution, often extending into Central America. In contrast, most of those that occur in the western center are autochthonous to the Sierra Madre Occidental and vicinity. Of the 217 species that occur in Mexico, about 83 are restricted within the country's political boundaries, accounting for only 38% of the morning glory flora. A significant number of these are *Ipomoea* (67 spp. = 46% of the genus). If Mexico is taken as a more natural biogeographic unit, however, including the regions of the Sonoran and Chihuahuan Deserts that stretch into the United States, and the tropical regions from the Sierra de Soconusco of Chiapas that extend as far as Nicaragua (e.g., MegaMexico III, sensu Rzedowski, in press), the percentage of endemism is substantially higher (130 spp. = 60%). This figure is slightly less than the estimated rate of endemism for the entire flora of MegaMexico III (i.e., 70%; Rzedowski, in press). Of the species endemic to MegaMexico III, 65 are narrow endemics (e.g., existing in two adjacent states or less), 46 of which are *Ipomoea*. Only two genera are 100% endemic (or nearly so) to MegaMexico III at the species level: *Bonamia* (6/7 spp.; 86%) and *Itzaea* (1/1 sp.; 100%). The
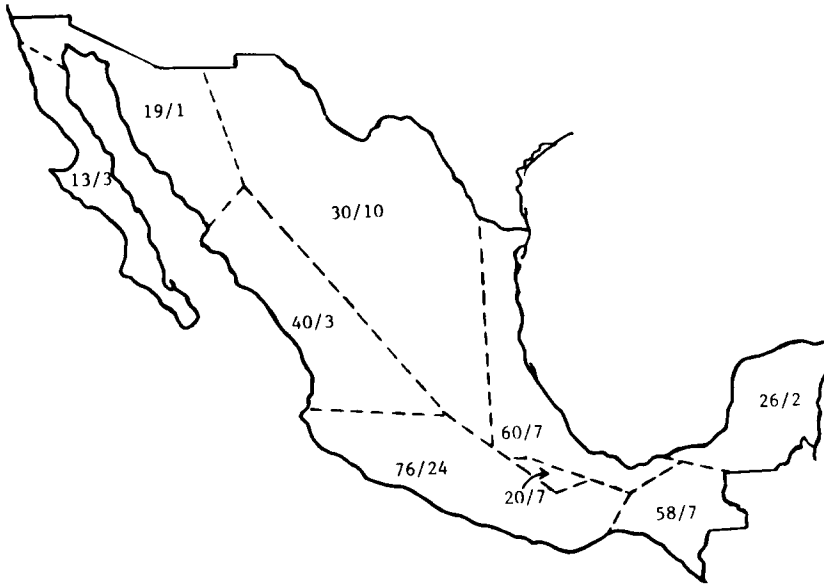
Fig. 1. Distribution of species richness for Mexican *Ipomoea*. The first number represents the number of *Ipomoea* species occurring in each region, the second gives the number of species endemic to the region. Note the center of species richness and endemism in southwestern Mexico.
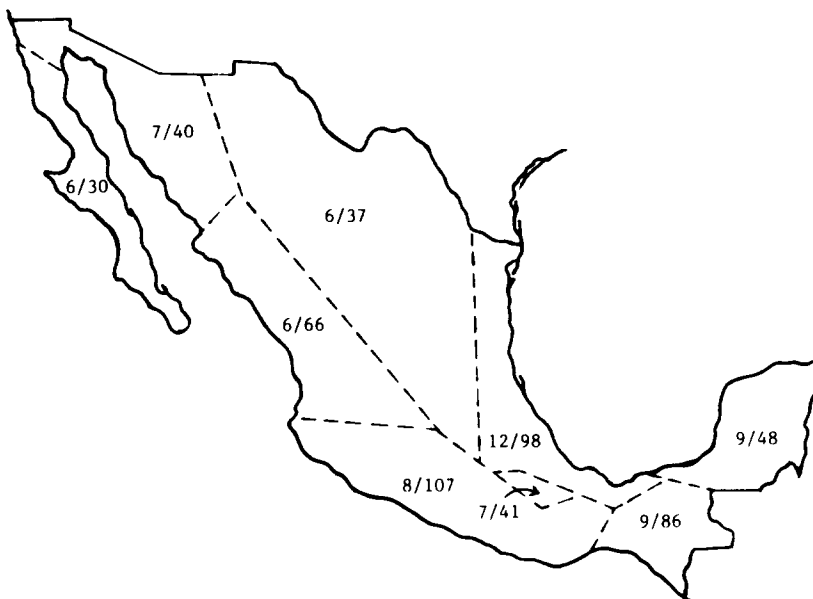

