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HOST-PLANT COEVOLUTION AND THE DIVERSITY OF BEES IN RELATION TO THE FLORA OF NORTH AMERICA

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That California supports an extremely high level of species diversity of bees (ca. 1500) was preliminarily documented in Moldenke & Neff (1974) and referred to subsequently in Moldenke (1976). This extraordinarily high number of resident bee species is however somewhat misleading, since the political boundaries of the state artificially encompass a wide spectrum of biotic realms and climatic patterns. This paper is an attempt to examine the levels of bee species richness throughout North America in order to demonstrate more appropriately respective levels of bee diversity in light of species/area relations, paleohistorical lineages and the role of specialized-feeding habits -- all so important in a basic understanding of the pollination ecology of any region.

The subject matter of this paper entails more directly an interest on my part, than the suitability/maturity of the data base for analysis. Judgments I make in this paper on the basis of the published literature and museum specimens are likely at times to be subsequently proven incorrect. In very general terms, two of the largest and most diverse bee genera in North America are only partially taxonomically revised at this time (e.g., Andrena, Osmia), and two other genera (e.g., Dialictus, Evylaeus) are awaiting revision. Dr. Eickwort however, has been revising Dialictus for the past several years and has been gracious enough to provide me at times with preliminary data. Though the host-plant associations of bees within the state of California are "relatively" well known, a large majority await the type of documentation and study necessary for absolute assurance; the bees of other regions (particularly the

Information included in this report is largely the result of several requests for information from students working on disparate questions in different parts of the U.S.A.; in providing them with this information in order to assist them to generalize their conclusions, I felt that much of this essentially raw data should be presented publicly so that other workers could have access to it, in the ultimate hope that additional data could be generated along this aspect of inquiry to supplement the information presently available to me. It is in this spirit, that this preliminary information is presented.

eastern U.S.) are much more poorly understood in terms of host-associations.

Nevertheless, judging from my own collections and those of my associates as well as a large published data base of floral collection records, and placing much weight upon the conservative nature of such host-association patterns (in lieu of specific evidence to the contrary, and oftentimes meager specifically relevant floral association data) -- I feel relatively confident that the major conclusions presented in this paper will, upon subsequent documentation, prove to be essentially correct. Many new species of bees are still awaiting collection in the United States, and many distributional patterns are very incompletely known, however, I expect that thanks in part to the compendia published by Mousebeck et al (1951) and Mitchell (1960, 1962)(which I have subsequently amended in light of more recent monographic treatments) faunistic species totals will not vary by more than 5-10%. This level of inaccuracy will not affect the major conclusions. Since this paper involves such a preliminary analysis of pollination systems, data is presented in a form which will facilitate adjustments in numerical analysis in light of yet to be published research. Likewise, this paper is being presented in a primarily botanical journal in order to acquaint botanists with much of the information that is accessible to entomologists, but much less accessible to botanists interested in pollination ecology.

Utilizing twelve of the biotic units of North America recognized by Kuchler (1975) and Shelford (1963) reveals that the level of bee species richness only varies roughly three-fold (Table 1), excluding the climaticly extreme tundra and muskeg. The species totals for the Great Basin and the Southern Mixed Forest are low; reflecting both low actual total species diversity and relatively poorly collected/studied faunas. Though the bee faunas of these two regions will undoubtedly increase significantly upon subsequent study, I am confident they will still remain relatively the most impoverished.

The Chihuahuan and Sonoran deserts support nearly 900 known bee species. Species resident in the Mexican portions of this arid region have not been included since they remain largely uncollected, and those species which have been named remain poorly known. Therefore this total of 890 species is undoubtedly a very low estimate for the non-montane desert region as a whole.

	TOTAL BEE SPECIES	TOTAL SPECIALIST SPECIES	# PLANT GENERA WITH SPECIALIST BEES	# PLANT FAMILIES WITH SPECIALIST BEES
DESERT (D)	890	592	38	27
MEDITERRANEAN CALIF. (MdCf)	830	466	53	23
FORESTED CALIFORNIA (For.Cf)	600	252	38	22
ROCKY MOUNTAINS (RM)	500	90	20	22
GREAT PLAINS (GP)	500	184	28	19
BOREAL FOREST (BF)	450	77	19	14
OAK/HICKORY FOREST (OHF) / MIXED MESOPHYTIC FRST	450	106	28	23
PACIFIC NORTHWEST (PNW)	425	104	25	-
OAK/HICKORY/PINE FOREST (OHPF)	425	84	21	19
DESERT MOUNTAINS (DMt)	395	98	16	-
GREAT BASIN (GB)	333	165	27	20
SOUTHERN MIXED FOREST (SMF)	280	63	13	11
TUNDRA & MUSKEG (T)	84	13	6	5

TABLE 1. BEE SPECIES RICHNESS OF NORTH AMERICAN BIOTIC REALMS.

"Pacific Northwest" includes the mountain axis of southwestern Canada, Washington, Oregon and northernmost California; it does not include the Great Basin intermontane portions of this territory nor does it include the forested regions of the major mountain chains in California."Desert Mountains" includes montane and subalpine regions of Arizona and New Mexico.

The well-studied mediterranean climatic region of California contains approximately 830 species; this is a relatively robust estimate and does not include species which are primarily forested montane within California, only infrequently occurring in the regions of upper chaparral in the Sierra Nevada. The Rocky Mountain region and the Great Plains are next in abundance with approximately 500 resident species, followed by significantly lower levels within the three forested eastern provinces as well as the montane forested Pacific Northwest (Table 1).

Within the different geographic regions of California, likewise, there is only approximately a 3-fold difference in bee species richness. The southern more xeric regions are characterized by the highest levels of species richness, while the Great Basin, alpine, northern and immediate coastal regions are characterized by lower levels (Table 2). The total number of forested California bee species is approximately 600, well below the respective mediterranean and desert totals.

There is no particular correlation between the total bee species richness and the extent of the area occupied (Illus. 1). Regions of high bee diversity have in common an arid/semi-arid climate and relatively low canopy. However, the same features characterize the Great Basin and Great Plains, regions of distinctly less bee species. The number of bee species per 1,000 mi^2 varies from 0.5-3.0 for all regions (excluding the tundra) except for California, where forested montane California is characterized by approximately 12.0 and mediterranean California by 14.0 bee species. When the bee fauna for the entire eastern half of the United States (ca. 700, Meusebeck et al in Mitchell (1960)) is totalled, only approximately 0.5 bees per 1,000 mi^2 are encountered. Why the diversity of both forested montane and mediterranean California should be nearly ten times that of other regions of comparable altitudinal and climatic diversity is not known with certainty. On first examination, the crucial determinant would appear to be the mediterranean region, since a large percentage (theoretically difficult to estimate) of the forested bees in California are much more characteristic of the chaparral than the forest understory. The mediterranean climate regime is paleohistorically very novel, dating from only the past million years (Axelrod, 1966). The flora of California is also exceptionally diverse, both in terms of endemic relict species and rapidly evolving contemporary lineages; the former group is basically forest-associated while the latter is a feature of the

	TOTAL BEE SPECIES	TOTAL SPECIALIST SPECIES	# PLANT GENERA WITH SPECIALIST BEES
NO. GREAT BASIN (NGB)	213	118	17
GREAT BASIN (GB)	179	98	14
OWENS VALLEY (OV)	394	253	33
MOJAVE DESERT (MD)	456	271	33
COLORADO DESERT (CD)	482	299	35
TRINITY/SISKIYOU MTS. (T/S)	220	86	11
ALPINE SIERRA NEVADA (AS)	183	89	13
NORTHERN SIERRA NEVADA (NS)	398	170	28
SOUTHERN SIERRA NEVADA (SS)	516	219	38
MONTANE SOUTHERN CALIF. (MSC)	422	186	30
COASTAL DUNES & SAGE (C)	172	52	12
NO. COAST RANGES (NCR)	377	152	33
SO. COAST RANGES (SCR)	520	262	44
CISMONTANE SO. CALIF. (CSC)	555	253	47
NO. CENTRAL VALLEY (NCV)	238	108	29
SO. CENTRAL VALLEY (SCV)	282	161	36

TABLE 2. BEE SPECIES RICHNESS OF CALIFORNIA GEOGRAPHIC REALMS.

Data slightly corrected from that presented in Moldenke (1976b) in light of recent monographs and personal observations.

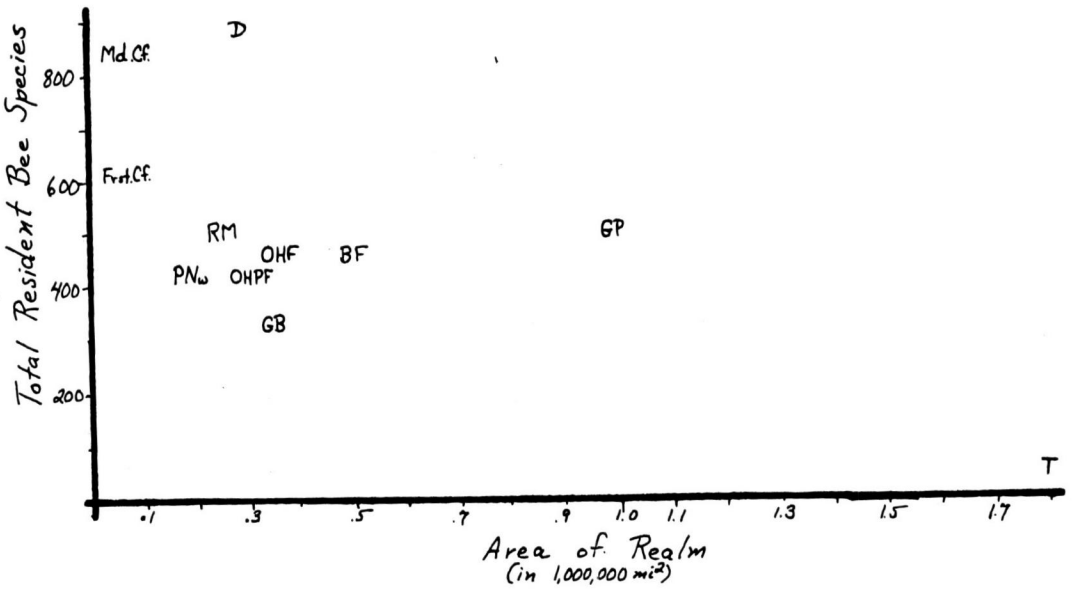

ILLUSTRATION 1

RELATIVE RICHNESS OF THE BIOTIC REGIONS OF NORTH AMERICA.
Abbreviations as in Table 1

arid ecosystems (Raven, 1977). The high proportion of forest floral endemics in California has been attributed to the relatively milder conditions during the Tertiary in California relative to more continental climates in North America. Perhaps a diverse assemblage of bee lineages also survived in the California forests under these conditions, and under the increasing aridity initiating in the Neogene have secondarily invaded the non-forested regions of the nascent mountain systems and rapidly speciated from this initially enriched stock.

. . .

Bee species with specialized feeding habits are frequent in all regions of the United States; so are species with established generalist feeding strategies. The vast majority of feeding strategies are not known with established certainty. Extrapolating from the habits of known close relatives (in the absence of conflicting data) does allow us to form general conclusions about the nature of food-choice preferences for the vast majority of species though. "Specialist-feeding" bee species should not be regarded as monoleges -- absolute specialization by a bee on only one species of plant host throughout its range is seldom, if ever, realized when the plant genus is not monotypic in the region concerned (e.g., Larrea) or the bee species very highly restricted in distribution. Specialist-feeding bees are usually restricted to the generic (or occasionally subgeneric) or closely-related generic group level (i.e., Potentilla, Ivesia, Chamaebatia & Horkelia). Some semi-specialists visit only a restricted subset of species of the families Compositae or Leguminosae. Specialists are usually faithful to the same "host-plant" throughout their range, though seldom have studies been undertaken to conclusively demonstrate this accepted working hypothesis.

For instance, Nomadopsis fracta visits the shrub Eriodictyon (Hydrophyllaceae) throughout its extensive range exclusively, except for regions of volcanic ash on Mount Shasta where it visits only the acaulescent Nama rothrockii (Hydrophyllaceae), Eriodictyon not being present (Moldenke, unpub. obs.)(one series bearing pollen and collected on Phacelia brachyloba (Hydrophyllaceae) in the San Bernardino Mountains exists in collections; and Rozen (1958) cites one possible instance on P. douglasii). Likewise, the very abundant Nomadopsis edwardsii is one of a sibling pair of species visiting Potentilla and closely related genera (Rosaceae) throughout extensive portions of the Pacific

Coast, however, at Mammoth Lakes, California, the population is morphologically dimorphic -- the larger individuals collecting the pollen and nectar of Calochortus (Liliaceae) apparently exclusively (Moldenke, unpub. obs.). I cite these examples from Nomadopsis, because the host-selections of most of these species have been clearly well-documented by Rozen (1958), and all the known species (except one) are clearly some of the most specialized bees known, but even in this group there are clearly some issues that need further study.

In the section that follows, I do not mean to imply that host-selection habits are fully known, or that when fully known there may not be many minor variations to the behavior noted, however, I confidently expect the general scheme I am presenting will not be grossly distorted. Poorly known groups clearly in need of subsequent study are indicated.

The series of phylogenies (Illustration 2) is presented in an oversimplified diagrammatic fashion to represent both the sequences of host shifts ("⟿") and the notable range extensions that have occurred in the evolution of North American bees. I recognize that the categories for range distribution are overgeneralized and perhaps overly simplistic in that they recognize basically only arid versus humid forest classes. At this stage of analysis, increasing the number of categories obscures the basic floristic relationships and patterns of plant associations. I have treated these categories somewhat liberally, for instance if a group is characterized by a basically arid western desert distribution, but does indeed inhabit a considerable portion of the southern prairies I have not noted that as a significant range expansion, but only have done so when such a distribution has clearly enlarged to include the eastern plains or the understory of the eastern forests. On the other hand, typical montane forested cool temperate species are noted in the xeric region only if they significantly inhabit xeric regions, rather than the isolated forested mountain tops throughout the western basins and deserts. Presumed paleogeographic lineages (based largely on the circular reasoning of present distributions) are basically unchanged from those presented in Moldenke (1976), and represent the published conclusions of taxonomic specialists or educated guesses on my part. Those of the Dufoureinae represent unpublished studies of Bohart, Lincoln and myself; these studies will be published in more detail subsequently.