Fig. 2. Distribution of generic and species richness of Mexican Convolvulaceae. The first number represents the number of genera in each respective region, the second number represents the total number of species in all genera.

remainder of genera exhibit varying degress of endemism: *Evolvulus* (5/12; 41%), *Jacquemontia* (10/19; 52%), *Ipomoea* (104/160; 65%) and *Merremia* (4/12; 33%), etc. (Appendix).

The majority of endemic species in every genus but *Ipomoea* have arisen in arid regions. *Dichondra, Evolvulus, Bonamia* and *Jacquemontia* all have more xerophytic endemics than tropical endemics (Appendix). Not one of the above genera has evolved a mesophytic endemic. The split between tropical and xerophytic endemics is about equal in *Merremia* (see Appendix). *Ipomoea* stands out uniquely as a source of tropical endemics (ca. 42 spp.), which almost double in number the arid endemics (ca. 23 spp.). In keeping with the tropical nature of morning glories, very few *Ipomoea* species (e.g., *I. monticola, I. purga, I. signata*) are endemic to mesic enviroments. It is especially noteworthy that due to the proponderance of endemism in tropical-deciduous vegetation, fewer endemics of *Ipomoea* occur in the eastern side of Mexico than on the drier western side (Fig. 2). Only two *Ipomoea* are endemic to Veracruz and adjacent regions (*I. eximia* and *I. purga;* McDonald, unpubl. data), while at least 20 endemics are found in a region of equal area from Jalisco to Oaxaca (Fig. 2). A secondary source of endemism for *Ipomoea* is found in the arid, central plateau of the North (Fig. 2).

At the subgeneric level, many species complexes of *Ipomoea* can be generally characterized by habitat preference. The series *Tyrianthinae* is best represented in the altiplano grasslands and deserts of central and northern Mexico. Most of the endemic elements of section *Quamoclit* occupy mesic-tropical habitats, while the series *Mirandinae, Arborescentes* and the Microsticta complex (Appendix) have proliferated in tropical, seasonally arid regions. The series *Pedatisectae* includes a subgroup of endemics in the northern deserts, and another subgroup that has radiated in the tropical deciduous vegetation of southwestern Mexico. Section *Exogonium* is a relatively more versatile group, with endemics from arid regions, tropical deciduous forests, tropical mesic forests and temperate forests (see Appendix).

In comparison to other countries, the high degree of endemism in the Convolvulaceae of Mexico is extraordinary. The United States has only a few endemic species of *Ipomoea,* a handful of *Stylisma* species, and around 20 endemic species of *Calystegia* or *Convolvulus.* Species endemics total less than 30 in the United States, a very low count in absolute numbers when compared to that for Mexico. This difference may be explained, in part, by the general tropical affinity of the Convolvulaceae. However, even less endemism is found in Central American countries. The floras of Nicaragua and Panama include no endemic morning glories, even though they are rich in Convolvulaceae (15 genera/78 species and 13 genera/58 species, respectively). Costa Rica has only a couple of endemic *Ipomoea* (pers. obs.), as does Guatemala (Standley and Williams, 1970). Thus, even when Central America is taken as a whole, there are no more than four endemic species from Guatemala to Panama. This I would presume is attributable to the relatively continuous corridors of humid climates across Central America, allowing for easy migration and widespread distribution of weedy, tropical morning glory species. Mexico's geographic antiquity, expansive and dissected terrain (Ferrusquía-Villafranca, in press), under the influence of climatic vacillations and

associated cycles of aridity (Rzedowski, 1973; in press; Toledo, 1982), apparently account for the country's high rates of morning glory endemism.

Morphological Diversity. In addition to species numbers, the biodiversity of a given region is also reflected in the variety of life forms found within its boundaries, as another crude reflection of its genetic heterogeneity. Thus, while the Convolvulaceae may not rank with the ten most species-rich families in Mexico (Rzedowski, in press), they equal or exceed most families in their wide scope of habitat preferences, growth habits, and general morphology.

Interestingly, the majority of morning glory genera in Mexico do not exhibit any extraordinary breadth in morphological variation. Most genera are characterized as herbaceous or lignescent, prostrate, trailing or twining vines. They generally have simple leaves, some of which are variably lobed, and only one native group, *Merremia,* includes species with palmately compound leaves. Their flowers are generally adapted for insect (usually bee) pollination, and their fruits vary little in regard to dispersal mechanisms (compare, for example, the wide variety of seed dispersal syndromes in fruits of the Cucurbitaceae, an ecological associate). Nevertheless, morphological diversification has run rampant in *Ipomoea,* a highly advanced group comprising about 145 species in Mexico. The many and varied elements of this genus exhibit extreme environmental versatility and a wide spectrum of morphological specializations.

Several xerophytic *Ipomoea (I. costellata, I. madrensis)* exist as herbaceous, annual or perennial hemicryptophytes, producing short, prostrate stems that in a dry year will flower and fruit just with a few nodes of growth. The large majority of *Ipomoea* are robust vines, with twining stems reaching from 1-5 m, while a few tropical lianas reach as high as 15 m *(I. phillomega, I. santillanii).* Several species of *Ipomoea* section *Erpipomoea (I. imperata, I. pes-caprae)* grow to equal lengths, but they have lost their twining habit, exhibiting a prostrate habit that forms dense cover over coastal sands. Other *Ipomoea* of deserts *(I. stans)* or grasslands *(I. sescossiana, I. durangensis)* are self-supporting, perennial, cespitose, suffrutescent shrubs that grow to 1 m in height. *Ipomoea carnea* subsp. *fistulosa* exists as a tropical, woody shrub growing from 2-4 m, and most species of *Ipomoea* series *Arborescentes* grow into soft-wooded trees from 3-9 m, occasionally dominating tropical deciduous forests of southwestern Mexico. Several species of the arborescent complex betray their vining ancestry by exhibiting circumnutation in young stems (e.g., *I. arborescens, I. pauciflora*).

A wide variety of leaf types is also represented in *Ipomoea.* The most common leaf shape is cordiform, being generally associated with the common, vining growth habit. Several xerophytes have independently derived highly dissected leaves, which are pinnatifid in the series *Tyrianthinae (I. sescossiana, I. ancisa)* and palmatifid in the series *Pedatisectae (I. capillacea, I. chamelana).* Arborescent *Ipomoea* generally produce leaves typical of tall trees: elliptical, apically attenuate, and lacking cordate leaf bases. The palmately compound leaf condition found so commonly in the genus *Merremia* and occasionally in some Old World *Ipomoea* is lacking in New World *Ipomoea.*

The reproductive biology of Mexican *Ipomoea* is also considerably varied. Based on field experience and cultivated greenhouse specimens (totalling ca. 90

taxa), only about 25 of the 144 species of *Ipomoea* are autogamous. Allogamy, the more prevalent breeding system, is maintained in two distinct ways: herkogamy (heteromorphic stamens that do not reach up to the stigma) and self-incompatibility (Bullock *et al.*, 1987; Devall and Thien, 1989; Martin, 1970). Either or both of these reproductive barriers may be functional, as some herkogamous species occasionally produce reduced seed set when artificially selfed (pers. obs.). In association with out-breeding systems, most *Ipomoea* have well-developed floral features that attract a myriad of pollinators.