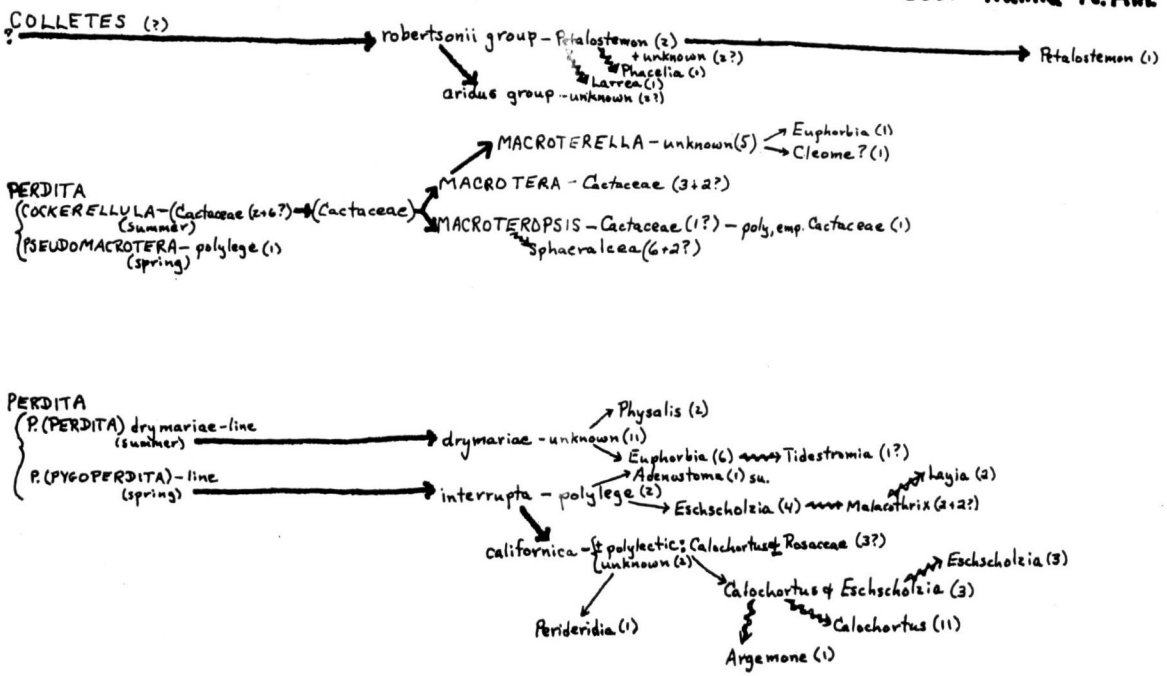

ILLUSTRATION 2 (and following)

~~~~ refers to host switches from one specialist to another.
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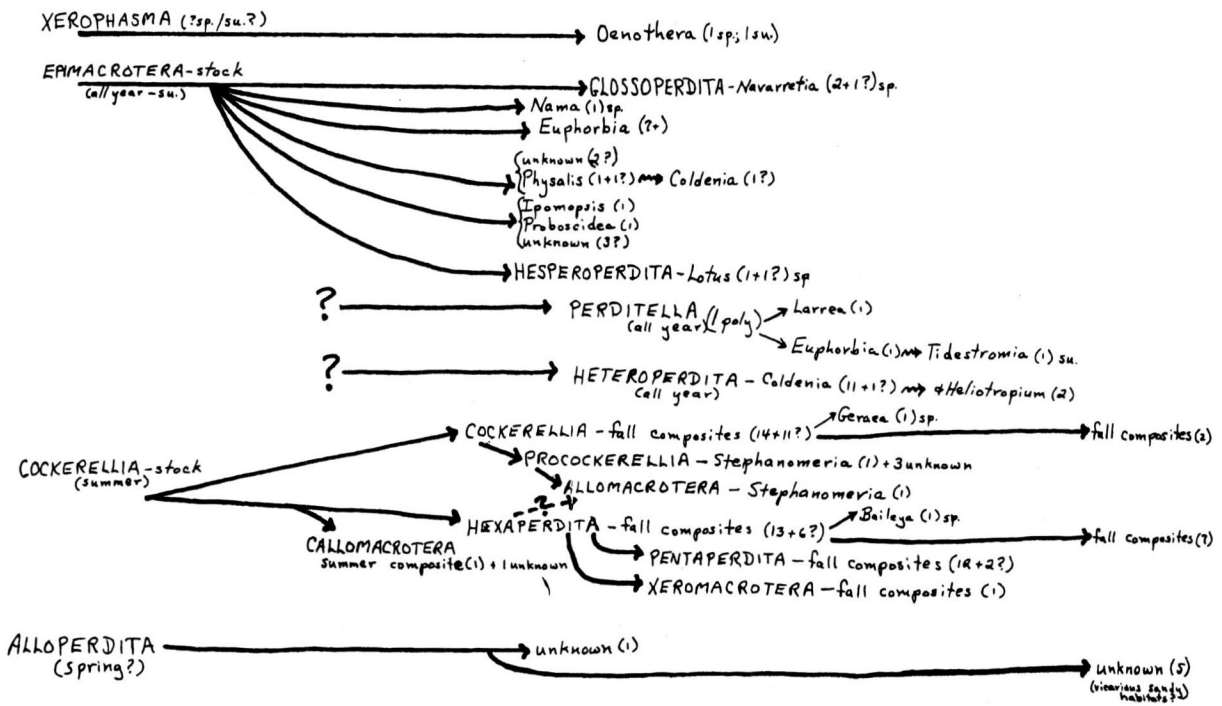
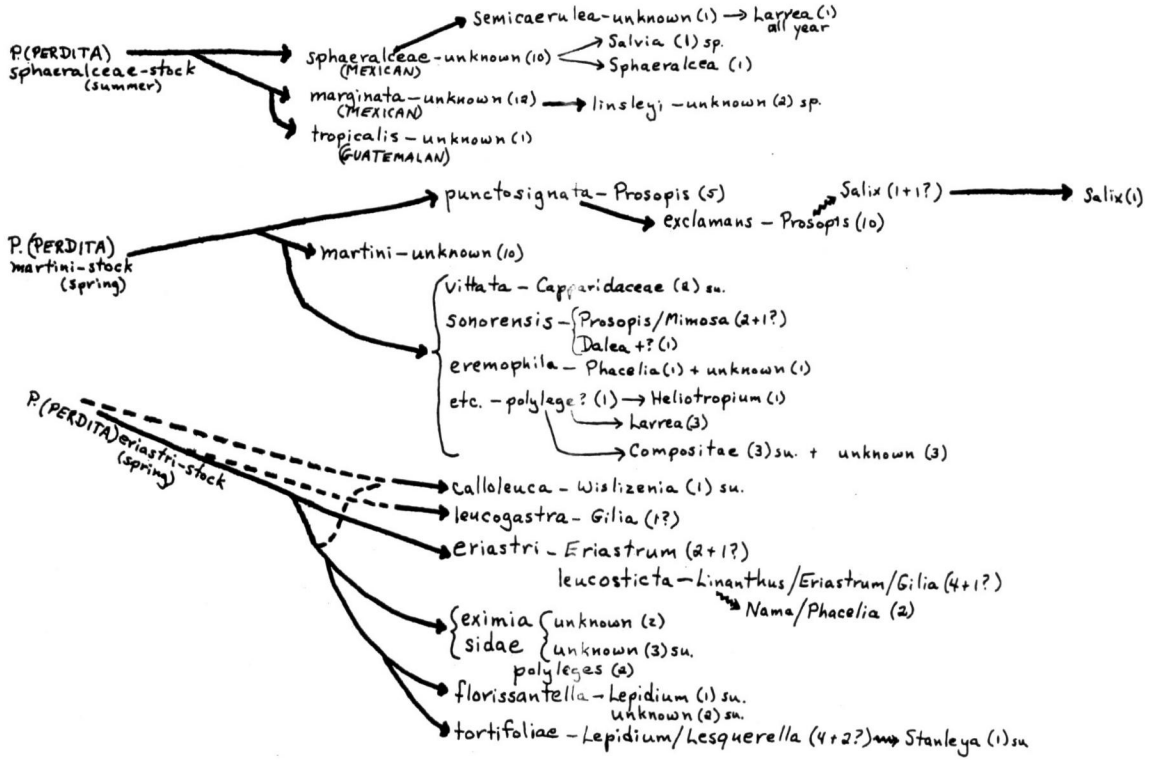
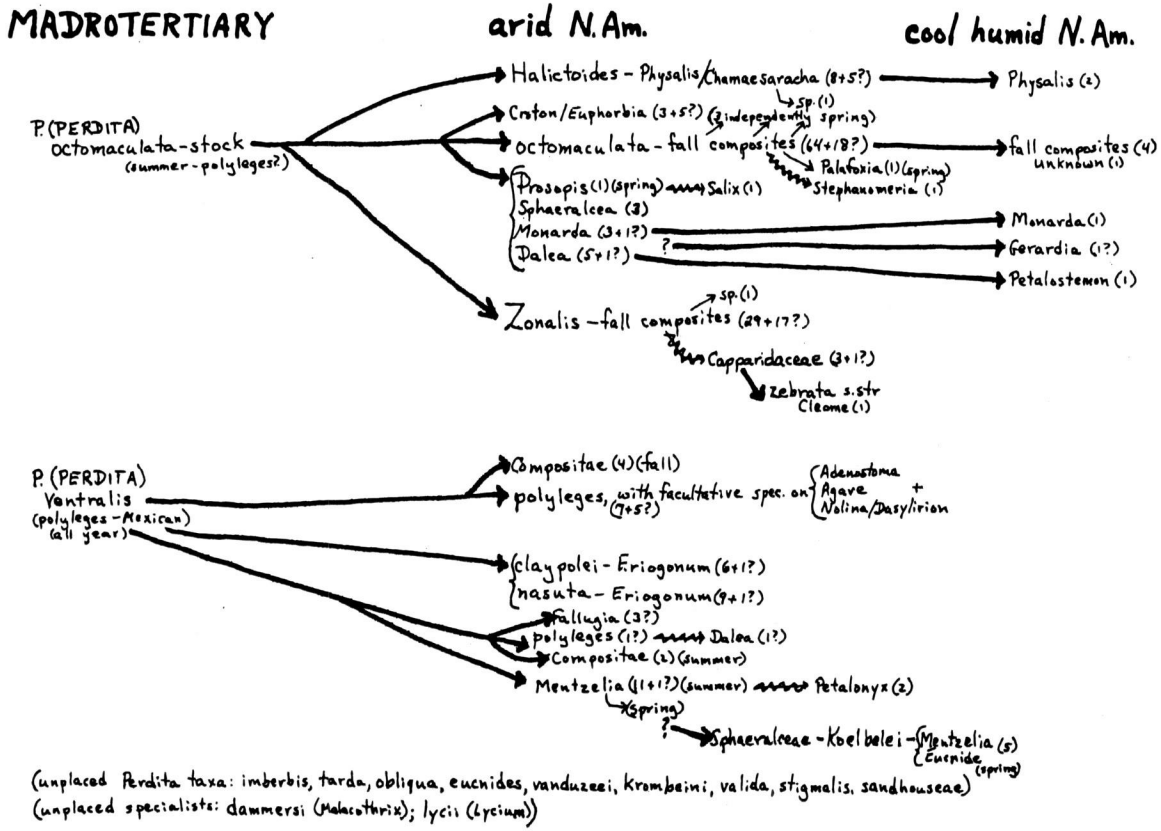
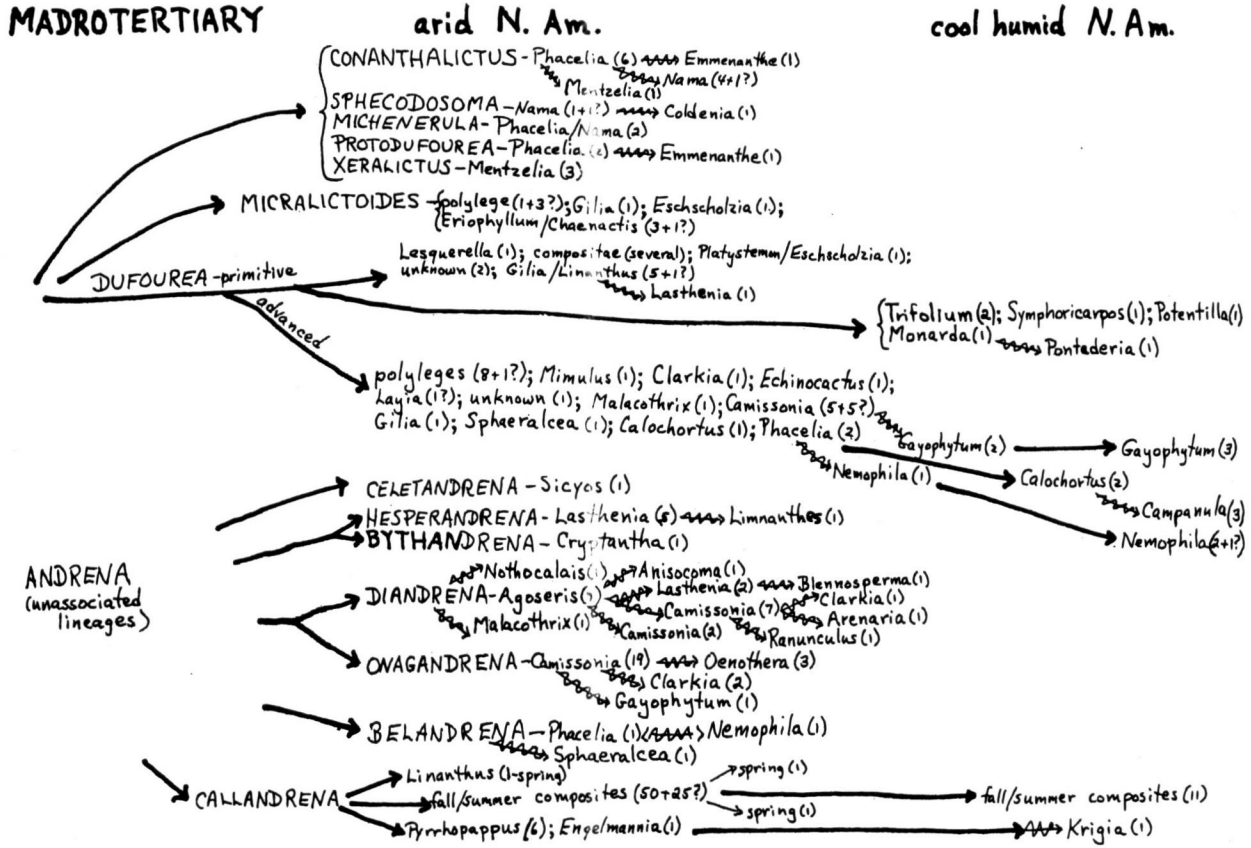
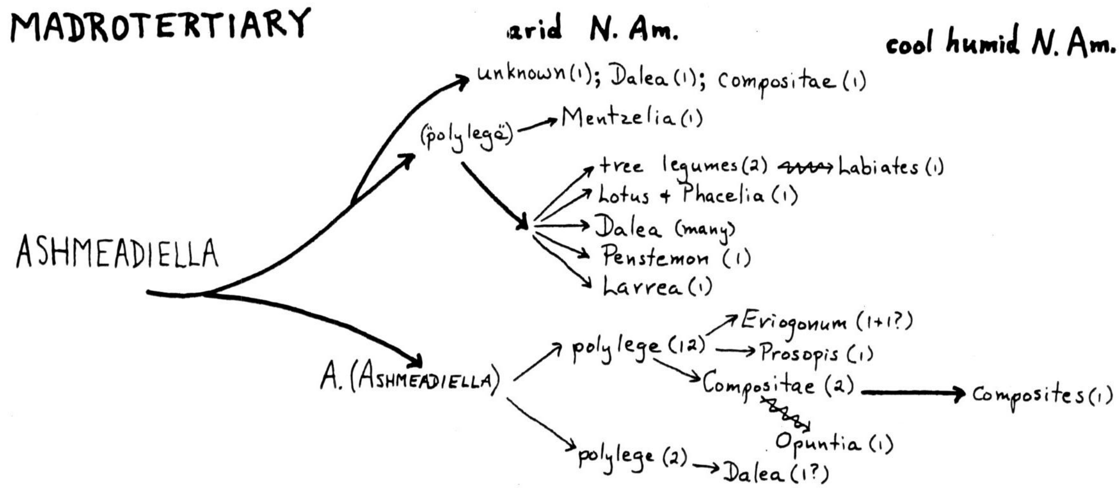

MADROTERTIARY
arid N.Am.
cool humid N. Am.
XEROPHASMA (?sp./su.?)
Oenothera (1sp; 1su.)
EPIMACROTERA-stock
(all year-su.)
GLOSSOPERDITA-Navarretia (2+1?)sp.
Nama (1)sp.
Euphorbia (?+)
(unknown (2?)
Physalis (1+1?) → Coldenia (1?)
Ipomopsis (1)
Proboscidea (1)
(unknown (3?)
HESPEROPERDITA-Lotus (1+1?) sp.
?
PERDITELLA
(all year)
(1 poly)
Larrea (1)
Euphorbia (1) → Tidestromia (1) su.
?
HETEROPERDITA - Coldenia (11+1?) → ± Heliotropium (2)
(all year)
COCKERELLIA-stock
(summer)
COCKERELLIA - fall composites (14+11?)
Geraea (1) sp.
fall composites (2)
PROCOCKERELLIA - Stephanomeria (1) + 3 unknown
ALLOMACROTERA - Stephanomeria (1)
HEXAPERDITA - fall composites (13+6?)
Baileya (1) sp.
fall composites (?)
CALLOMACROTERA
summer composite (1) + 1 unknown
PENTAPERDITA - fall composites (1R+2?)
XEROMACROTERA - fall composites (1)
ALLOPERDITA
(spring?)
unknown (1)
unknown (5)
(vicarious sandy habitats)


MADROTERTIARY
arid N.Am.
cool/ humid N.Am.
P.(PERDITA) sphaeralceae-stock (summer)
sphaeralceae - unknown (10) (MEXICAN)
Semicaerulea - unknown (1) → Larrea (1) all year
Salvia (1) sp.
Sphaeralcea (1)
marginata - unknown (12) (MEXICAN) → linsleyi - unknown (2) sp.
tropicalis - unknown (1) (GUATEMALAN)
P. (PERDITA) martini-stock (spring)
punctosignata - Prosopis (5)
Salix (1+1?) → Salix (1)
exclamans - Prosopis (10)
martini - unknown (10)
vittata - Caparidaceae (2) su.
sonorensis - Prosopis/Mimosa (2+1?)
Dalea +? (1)
eremophila - Phacelia (1) + unknown (1)
etc. - polylege? (1) → Heliotropium (1)
→ Larrea (3)
→ Compositae (3) su. + unknown (3)
P. (PERDITA) eriastri-stock (spring)
calloleuca - Wislizenia (1) su.
leucogastra - Gilia (1?)
eriastri - Eriastrum (2+1?)
leucosticta - Linanthus/Eriastrum/Gilia (4+1?)
→ Nama/Phacelia (2)
eximia - unknown (2)
sidae - unknown (3) su.
polyleges (2)
florissantella - Lepidium (1) su.
unknown (2) su.
tortifoliae - Lepidium/Lesquerella (4+2?) → Stanleya (1) su

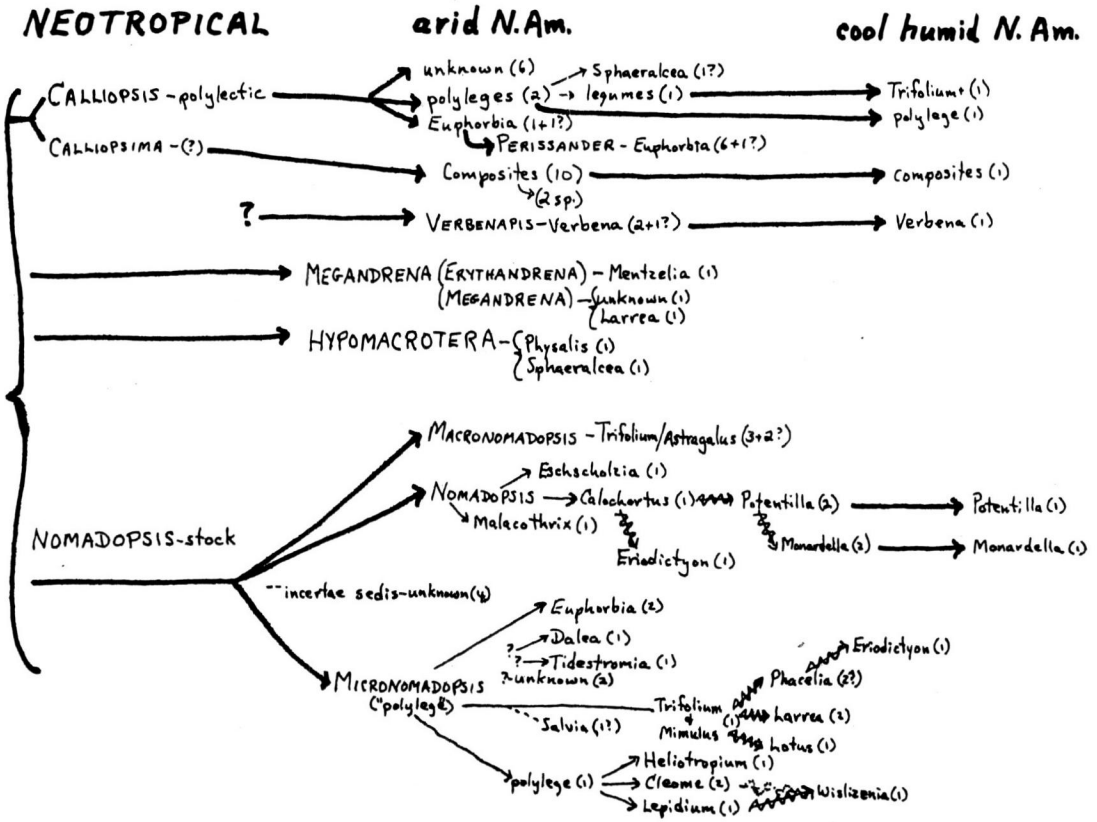


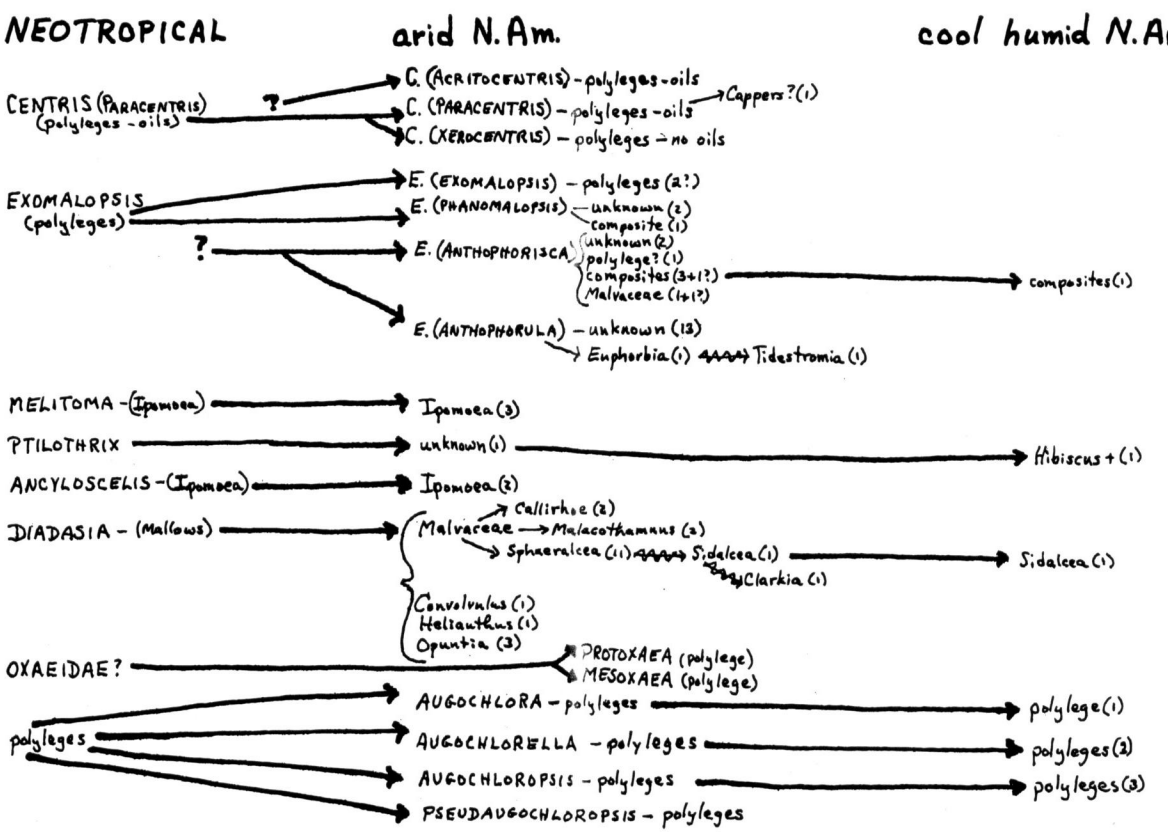
(unplaced Perdita taxa: imberbis, tarda, obliqua, eucnides, vanduzeei, krombeini, valida, stigmalis, sandhouseae)
(unplaced specialists: dammersi (Malacothrix); lycii (Lycium))

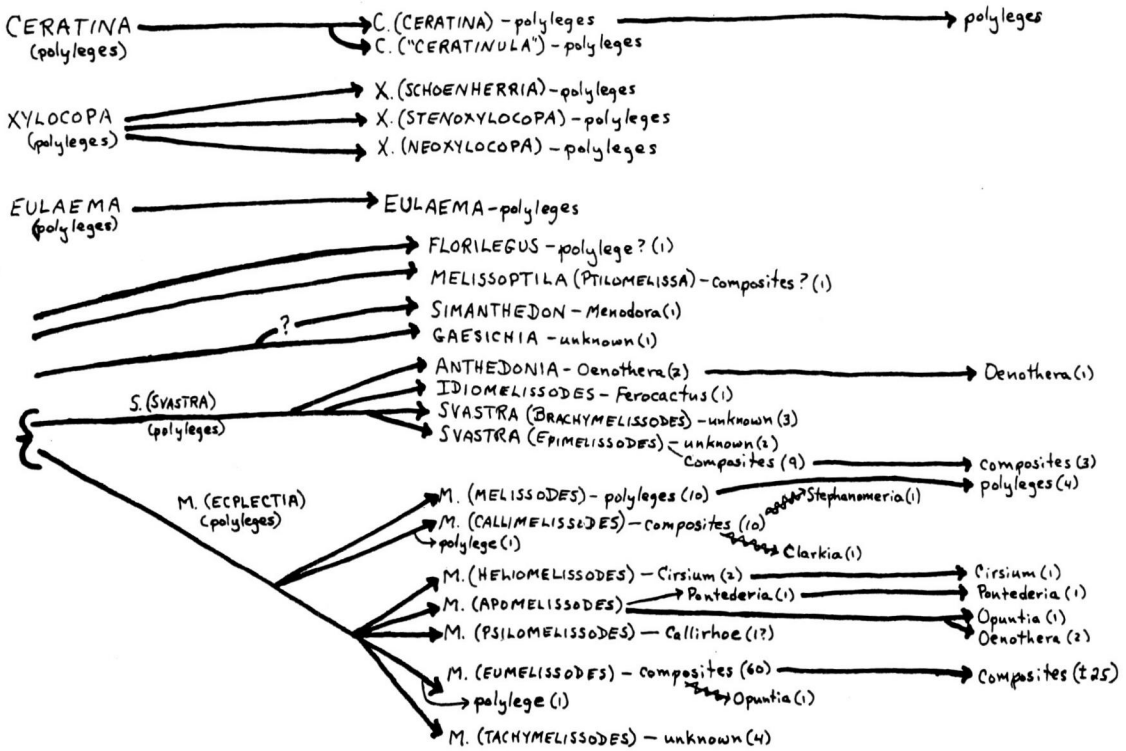

MADROTERTIARY
arid N. Am.
cool humid N. Am.
CONANTHALICTUS - Phacelia (6) → Emmenanthe (1)
Mentzelia (1)
Nama (4+1?)
SPHECODOSOMA - Nama (1+1?) → Coldenia (1)
MICHENERULA - Phacelia/Nama (2)
PROTODUFOUREA - Phacelia (2) → Emmenanthe (1)
XERALICTUS - Mentzelia (3)
MICRALICTOIDES - polylege (1+3?); Gilia (1); Eschscholzia (1); Eriophyllum/Chaenactis (3+1?)
DUFOUREA - primitive
Lesquerella (1); compositae (several); Platystemon/Eschscholzia (1); unknown (2); Gilia/Linanthus (5+1?) → Lasthenia (1)
Trifolium (2); Symphoricarpos (1); Potentilla (1)
Monarda (1) → Pontederia (1)
advanced
polyleges (8+1?); Mimulus (1); Clarkia (1); Echinocactus (1); Layia (1?); unknown (1); Malacothrix (1); Camissonia (5+5?) Gilia (1); Sphaeralcea (1); Calochortus (1); Phacelia (2)
Gayophytum (2) → Gayophytum (3)
Nemophila (1)
Calochortus (2)
Campanula (3)
Nemophila (6+1?)
CELETANDRENA - Sicyos (1)
HESPERANDRENA - Lasthenia (5) → Limnanthes (1)
BYTHANDRENA - Cryptantha (1)
ANDRENA (unassociated lineages)
Nothocalais (1)
Anisocoma (1)
DIANDRENA - Agoseris (?)
Lasthenia (2) → Blennosperma (1)
Clarkia (1)
Camissonia (7)
Arenaria (1)
Malacothrix (1)
Camissonia (2)
Ranunculus (1)
OWAGANDRENA - Camissonia (19) → Oenothera (3)
Clarkia (2)
Gayophytum (1)
BELANDRENA - Phacelia (1) → Nemophila (1)
Sphaeralcea (1)
CALLANDRENA
Linanthus (1-spring)
fall/summer composites (50+25?)
spring (1)
spring (1)
fall/summer composites (11)
Pyrrhopappus (6); Engelmannia (1) → Krigia (1)

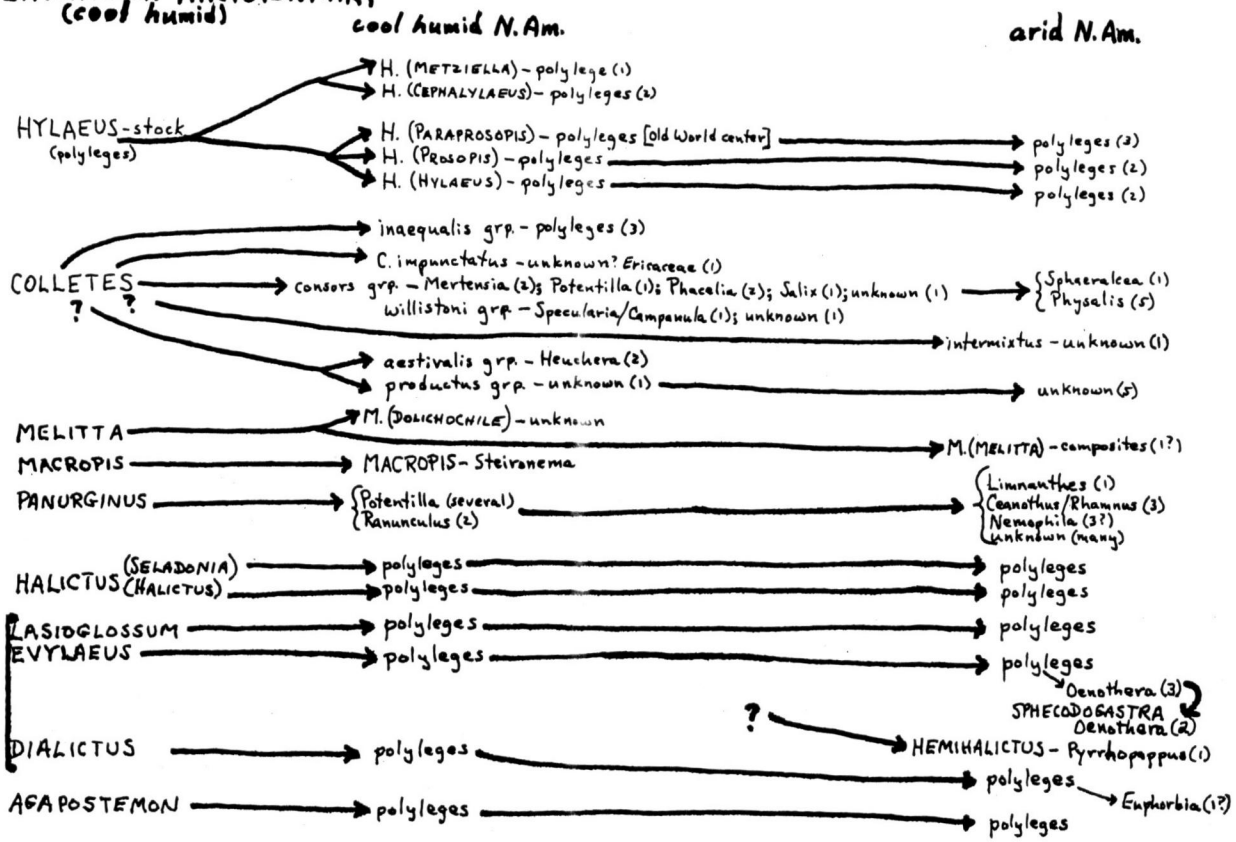

MADROTERTIARY
arid N. Am.
cool humid N. Am.
ASHMEADIELLA
unknown (1); Dalea (1); Compositae (1)
(polylege) Mentzelia (1)
tree legumes (2) Labiates (1)
Lotus + Phacelia (1)
Dalea (many)
Penstemon (1)
Larrea (1)
A. (ASHMEADIELLA)
polylege (12)
Eriogonum (1+1?)
Prosopis (1)
Compositae (2)
Composites (1)
Opuntia (1)
polylege (2)
Dalea (1?)

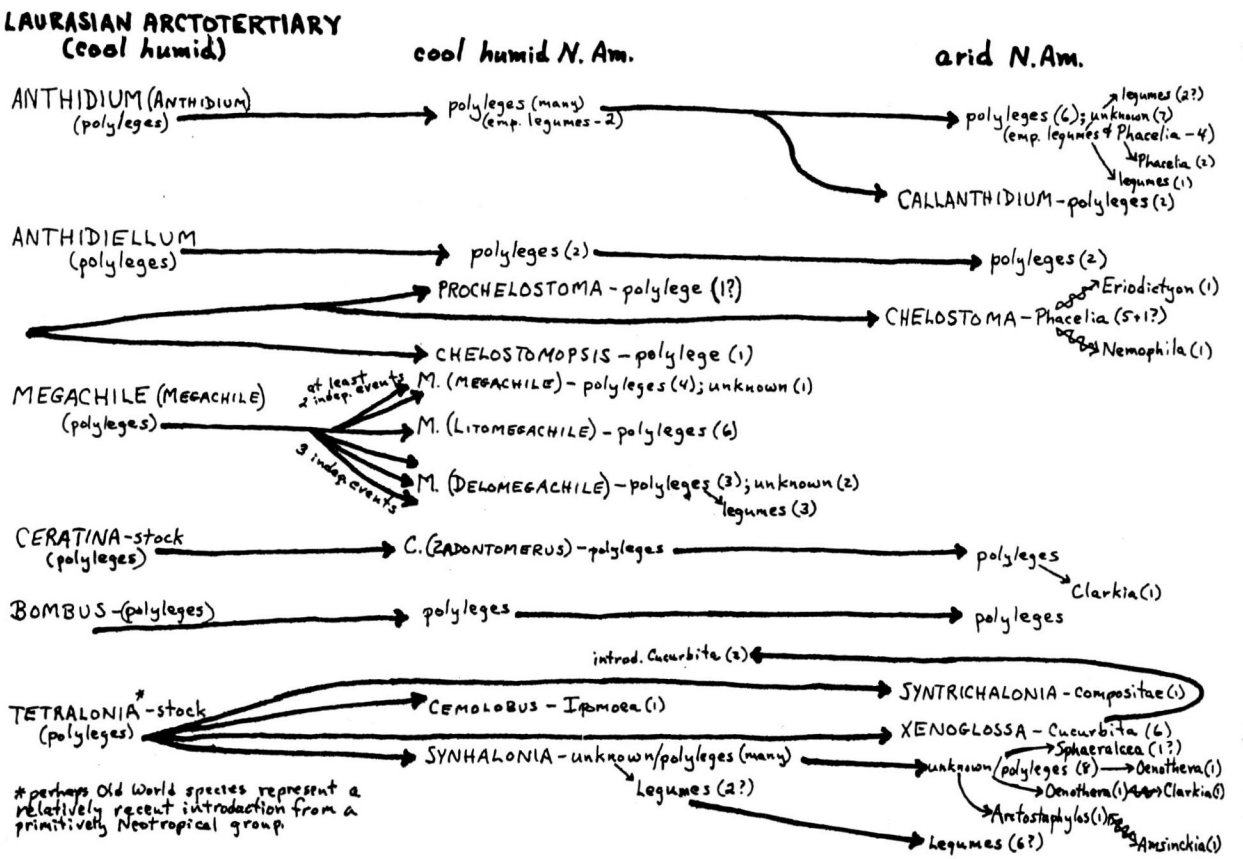

NEOTROPICAL
arid N. Am.
cool humid N. Am.
PSAENYTHIA (ROTANDRENA)
XENOPANURGUS - unknown (1)
unknown (many); Euphorbia (1?); Tidestromia (3?); composites (1±2?)
polylege (1?)
polylege (1?)
METAPSAENYTHIA - Monarda + ? (1)
Monarda? (1)
PSEUDOPANURGUS - compositae (6+1?)
composites (2)
ANTHEMURGUS - Passiflora (1)
HETEROSARUS - unknown (many); Euphorbia (1?); fall composites (1); Sphaeralcea (1?); polyleges (2?)
unknown (several); Ceanothus (2?)
PTEROSARUS - unknown (many); composite vernal (1)
HYLAEUS s. lato
polyleges
HYLAEANA
H. (HYLAEANA) - polyleges
H. (PROSOPELLA) - polyleges
COLLETES
? ancestry
C. titusensis - unknown (1)
C. longifacies - unknown (1)
C. wootoni - unknown (1)
C. latitarsis grp. - unknown (1)
unknown (1)
C. bulbotibialis - unknown (1)
C. platycnema - Acacia (1)
EULONCHOPRIA - Acacia
Acacia (1)
CAUPOLICANA - polyleges
polyleges
PTILOGLOSSA - polyleges
polyleges?
LITHURGUS - Cactaceae
L. (LITHURGOMMA) - Opuntia + (4+1?)
Echinocactus (1)
Opuntia (1)
MEGACHILE (CRESSONIELLA)
M. (CRESSONIELLA) - unknown (1?)
M. (NEOMEGACHILE) - unknown (2?)
MEGACHILE (PSEUDOCENTRON)