The majority of *Ipomoea* are pollinated by a variety of bees, such as *Ancylocelis, Ceratina, Melitoma, Ptilothrix,* among others (McDonald, 1982; Schlising, 1970). They attract their pollinators with diurnal, blue, purple, lavender or yellow, infundibular corollas. Bees generally exploit the nectar rewards presented by a glandular disc at the base of the ovary, and collect the characteristically large morning glory pollen grains (50-120 µm in diam.). Hummingbird pollination syndromes have evolved convergently from this presumably primitive pollination mode in such groups as section *Quamoclit,* series *Exogonium* and *Mirandinae* (Austin, 1977; McDonald, 1987b). Species of these complexes present red, salverform corollas with exserted stamens and styles, and secrete large quantities of nectar. Their independent derivations are not only evident by the fact that each of these groups shares close relationships with a melittophilous sister group, but they also exhibit floral features that suggest independent origins. The stamens of species in series *Exogonium,* for example, are found fused to the length of the corolla tube, suggesting that the narrow corolla tubes elongated by extending at the base of the corolla where the stamens are adnate to the corolla. In contrast, the subgenus *Quamoclit* presents free stamens, suggesting that the corolla tubes elongated somewhere along the middle of the tube, free from the basal point of adnation between corolla and stamens. This and other cases of convergence in pollinations modes can be observed in the genus. The hawk-moth pollination syndrome, for example, associated with white, nocturnal, often aromatic, salverform corollas, and exserted stamens and styles, is observed in the distantly related *I. alba* (series *Caloncyction*), *I, igualensis* (series *Involucratae*), *I. zimmermanii* (series *Jalapae*) and *I. tenuiloba* (series *Pedatisectae*).

Bats are not common as pollinators in *Ipomoea,* but they are apparently dependent on the genus in southwestern Mexico during the annual dry season (Álvarez and González, 1970). *Ipomoea murucoides* is probably the main food source of bats, as this species exhibits the typical syndrome of floral features associated with chiropterophily: flowers white, leathery, nocturnal (also diurnal in this species), tube wide, the base of the tube forming a thimble-sized well for copious nectar secretions. *Ipomoea murucoides* is also legitimately visited by beetles and bees during the day (pers. obs).

Although beetles are generally associated with polypetalous flowers that provide a large landing platform for these clumsy pollinators (Faegri and van der Pijl, 1971), they apear to be specialized to exploit nectar sources of *Ipomoea* section *Tricolor* (McDonald, 1982) and series *Tyrianthinae.* Flowers of *I. tricolor, I. stans* and *I. orizabensis* are usually occupied by hairy, pollen-laden scarab beetles of the genus *Euphoria* (pers. obs.). Beetles are absent from all other *Ipomoea* that I

have observed over the years, except for occasional visitations on the aforementio-
ned group of arborescent *Ipomoea,* which are visited by unique species of scarabs
(pers. obs.). In addition to the uncommon specializations for coleopterophily, *Ipo-
moea* also attract butterflies (*I. quamoclit;* pers. obs.) and long-tongued flies (*I.
expansa, I. microsepala:* McDonald, 1982).

The activity of nectar robbers has also played an important role in the evolu-
tion of morning glory flower parts, as many *Ipomoea* have evolved a number of
morphological features that protect their corolla tubes from nectar parasites. The
fragile construction of morning glory flowers makes them particulary susceptible
to nectar robbing carpenter bees *(Xylocopa),* which cling to sepals and perforate
the base of the corolla tubes with mouth parts to extract nectar (Keeler, 1977; pers.
obs.). As an adaptation to insure the presence of a nectar reward for legitimate
pollinators, some morning glories produce long, thick, impenetrable sepals that
protect the nectar gland at the base of the ovary *(I. clavata, I. ampullacea).* Another
group produces long fleshy setae on their sepals to impede the xylocopas from
landing near the corolla tube *(I. crinicalyx, I. silvicola). Ipomoea mairetii* and *I.
igualensis* produce large, bracteate, capitate inflorescences that make the corolla
tubes inaccessible. Many species provide aggressive and protective wasps and
ants with extrafloral nectaries on the sepals (*I. carnea;* Keeler and Kaul, 1984;
Keeler, 1977), while yet other species protect their nectar by enveloping the corolla
tubes with large bracts *(I. bracteata, I. suffulta)* or leaves *(I. seducta).* The interesting
dynamics of these parasite-host relationships have yet to be investigated adequa-
tely.

Seed dispersal syndromes are not nearly so varied as pollination syndromes.
A few species have apparently accomplished long-distance dispersal, including *I.
dumetorum* (ser. *Exogonium*), *I. pubescens* (ser. *Heterophyllae*), and *I. plummerae*
(ser. *Pedatisectae*). These species are weedy xerophytes with amphitropical dis-
junct distributions between the deserts of Argentina and northern Mexico. They
produce small (3-4 mm diam.), dark, hard-coated seeds that possibly reached
South America by means of endozoic bird dispersal (McDonald, 1984), given the
unlikelihood of a continuous, xeric habitat across Central America during the last
few million years (Raven, 1963). Nevertheless, species with this distribution
pattern account for less than 2% of the *Ipomoea* of Mexico and South America. A
second possible means of dispersal in *Ipomoea* is by water. The pantropical
distribution of the littoral-maritime species, *I. imperata, I. pes-caprae* and *I. viola-
cea,* is due in part to their hairy, long-lived, buoyant seeds adapted for sea drift
(Gunn, 1976; Guppy, 1917). This relatively uncommon means of dispersal is also
found in distantly related lineages of other Convolvulaceae associated with ripa-
rian habitats. The light, air-filled, indeshiscent fruits of *Bonamia sulphurea, Ipo-
moea corymbosa* (=*Turbina corymbosa* (L.) Raf., *pro syn.*) and *Merremia discoides-
perma,* generally float for many days, as do their seeds. Their fruits abort 3 of the
original 4 ovules, presumably as an adaptation to lighten the fruit's load. Despite
the capacity for long-term flotation, none of the above three species has become
established on distant continents.

ACKNOWLEDGEMENTS

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APPENDIX

Native morning glory species of Mexico are listed with their known distributions. Genera are organized by tribes, beginning with primitive tribes and ending with the more advanced. *Ipomoea,* due to its large size, is further broken into tentative species groups, based on my present interpretations. Generic names are followed by numbers included in parentheses. The first number notes the number of species present in Mexico, the second records the approximate number of species in the genus. The continental distributions of each genus follows. Distributional aspects and habitat preference of each species is given, using the following key:

M-Distribution endemic to MegaMexico III (sensu Rzedowski, 1990); *—Distribution within the political boundaries of Mexico; !—Narrow endemic (found in two states or less); x—Xerophytic; t—Tropical; m—Mesophytic.

DICHONDREAE

Dichondra Forst. & Forts. (6/13) Mexico, South America, New Zealand, Australia

D. argentea H.B.K.	x
D. brachypoda Wooton & Standley	Mx
D. micrantha Urban	x
D. nivea (Brand.) Tharp & Johnston	*!x
D. occidentalis House	!Mx
D. sericea SW.	t

EVOLVULEAE

Evolvulus L. (12/100) South America, Mexico, Antilles, Central America

E. alsinoides L.	t
E. cardiophyllus Schlecht.	t
E. choapanus McDonald	*!t
E. glaber Spreng.	t
E. hallieri V. Ooststr.	*!t
E. nummularius L.	t
E. ovatus Fernald	t
E. pohlii Meissn.	t
E. prostratus Robins.	*t
E. purpusii v. Ooststr.	*!t
E. rotundifolius (s. Watson) Hall.f.	*!t
E. sericeus Sw.	t