M. (MELANOSARUS) - compositae (2?)
M. (LEPTORACHIS) - polylege (1)
M. (PSEUDOCENTRON) - polyleges (2)
M. (ACENTRON) - polylege (1?)
? MEGACHILE (SAYAPIS)?
M. (SAYAPIS) - polylege (1)
composites (5+1?)
Prosopis/Acacia + (1)
composites (3)

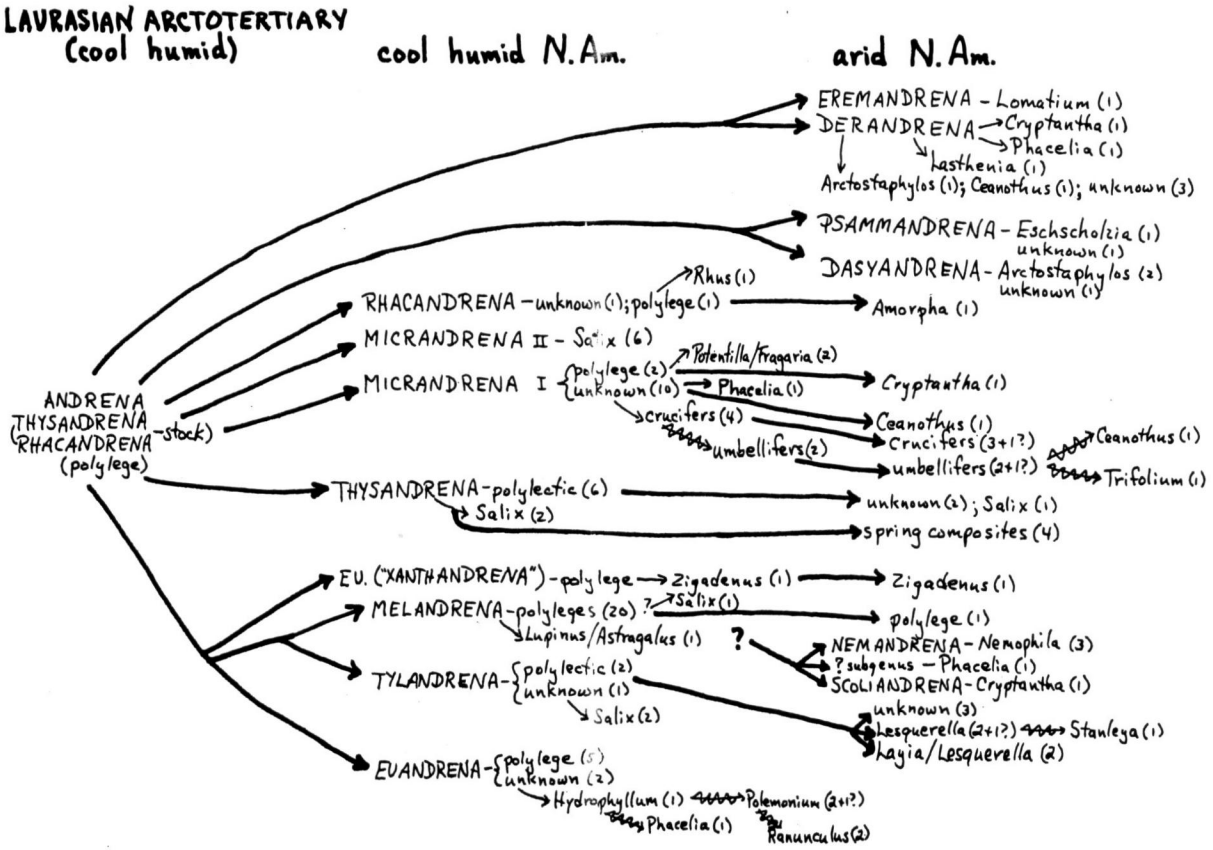

NEOTROPICAL
arid N.Am.
cool humid N.Am.
CALLIOPSIS - polylectic
CALLIOPSIMA - (?)
unknown (6)
Sphaeralcea (1?)
polyleges (2)
legumes (1)
Trifolium+ (1)
Euphorbia (1+1?)
polylege (1)
PERISSANDER - Euphorbia (6+1?)
Composites (10)
composites (1)
(2 sp.)
?
VERBENAPIS - Verbena (2+1?)
Verbena (1)
MEGANDRENA (ERYTHANDRENA) - Mentzelia (1)
(MEGANDRENA) - unknown (1)
larrea (1)
HYPOMACROTERA - Physalis (1)
Sphaeralcea (1)
NOMADOPSIS-stock
MACRONOMADOPSIS - Trifolium/Astragalus (3+2?)
NOMADOPSIS
Eschscholzia (1)
Calochortus (1)
Potentilla (2)
Potentilla (1)
Malacothrix (1)
Eriodictyon (1)
Monardella (2)
Monardella (1)
incertae sedis - unknown (4)
Euphorbia (2)
Dalea (1)
Tidestromia (1)
unknown (2)
MICRONOMADOPSIS ("polyleges")
Eriodictyon (1)
Phacelia (2?)
Trifolium (1)
larrea (2)
Mimulus
Salvia (1?)
lotus (1)
polylege (1)
Heliotropium (1)
Cleome (2)
Wislizenia (1)
Lepidium (1)

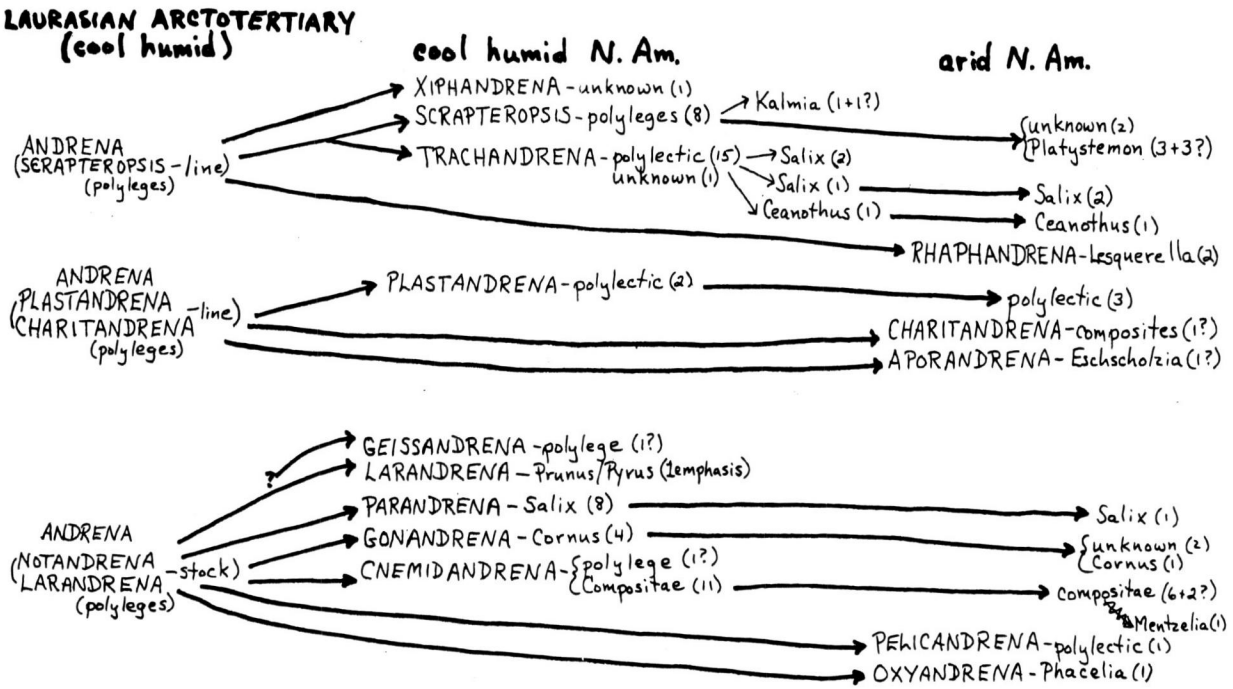

NEOTROPICAL
arid N.Am.
cool humid N.Am.
CENTRIS (PARACENTRIS) (polyleges - oils)
?
C. (ACRITOCENTRIS) - polyleges - oils
C. (PARACENTRIS) - polyleges - oils
Cappers? (1)
C. (XEROCENTRIS) - polyleges - no oils
EXOMALOPSIS (polyleges)
E. (EXOMALOPSIS) - polyleges (2?)
E. (PHANOMALOPSIS)
unknown (2)
composite (1)
?
E. (ANTHOPHORISCA)
unknown (2)
polylege? (1)
composites (3+1?)
Malvaceae (1+1?)
composites (1)
E. (ANTHOPHORULA) - unknown (13)
Euphorbia (1)
Tidestromia (1)
MELITOMA - (Ipomoea)
Ipomoea (3)
PTILOTHRIX
unknown (1)
Hibiscus + (1)
ANCYLOSCELIS - (Ipomoea)
Ipomoea (2)
DIADASIA - (Mallows)
Malvaceae
Callirhoe (2)
Malacothamnus (2)
Sphaeralcea (11)
Sidalcea (1)
Sidalcea (1)
Clarkia (1)
Convolvulus (1)
Helianthus (1)
Opuntia (3)
OXAEIDAE?
PROTOXAEA (polylege)
MESOXAEA (polylege)
polyleges
AUGOCHLORA - polyleges
polylege (1)
AUGOCHLORELLA - polyleges
polyleges (2)
AUGOCHLOROPSIS - polyleges
polyleges (3)
PSEUDAUGOCHLOROPSIS - polyleges


NEOTROPICAL
arid N. Am.
cool humid N. Am.
CERATINA (polyleges)
C. (CERATINA) - polyleges
C. ("CERATINULA") - polyleges
polyleges
XYLOCOPA (polyleges)
X. (SCHOENHERRIA) - polyleges
X. (STENOXYLOCOPA) - polyleges
X. (NEOXYLOCOPA) - polyleges
EULAEMA (polyleges)
EULAEMA - polyleges
FLORILEGUS - polylege? (1)
MELISSOPTILA (PTILOMELISSA) - composites? (1)
SIMANTHEDON - Menodora (1)
GAESICHIA - unknown (1)
?
S. (SVASTRA) (polyleges)
ANTHEDONIA - Oenothera (2)
Oenothera (1)
IDIOMELISSODES - Ferocactus (1)
SVASTRA (BRACHYMELISSODES) - unknown (3)
SVASTRA (EPIMELISSODES) - unknown (2)
composites (9)
composites (3)
polyleges (4)
Stephanomeria (1)
M. (ECPLECTIA) (polyleges)
M. (MELISSODES) - polyleges (10)
M. (CALLIMELISSODES) - composites (10)
polylege (1)
Clarkia (1)
M. (HELIOMELISSODES) - Cirsium (2)
Cirsium (1)
M. (APOMELISSODES)
Pentstemon (1)
Pentstemon (1)
Opuntia (1)
Oenothera (2)
M. (PSILOMELISSODES) - Callirhoe (1?)
M. (EUMELISSODES) - composites (60)
composites (± 25)
Opuntia (1)
polylege (1)
M. (TACHYMELISSODES) - unknown (4)

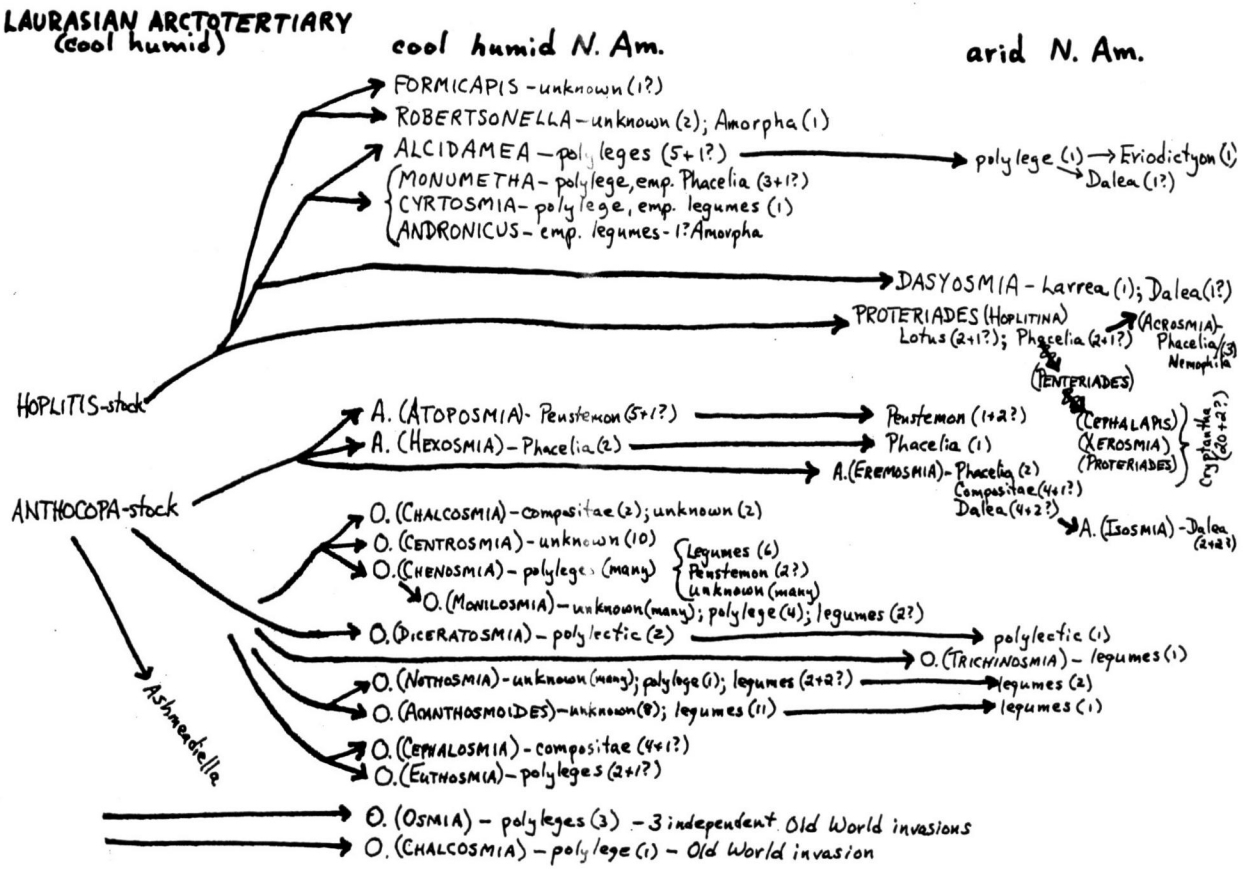

LAURASIAN ARCTOTERTIARY
(cool humid)
cool humid N. Am.
arid N. Am.
HYLAEUS-stock
(polyleges)
H. (METZIELLA) - polylege (1)
H. (CEPHALYLAEUS) - polyleges (2)
H. (PARAPROSOPIS) - polyleges [Old World center]
H. (PROSOPIS) - polyleges
H. (HYLAEUS) - polyleges
polyleges (3)
polyleges (2)
polyleges (2)
COLLETES
inaequalis grp. - polyleges (3)
C. impunctatus - unknown? Ericaceae (1)
consors grp. - Mertensia (2); Potentilla (1); Phacelia (2); Salix (1); unknown (1)
willistoni grp. - Specularia/Campanula (1); unknown (1)
Sphaeralcea (1)
Physalis (5)
intermixtus - unknown (1)
aestivalis grp. - Heuchera (2)
productus grp. - unknown (1)
unknown (5)
MELITTA
M. (DOLICHOCHILE) - unknown
M. (MELITTA) - composites (1?)
MACROPIS
MACROPIS - Steiranema
PANURGINUS
Potentilla (several)
Ranunculus (2)
Limnanthes (1)
Ceanothus/Rhamnus (3)
Nemophila (3?)
unknown (many)
HALICTUS
(SELADONIA)
(HALICTUS)
polyleges
polyleges
polyleges
polyleges
LASIOGLOSSUM
EVYLAEUS
polyleges
polyleges
polyleges
Oenothera (3)
SPHECODOGASTRA
Oenothera (2)
DIALICTUS
polyleges
HEMIHALICTUS - Pyrrhopappus (1)
polyleges
Euphorbia (1?)
AGAPOSTEMON
polyleges
polyleges

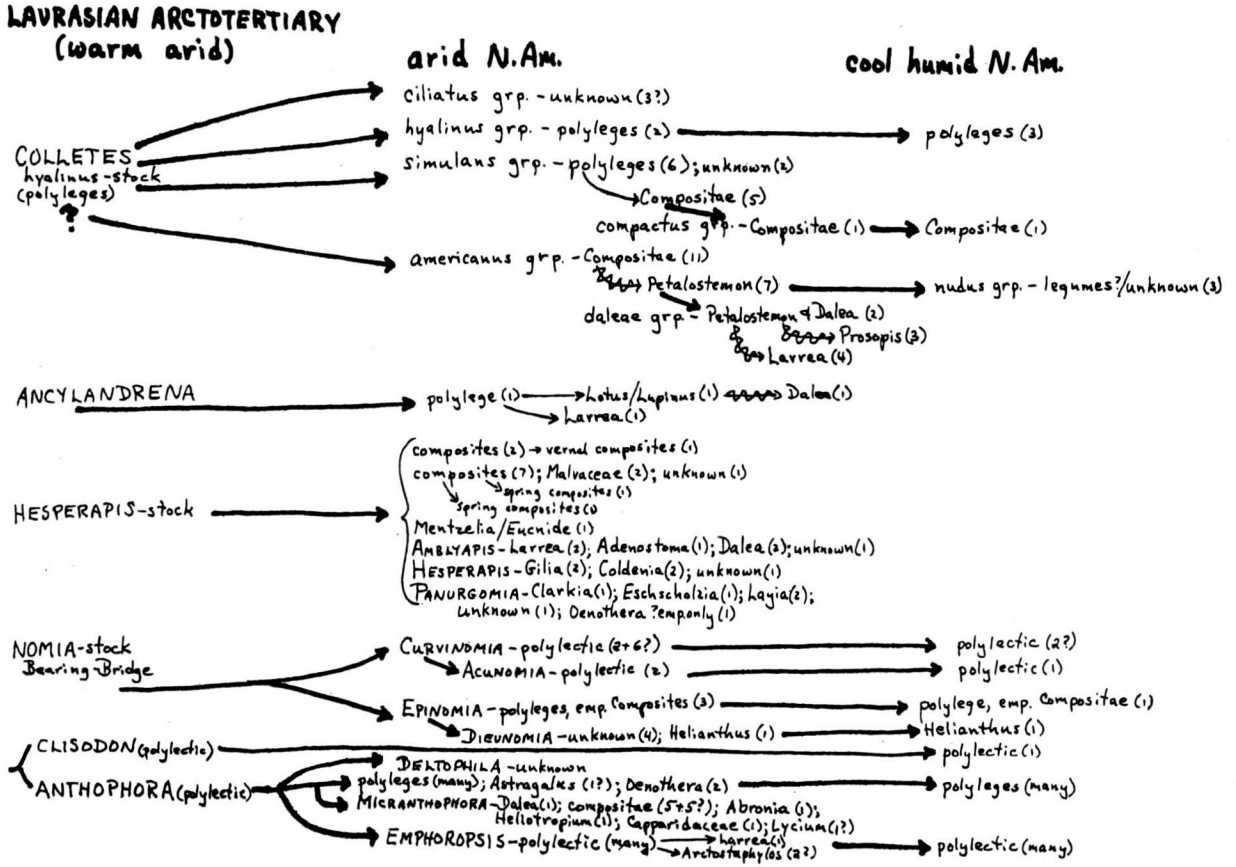

LAURASIAN ARCTOTERTIARY
(cool humid)
cool humid N. Am.
arid N. Am.
ANTHIDIUM (ANTHIDIUM)
(polyleges)
polyleges (many)
(emp. legumes - 2)
polyleges (6); unknown (?)
(emp. legumes & Phacelia - 4)
legumes (2?)
Phacelia (2)
legumes (1)
CALLANTHIDIUM - polyleges (2)
ANTHIDIELLUM
(polyleges)
polyleges (2)
polyleges (2)
PROCHELOSTOMA - polylege (1?)
CHELOSTOMA - Phacelia (5+1?)
Eriodictyon (1)
Nemophila (1)
CHELOSTOMOPSIS - polylege (1)
MEGACHILE (MEGACHILE)
(polyleges)
at least 2 indep. events
M. (MEGACHILE) - polyleges (4); unknown (1)
M. (LITOMEGACHILE) - polyleges (6)
3 indep. events
M. (DELOMEGACHILE) - polyleges (3); unknown (2)
legumes (3)
CERATINA - stock
(polyleges)
C. (ZADONTOMERUS) - polyleges
polyleges
Clarkia (1)
BOMBUS - (polyleges)
polyleges
polyleges
introd. Cucurbita (2)
SYNTRICHALONIA - Compositae (1)
TETRALONIA* - stock
(polyleges)
CEMOLOBUS - Ipomoea (1)
XENOGLOSSA - Cucurbita (6)
SYNHALONIA - unknown/polyleges (many)
Sphaeralcea (1?)
unknown/polyleges (8)
Oenothera (1)
Oenothera (1)
Clarkia (1)
Legumes (2?)
Arctostaphylos (1)
Amsinckia (1)
Legumes (6?)
* perhaps Old World species represent a relatively recent introduction from a primitively Neotropical group