CRESSEAE

Bonamia Petit-Thouars (7/45) South America , Africa, Australia, Madagascar

B. elliptica (Smith & Schub.) Myint & Ward	*!t
B. mexicana McDonald	*!t
B. multicaulis (Brandg.) House	Mx
B. ovalifolia (Torr.) Hall. f.	*!x
B. repens (I. M. Johnston) Aust. & Stap.	M!x
B. sulphurea (Brandg.) Myint & Ward	t
B. sp. nov. McDonald (in prep.)	*!t

Calycobolus (1/25) Africa, South America, Mexico

C. nutans (Mart. & Gal.) Austin	*!t

Cressa L. (2/5) North America, South America, Asia, Africa, Australia

C. truxillensis H.B.K.	x
C. nudicaulis Griseb.	x

Itzaea Standl. & Steyerm. (1/1) México, Central America

I. sericea (Standl.) Standl. & Steyerm.	Mt

ERYCIBEAE

Maripa Aublet (1/19) South America, Central, America, México.

M. nicaraguensis Hemsl.	t

CONVOLVULEAE

Aniseia Choisy (2/5) South America, Central America, Mexico, Asia

A. martinicensis (Jacq. Choisy	t
A. minor (Choisy) McDonald (in prep.)	t

Calystegia R. Br. (2/25) North America, Europe

C. *macrostegia* (Greene) Brummitt	Mx
C. *sp.*	m

Convolvulus L. (4/200) Europe, North America, Asia, South America, Australia, Africa

C. *arvensis* L.	m
C. *equitans* Benth.	m
C. *simulans* L. Perry	M!x
C. *soldanella* L.	m

Jacquemontia Choisy (17/100) South America, Mexico

J. *abutiloides* Benth.	*!x
J. *albida* Wigg. & Roll.	*!x
J. *agrestis* (Choisy) Meissn.	t
J. *ciliata* Sandwich	t
J. *eastwoodiana* I. M. Johnston	*!x
J. *havanensis* Urb.	t
J. *mexicana* (Loes.) Standl.	Mt
J. *nelsonii* House	*t
J. *nodiflora* (Desr.) G. Don	t
J. *oaxacana* (Meissn.) Hall. f.	*t
J. *ovalifolia* (Vahl ex West) Hall. f.	t
J. *palmeri* S. Wats.	Mx
J. *pentantha* (Jacq.) G. Don	t
J. *polyantha* (Schlecht. & Cham.) Hall. f.	*tm
J. *pringlei* A. Gray	Mx
J. *pycnocephala* Benth.	*!x
J. *smithii* Rob. & Greenm.	*!x
J. *sphaerostigma* (Cav.) Rusby	t
J. *tamnifolia* (L.) Griseb.	t
J. *verticillata* (L.) Urban	t

Odonellia (Mart. & Gal.) Roberston (1/2) North America, South America

O. *hirtiflora* (Mart. & Gal.) Roberston	t

MERREMIEAE

Operculina S. Manso (2/20) Asia, Africa, South America, Mexico

O. *pinnatifida* (H.B.K.) O'Donell	t
O. *pteripes* (G. Don) O'Donell	t

Merremia Dennst. (12/80) Asia, South America, Mexico, Africa

M. *aegyptia* (L). Urban	t
M. *aturensis* (H.B.K.) Hall. f.	t
M. *aurea* (Kellogg) O'Donell	*!x
M. *austinii* McDonald	*!t
M. *cissoides* (Lam. Hall. f.	t
M. *discoidesperma* (Donn.-Sm.) O'Donell	!Mt
M. *dissecta* (Jacq.) Hall f.	t
M. *palmeri* Hall. f.	*!x
M. *platyphylla* (Fern.) O'Donell	*t
M. *quinquefolia* (L.) Hall. f.	t
M. *tuberosa* (L.) Rendle	t
M. *umbellata* (L.) Hall. f.	t

IPOMOEEAE
   Ipomoea L. (141/500) Mexico, South America, Africa, Southeast Asia, Australia
Subgenus *Eriospermum* (H. Hallier) Verdcourt
  Section *Eriospermum* H. Hallier
    Series *Anisomeres* (House) Austin

I. lindenii Mart. & Gal.	t
I. squamosa Choisy	t
I. wallii (Morren.) Hemsl.	t

    Series *Arborescentes* (Choisy) Austin (10/10)

I. arborescens (H.B.K.) G. Don	*xt
I. chilopsidis Standl.	*!xt
I. cuernavacensis House	*!xt
I. intrapilosa Rose	*t
I. murucoides Roem. & Schult.	*t
I. pauciflora Mart. & Gal.	*t
I. populina House	*t
I. praecana House	Mt
I. teotitlanica McPherson	*!x
I. wolcottiana Rose	tx

    Series *Bombycospermum* (Presl) Austin 2/2)

I. bombycina (Choisy) Benth.	*!t
I. sp. nov. McDonald (in prep.)	*!x

    Series *Jalapae* (House) Austin (8/10)

I. amnicola Morong	x
I. jalapa (L.) Pursh	t
I. leonensis Robinson	*!x
I. rupicola House	*x
I. sagittata Lam.	t
I. scopulorum Brandg.	*!x
I. zimmermanii McDonald	*!x
I. sp. nov. McDonald (in prep.)	*!x

    Microsticta complex (fide McPherson, 1979)

I. auratiaca L. Wms.	M!xt
I. batatoides Choisy	t
I. heterodoxa Standl. & Steyerm.	Mt
I. lottiae Mcdonald	*!t
I. microsticta Hall. f.	t
I. proximum Mart. & Gal.	*t
I. pseudoracemosa McPherson	*!tx
I. reticulata O'Donell	t
I. robinsonii House	*!t
I. suaveolens (Mart. & Gal.) Hemsl.	Mt
I. sp. nov. McDonald (in prep.)	Mt

    Series *Mirandinae* Austin (6/26)

I. concolor (Matuda) D. Austin	*!tx
I. conzattii Greenm.	*!x
I. crocea McPherson (nom. nov. ined.)	*xt
I. steerei (Standl.) L. Wms.	Mt
I. tuxtlensis House	t
I. sp. nov. McDonald (in prep.)	*!t

    Series *Setosae* (House) Austin (6/6)

I. crinicalyx Moore	t
I. pedicellaris Benth.	Mt
I. sepacuitensis Donn.—Sm.	Mt
I. setosa Ker	t

I. silvicola House	Mt
I. tentaculifera Greenm.	*!x

Section *Erpipomoea* Choisy (4/5)

I. asarifolia (Desr.) Roem. & Schult.	t
I. imperata (Vahl) Griseb.	t
I. pres-caprae (L.) Sweet	t
I. violacea L.	t

Subgenus *Ipomoea*
  Section *Ipomoea*
    Series *Ipomoea*

I. ampullacea Fernald	*t
I. igualensis Weatherby	*!t
I. laeta A. Gray	*!t
I. mairetii Choisy	Mt
I. villifera House	Mt

Section *Pharbitis* (Choisy) Griseb.
  Series *Pharbitis* (House) Austin

I. barbatisepala A. Gray	Mt
I. decasperma Hall. f.	x
I. purpurea (L.) Roth	mt

Series Heterophyllae (House) Austin

I. hallieri I. M. Johnston	*!x
I. indica (Burm.) Merr.	t
I. lindheimeri A. Gray	Mt
I. nil (L.) Roth	t
I. pubescens Lam.	x

Series *Tyrianthinae* (House) Austin (9/9)