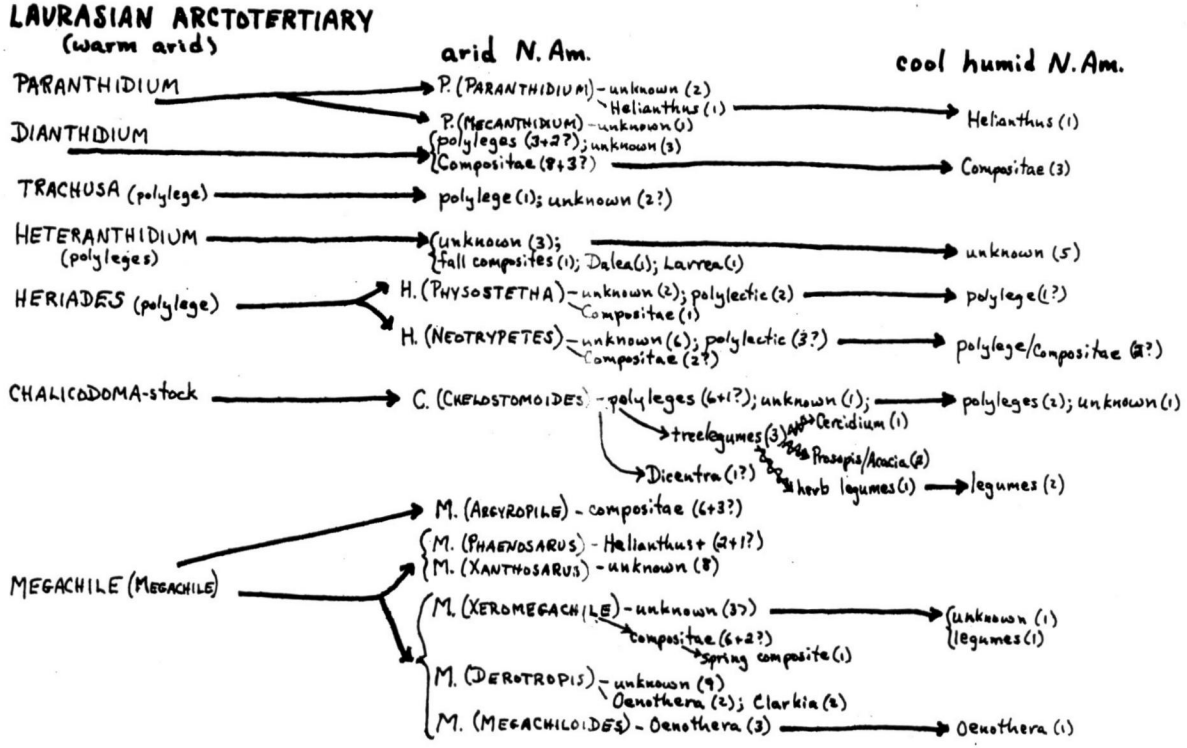

LAURASIAN ARCTOTERTIARY
(cool humid)
cool humid N. Am.
arid N. Am.
ANDRENA
THYSANDRENA
RHACANDRENA
(polylege)
-stock)
EREMANDRENA - Lomatium (1)
DERANDRENA
Cryptantha (1)
Phacelia (1)
Hasthenia (1)
Arctostaphylos (1); Ceanothus (1); unknown (3)
PSAMMANDRENA - Eschscholzia (1)
unknown (1)
DASYANDRENA - Arctostaphylos (2)
unknown (1)
RHACANDRENA - unknown (1); polylege (1)
Rhus (1)
Amorpha (1)
MICRANDRENA II - Salix (6)
MICRANDRENA I
polylege (2)
unknown (10)
Potentilla/Fragaria (2)
Phacelia (1)
Cryptantha (1)
crucifers (4)
umbellifers (2)
Ceanothus (1)
Crucifers (3+1?)
umbellifers (2+1?)
Ceanothus (1)
Trifolium (1)
THYSANDRENA - polylectic (6)
Salix (2)
unknown (2); Salix (1)
spring composites (4)
EU. ("XANTHANDRENA") - polylege
Zigadenus (1)
Zigadenus (1)
MELANDRENA - polyleges (20)
Salix (1)
polylege (1)
Lupinus/Astragalus (1)
?
NEMANDRENA - Nemophila (3)
? subgenus - Phacelia (1)
SCOLIANDRENA - Cryptantha (1)
TYLANDRENA
polylectic (2)
unknown (1)
Salix (2)
unknown (3)
Lesquerella (2+1?)
Stanleya (1)
Kayia/Lesquerella (2)
EVANDRENA
polylege (5)
unknown (2)
Hydrophyllum (1)
Polemonium (2+1?)
Phacelia (1)
Ranunculus (2)

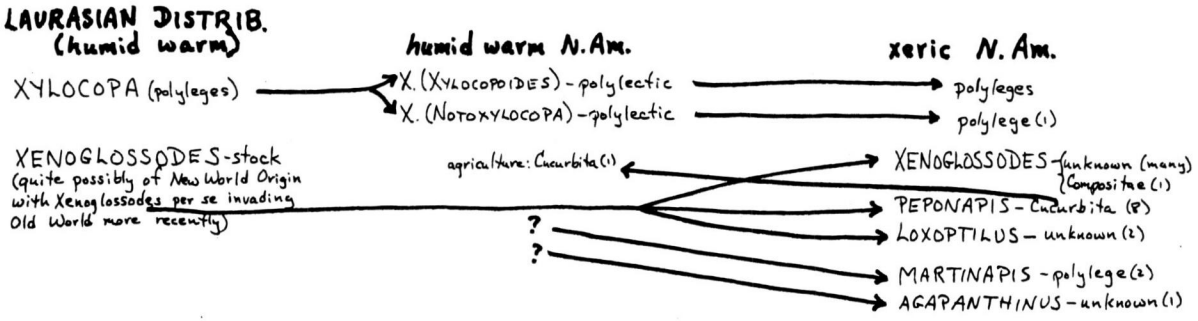


Not Illustrated:
Dactylandrena - Ribes (2+2?); Iomelissa - Viola (1); Ptilandrena [unknown (1); Claytonia (1)];
n. subg. - Nothoscordum (1); n. subg. - Erythronium (2); Leucandrena [unknown (many); Erythronium (1)];
Opandrena; Conandrena; Oligandrena; Simandrena (Platandrena, Stenandrena);
Chaulandrena; Taeniandrena.


LAURASIAN ARCTOTERTIARY
(cool humid)
cool humid N. Am.
arid N. Am.
FORMICAPIS - unknown (1?)
ROBERTSONELLA - unknown (2); Amorpha (1)
ALCIDAMEA - polyleges (5+1?)
polylege (1) → Eriodictyon (1)
Dalea (1?)
MONUMETHA - polylege, emp. Phacelia (3+1?)
CYRTOSMIA - polylege, emp. legumes (1)
ANDRONICUS - emp. legumes - 1? Amorpha
DASYOSMIA - Larrea (1); Dalea (1?)
PROTERIADES (HOPLITINA)
Lotus (2+1?); Phacelia (2+1?)
(ACROSMIA) - Phacelia (3) Nemophila
(PENTERIADES)
HOPLITIS-stock
A. (ATOPOSMIA) - Penstemon (5+1?)
Penstemon (1+2?)
A. (HEXOSMIA) - Phacelia (2)
Phacelia (1)
(CEPHALAPIS)
(XEROSMIA)
(PROTERIADES)
Cryptantha (20+2?)
A. (EREMOSMIA) - Phacelia (2)
Compositae (4+1?)
Dalea (4+2?)
A. (ISOSMIA) - Dalea (2+2?)
ANTHOCOPA-stock
O. (CHALCOSMIA) - Compositae (2); unknown (2)
O. (CENTROSMIA) - unknown (10)
O. (CHENOSMIA) - polyleges (many)
Legumes (6)
Penstemon (2?)
unknown (many)
O. (MONILOSMIA) - unknown (many); polylege (4); legumes (2?)
O. (DICERATOSMIA) - polylectic (2)
polylectic (1)
O. (TRICHINOSMIA) - legumes (1)
O. (NOTHOSMIA) - unknown (many); polylege (1); legumes (2+2?)
legumes (2)
O. (ACANTHOSMOIDES) - unknown (8); legumes (11)
legumes (1)
Ashmeadiella
O. (CEPHALOSMIA) - compositae (4+1?)
O. (EUTHOSMIA) - polyleges (2+1?)
O. (OSMIA) - polyleges (3) - 3 independent Old World invasions
O. (CHALCOSMIA) - polylege (1) - Old World invasion


LAURASIAN ARCTOTERTIARY
(warm arid)
arid N. Am.
cool humid N. Am.
COLLETES
hyalinus-stock
(polylleges)
?
ciliatus grp. - unknown (3?)
hyalinus grp. - polyleges (2)
polylages (3)
simulans grp. - polyleges (6); unknown (2)
Compositae (5)
compactus grp. - Compositae (1)
Compositae (1)
americanus grp. - Compositae (11)
Petalostemon (7)
nudus grp. - legumes?/unknown (3)
dalea grp. - Petalostemon & Dalea (2)
Prosopis (3)
Larrea (4)
ANCYLANDRENA
polylege (1)
lotus/Lupinus (1)
Dalea (1)
Larrea (1)
HESPERAPIS-stock
composites (2) → vernal composites (1)
composites (7); Malvaceae (2); unknown (1)
spring composites (1)
spring composites (1)
Mentzelia/Eucnide (1)
AMBLYAPIS - Larrea (2); Adenostoma (1); Dalea (2); unknown (1)
HESPERAPIS - Gilia (2); Coldenia (2); unknown (1)
PANURGOMIA - Clarkia (1); Eschscholzia (1); kayia (2);
unknown (1); Denothera ?emponly (1)
NOMIA-stock
Bearing Bridge
CURVINOMIA - polylectic (2+6?)
polylectic (2?)
ACUNOMIA - polylectic (2)
polylectic (1)
EPINOMIA - polyleges, emp. Composites (3)
polylege, emp. Compositae (1)
DIEUNOMIA - unknown (4); Helianthus (1)
Helianthus (1)
CLISODON (polylectic)
polylectic (1)
ANTHOPHORA (polylectic)
DELTOPHILA - unknown
polyleges (many); Astragalus (1?); Denothera (2)
polyleges (many)
MICRANTHOPHORA - Dalea (1); compositae (5+5?); Abronia (1);
Heliotropium (1); Capparidaceae (1); Lycium (1?)
EMPHOROPSIS - polylectic (many)
larrea (1)
Arctostaphylos (2?)
polylectic (many)


LAURASIAN ARCTOTERTIARY
(warm arid)
arid N. Am.
cool humid N. Am.
PARANTHIDIUM
P. (PARANTHIDIUM) - unknown (2)
Helianthus (1)
P. (MECANTHIDIUM) - unknown (1)
Helianthus (1)
DIANTHIDIUM
polylegas (3+2?); unknown (3)
Compositae (8+3?)
Compositae (3)
TRACHUSA (polylege)
polylege (1); unknown (2?)
HETERANTHIDIUM
(polyleges)
unknown (3);
fall composites (1); Dalea (1); Larrea (1)
unknown (5)
HERIADES (polylege)
H. (PHYSOSTETHA) - unknown (2); polylectic (2)
Compositae (1)
polylege (1?)
H. (NEOTRYPETES) - unknown (6); polylactic (3?)
Compositae (2?)
polylege/Compositae (2?)
CHALICODOMA-stock
C. (CHELOSTOMOIDES) - polyleges (6+1?); unknown (1);
polyleges (2); unknown (1)
tree legumes (3)
Cercidium (1)
Prosopis/Acacia (2)
Dicentra (1?)
herb legumes (1)
legumes (2)
MEGACHILE (MEGACHILE)
M. (ARGYROPILE) - compositae (6+3?)
M. (PHAENOSARUS) - Helianthus + (2+1?)
M. (XANTHOSARUS) - unknown (8)
M. (XEROMEGACHILE) - unknown (37)
unknown (1)
legumes (1)
compositae (6+2?)
spring composite (1)
M. (DEROTROPIS) - unknown (9)
Oenothera (2); Clarkia (2)
M. (MEGACHILOIDES) - Oenothera (3)
Oenothera (1)



"RECENT" INTRODUCTIONS:

Europe → Apis (polylege)
Europe → Hylaeus (H.) - polylege [perhaps relict]
Europe → Hylaeus (H.) – *Melilotus*?
Europe → Ceratina (Euceratina) – polylege