I. ancisa House	*!x
I. durangensis House	*!x
I. hartwegii Benth.	*t
I. jacalana Matuda	*!t
I. lenis House	*x
I. orizabensis (Pell.) Led. ex Steudl.	Mm
I. petrophila House	*!x
I. sescossiana Baillon	*x
I. stans Cav.	*x

Subgenus *Quamoclit* (Moench) Clark
  Section *Batatas* (Choisy) Griseb. (8/11)

I. batatas (L.) Lam.	t
I. cordatotriloba Dennstedt	m
I. ramosissimma Choisy	t
I. tabascana McDonald & Austin	*!t
I. tiliacea (Willd.) Choisy	t
I. trifida (H.B.K.) G. Don	t
I. triloba L.	tx
I. umbraticola House	t

Section *Calonyction* (Choisy) Griseb. (3/4)

I. alba L.	t
I. muricata (L.) Jacq.	t
I. santillanii O'Donell	Mt

Section **Exogonium** (Choisy) Griseb. (20/20)

I. bracteata Cav.	*t
I. dumetorum Willd. ex Roem. & Schult.	m

I. dumosa (Benth.) L. Wms.	t
I. elongata Choisy	Mxm
I. eximia House	*!t
I. expansa Mc Donald	*t
I. ignava House	*!xtm
I. jicama Brandg.	*!xt
I. mcvaughii McPherson	*!t
I. monticola McDonald	*!m
I. noctulifolia McPherson	*!t
I. puncticulata Benth.	*t
I. purga (Wender.)	*!m
I. schaffneri Watson	*!x
I. seducta House	Mt
I. signata House	Mm
I. simulans Hanbury	*t
I. suffulta (H.B.K.) G. Don	Mt
I. tastensis Brandg.	*!xt
I. urbinei House	*!t

Section *Microsepalae* (House) McDonald (stat. nov. in prep.) (2/2)

I. microsepala Benth.	Mt
I. minutiflora (Mart. & Gal.) House	t

Section *Pedatisectae* (House) McDonald (stat. nov. in prep.) (8/8)

I. capillacea (H.B.K.) G. Don	x
I. chamelana McDonald	*!t
I. costellata Torr.	Mx
I. madrensis Watson	*x
I. plummerae A. Gray	Mtx
I. perpartita McPherson	*!t
I. tenuiloba Torr.	Mx
I. ternifolia Cav.	t

Section *Quamoclit* Moench (12/15)

I. cholulensis H.B.K.	m
I. cristulata Hall. F.	Mx
I. decemcornuta O'Donell	*!t
I. funis Schlecht. & Cham.	*mt
I. hastigera H.B.K.	*t
I. hederifolia L.	t
I. lobata (Cerv.) Thellung	*t
I. lutea Hemsl.	Mt
I. neei (Spr.) O'Donell	t
I. quamoclit L.	t
I. sp. nov. McDonald (in prep.)	*!t
I. nom. nov. McDonald (in prep.)	*!m

Section *Tricolor* McDonald (in prep.) (4/4)

I. cardiophylla A. Gray	Mx
I. oocarpa Benth.	t
I. parasitica (H.B.K.) G. Don	t
I. tricolor Cav.	t

Species Inquirendae

I. carnea Jac.	t
I. ciervensis Painter	*!x
I. clavata (G. Don) V. Ooststr. & McBr.	t
I. corymbosa (L.) Roth	t
I. fimbriosepala Choisy	t
I. gentryi Standl.	*!t

I. invicta House   *!t
I. kruseana Matuda   *!t
I. lambii Fernald   *!t
I. lozanii Painter   *!t
I. meyeri (Spr.) G. Don   t
I. phillomega (Vell.) House   t
I. pruinosa McPherson   *!t
I. rhomboidea House   *!t
I. variabilis Schlecht. & Cham.   Mt
I. sp. nov. McDonald (in prep).   *!