Asia → Ceratina (Pithitis) – polylege
Europe → Hoplitis (Hoplitis) – Echium
Trop. Africa → Chalicodoma (Archimegachile) – unknown
Africa → Megachile (Eutricharaea) – polyleges (2)

I have found approximately 250 instances of host changes of the nature polylectic ⟶ specialist or specialist$_a$ ⟶ specialist$_b$ (this excludes some unmonographed subgenera of Andrena and Osmia) in the evolution of North American bees. Depending on one's point of view, this can be taken as either a surprisingly large or a surprisingly small number since no comparable data exist. I personally fall into the latter camp for it should be emphasized that many such instances of specialization or "shifts" have not been particularly "successful" gauged in terms of adaptive radiation subsequent to such host changes nor have many of such changes markedly affected the pollination ecology of the North American flora. Many bee taxa which demonstrate host-specialization and host-shifts most frequently are not the most important pollinators of their respective hosts. There are also very many abundant melittophilous plant groups in North America which have not coevolved with any specialist-feeding bees at all, indeed the flora of North America (except for certain dominant tree genera) is overwhelmingly melittophilous.

Illustration 2 reveals that the presumed primitive character state in most groups is generalized feeding. This is not based solely on theoretical concerns, but in fact in many groups the structurally least specialized species are known to be generalized feeders. In some of the groups we do not know, even by inference, what the ancestors may have fed upon, since the least specialized species are characterized by divergent feeding patterns; my most reasonable guess of ancestral feeding patterns is sometimes indicated in the left-hand column. It is notable, and surprising I think, that there are no instances of host changes of the type from specialist ⟶ polylege. Specialization appears to be an exclusively one way process. The only semblance of such a shift takes place in the evolution of our largely endemic Centris (Xerocentris) polyleges from ancestors within the genus Centris which while polylectic for pollen supplies still were obligately specialized to harvest oils instead of nectar (Neff unpub.).

In addition to the presumed and postulated ancient polylectic ancestors of our North American bee fauna, there have been at least 9 Neotropical, 2 Arctotertiary (with close present Old World ties) and two recent accidental introductions of formerly specialized lineages which have maintained their pattern of specialization here. Of the 250 instances of evolutionary host-plant specialization or switches, most have occurred in very few genera: more than 60 in Perdita.

24 in Dufourea, 18 in Nomadopsis, 15 in Colletes, 23 in the Eucerinae. Perdita and Andrena are the two most diverse genera in North America, hence their degree of specialization is not unexpected. The third largest genus, Dialictus, has speciated in the absence of host-plant specialization; all North American species are generalized feeders with the possible exception of one desert species implicated in association with Euphorbia (Eickwort, pers. comm.). Both Dialictus and Evylaeus (considered by some workers congeneric) are apparently generally polylectic throughout their range, seldom specializing either in the Old World or the New World (Ebmer & Pauly, pers. comms.). I presume that this indicates that these and other halictine bees do not have the same type of genetic host-selection mechanisms possessed by most other bees.

Nearly all of the specialization events noted are those from polylege ⟶ specialist, only 53 are possibly switches between different non-confamilial individual plant hosts, again implying the unidirectional and apparently "dead end" nature of such switches. Interestingly, about half of the switches that apparently do occur take place in the Sonoran Desert and the other half in the Mediterranean regions of California, practically none in the other regions of North America. Though the arid regions do support greater diversities, this degree of difference cannot be accounted for on that basis alone. Climates are less predictable and smaller shifts in amplitudes in these regions produce greater effects on the flora and fauna perhaps by altering germination cues and the temporal synchronization of host plant and bee disproportionately.

Of these 53 non-confamilial host-shifts, only 10 occur between taxa which appear visually rather similar (at least to human eyes). Though relevant data on chemical cues are lacking for most taxa, it is reasonable to suppose that many such switches have indeed occurred between taxa which are in fact extremely dissimilar. In certain cases the recipient host is a dominant plant (e.g., Larrea, Prosopis) that the former species could reasonably be expected to have continual exposure to, or in some cases the novel host is one of the very few other plants to bloom during the particular time of year the original host was in bloom (e.g., Tidestromia, Limnanthes), but in many instances logical "explanations" for such shifts elude me. Examination of the lineage diagrams also reveals an additional ca. 30 confamilial host-shifts, occurring between visually rather dissimilar plants (Phacelia/Nemophila; Clarkia/Camissonia; Lesquerella/Stanleya; Mentzelia/Petalonyx);

it is reasonable to presume tentatively that such shifts were facilitated by the recognition of certain phylogenetically shared chemical characteristics, however such assumptions must be tested by subsequent chemical analysis.

In an analysis of evolutionary host-shift patterns, it is of course of utmost importance to determine as precisely as possible the cladistic relationships amongst the species themselves. I have accepted the published opinions of taxonomists wherever available. I have tried in all possible instances to examine their implied/stated cladograms with a skeptical eye, but seldom have I felt that an application of Occam's Razor (solely in light of known/postulated host associations) would change their point of view, except in instances of very rare incompletely known taxa which were unknown from the standpoint of host associations as well. Minor differences, either of conscious design on my part or misinterpretation, will be apparent since I have chosen to present diagrammatic cladograms to facilitate data examination in problem phylogenies. It is important to note that seldom (if ever) have bee taxonomists considered host-association or weighted it heavily in constructing their published phylogenetic speculations; such relationships are generally based on morphological structures, particularly the male genital apparatus. Indeed, recent monographers of Andrena have considerably revised the postulated relationships of this very large genus by not treating specific floral adaptations in their phylogenetic schemes.

I believe that the only conscious changes I have incorporated herein are: 1) the sinking and remixing of A. (Scaphandrena) into A. (Micrandrena)(a separation termed possibly artifactual by the latest monographer -- Ribble, 1974) which entails the lumping of the crucifer-feeding M. piperi-group, M. primulifrons-group and all crucifer-feeding Scaphandrena; uniting M.(I) chlorogaster with S. merriami; S. lomatii, mackiae, S. plana with M.(I) microchlora; M. (I) melanochroa perhaps united with Derandrena ziziaeformis; 2) the lumping of possible Polemonium A. (Euandrena) feeders (i.e. A. polemonii to A. segregans) by application of Occam's Razor; 3) the uniting (largely) on the basis of similarities of the 8th sternum from various tentative placements of a group of species related to the Perdita vittata/sonorensis groups (since many of these species, e.g., P. heliotropii, covilleae, punctulata, plucheae, perixantha, paryella, ambigua, tarda, have unknown hosts, at this preliminary level of analysis, the point is largely moot); 4) the uniting, by Occam's Razor only, of the P. koebelei-group with other

Mentzelia-feeding Perdita; 5) uniting the Lesquerella-feeding A. (Tylandrena); 6) removing Colletes larreae & C. turgiventris from the C. robertsoni group on the basis of their distinct genital apparati; 7) linking P. (Alloperdita) to P. (Procockerellia) by Occam's Razor alone; 8) removing the long-faced Perdita hurdi and P. giliae from the long-tongued P. (Glossoperdita) and placing them in P. (Epimacrotera); 9) transfering Perdita erythropyga & P. fulvicauda from the ventralis-group to the octomaculata-group on the basis of the similarities of the eighth sternum; 10) linking by Occam's Razor the Dalea-oligoleges in Ashmeadiella (Rhamphorhyncha, Cubitognatha & Corythochila); 11) postulating monophyly in each of the composite-, Dalea- and Phacelia-feeding groups of Anthocopa (Eremosmia/Isosmia); 12) lumping as monophyletic the legume oligoleges in Osmia (Nothosmia & Acanthosmoides) on the basis of Occam's Razor alone in the absence of any conflicting information.

In groups which have not been recently monographed, cladistic sequences were not attempted, and are not indicated in Illustration 2, nor are the switches (whatever form they may really take) counted in textual analysis. Cladograms of Colletes and Perdita are original but attempt to agree with the taxonomic specialist's published anecdotal remarks.

Of the host-specialization relationships elucidated in this manner, most are represented in the western United States. Indeed, California is uniquely situated in which to study the precise forms that such adaptation can produce since all the trophic couplings between particular plant genera and specialist-feeding groups except 30 occur within the state; there are another six resident plant groups with specialist feeders in closely adjacent regions which subsequent field work will probably discover in California as well (i.e., Cornus, Nothocalais, Stanleya, Descurainia, Wislizenia, Polemonium).

. . .

Illustration 2 represents approximately 50 bee lineages that are suspected of ancient Arctotertiary Floral ties to closely related species in the Old World, 40 Neotropical, 25 endemic Madrotertiary Flora and 35 old North American Tropical. Since these lineage ancestries are by definition highly speculative, these results should be taken to indicate only relatively heavy phylogenetic inputs from the three external source paleohistorical realms to the present bee fauna of North

America. The terms Arctotertiary and Madrotertiary refer primarily to the floral associates of the bee lineages since the paleohistorical age of most bee groups is completely unknown in the absence of relevant fossils. Most bee taxonomists (unlike myself) believe that most bee lineages are of much more recent derivation than these basic floral assemblages. Both Arctotertiary and Neotropical (open savanna and humid forest not distinguished) stocks have contributed heavily to the semi-arid/arid regions of the southwestern United States; contributing by my count approximately 45 stocks each. Neotropical stocks have undoubtedly contributed even more heavily, since I am thoroughly unfamiliar with the bee fauna of semi-arid Mexico, and it is quite probable that no additional Arctotertiary elements (not already counted) have contributed. Twenty Neotropical stocks have also contributed heavily to the forested regions of the southeastern U.S.A., though many of these elements may have been archaically associated with North America rather than with temperate South America whose faunistic contribution may be limited to late Pliocene. Twenty-one separate lineages traceable to basically arid stock but not definitely associated with either Neotropical or Arctotertiary ancestries (termed "endemic Madrotertiary") have contributed to the present cool temperate North American fauna as well.

True range expansions of lineages into novel geofloras, usually involve polylectic species, or species which have followed a successful invasion by their host plant (i.e., Cucurbita, Opuntia, Oenothera?, Petalostemon) or species which were basically "family-oligoleges" and which were able to switch to alternate but closely related host plants. Range extensions associated with specialization upon a totally new plant host characteristic of the recipient floristic realm are not frequent; all such examples cited in Illustration 2 represent cool humid forest ⟶ semi-arid scrub shifts, except for two independent Prosopis ⟶ Salix shifts. (Too little data is available to cite any potential Neotropic ⟶ Madrotertiary extensions accompanied by major host jumps; such examples most certainly exist, however, I know too little about the pattern of host-selection in most truly Neotropical genera).

An interesting case in point involves Andrena (Callandrena), a group clearly associated with the Compositae (except one very distinct species, A. levipes) of the arid portions of Mexico and southwestern United States. LaBerge has carefully monographed (1967) the group and provided detailed postulates of

cladistic relationships. Of the twenty species which are not primarily distributed in the desert United States or Mexico, there are eleven distinct lineages (treating the genitalicly distinct A. haynesi as a monotypic group). Though host generic identity of the Mexican and southwestern United States species are not known, it is clear that nearly all of the basic lineages within the subgenus were able to expand into the adjacent portions of North America by specializing upon one particular genus (or several closely related ones) which then provided an access route to great geographic expansion (presumably through limited competition); though several species utilize apparently the same genus, the overlap was apparently circumstantial and not determined by the nature of their as yet unknown ancestral Mexican hosts (e.g., A. aliciae - Helianthus/Rudbeckia; A. melliventris - Gaillardia & A. rudbeckiae - Rudbeckia/Ratibida; A. accepta - Helianthus; A. crawfordi/sitiliae - Pyrrhopappus & A. krigiana - Krigia; A. simplex - Aster/Solidago & A. placata - Solidago & A. asteris/asteroides - Aster; A. fulvipennis - ?oligolectic?; A. haynesi - Helianthus; A. helianthi - Helianthus & bracata - Solidago & A. vulpicolor - autumnal Chrysothamnus & A. irrasus - Amphiachrys/Gutierrezia; A. helianthiformis - Echinacea; A. gardineri - vernal Senecio & A. ardis - Chrysothamnus/Gutierrezia). Thus the United States assemblage of species are not closely related as one might initially expect but seem to represent a diverse array of independent phylads, each of which owes its range expansion in some way to a separate instance of host specialization -- quite probably involving generic shifts from the ancestral host in many cases.

Table 3 summarizes the information in the phyletic charts as to plant genera within North America that are known to support specialist-feeding bees. In each case the probable number of independent evolutionary switches leading to that particular host association is indicated in parenthesis. Generic specialization within the Compositae, other than Cichoreae is omitted for brevity sake. The largest number of independent specialist groups are associated with the Compositae (38 summer & fall composites; 13 spring Lasthenia, Layia, Blennosperma; 5 spring cichoriacs Agoseris, Malacothrix, Anisocoma; 5 summer Stephanomeria, Pyrrhopappus); this group contains in excess of 525 species of which the host choices are relatively certain, well in excess of one third of all the specialized-feeding bee species in North America.

TABLE 3

Classes of Plants with specialist-pollinators:

(# species; # independent lineages)

I Blooms at odd-time of the day:

Blooms early in the morning	Blooms in the evening
Calystegia (1;1)	Camissonia (several)
Camissonia (36;4)	Oenothera (25;11)
Cucurbita (14;2)	Mentzelia (several)
Ipomoea (6;3)	
Agoseris/Malacothrix(14+2?;5)	
Pyrrhopappus/Krigia (8;2)	
Sicyos (1;1)	

II Blooms at odd-times of the year:

Blooms in the early spring	Blooms at the very end of the season
Amsinckia (1;1)	Aster
Erythronium (3;2)	Baccharis
Limnanthes (2;2)	Chrysothamnus/Haplo-pappus (many)
Lomatium/Sanicula (2;1)	Gutierrezia/Hetero-theca
Ribes (2+?;1)	Solidago
Salix (29;11)	Gayophytum (5;2)
Zigadenus (1;1)	Perideridia (1;1)
Ranunculus (3;2)	
Claytonia (1;1)	
Vaccinium (1?;1)	
spring dandelions(14+2?;5)	
spring composites(29+8?;14)	

III Dominant plant in community (or most abundant):

Adenostoma (2;2)	Prosopis (30+2?;9)
Arctostaphylos (4+2?;3+1)	Helianthus (many)
Ceanothus/Rhamnus (4+1?;5)	Eschscholzia (15;7)
Chrysothamnus/Haplopappus (many)	Eriogonum (16+3?;2)
Larrea (22;12+3?)	Potentilla (alpine)(6;4)
Lasthenia/Layia(26+7?;11)	Cercidium (1;1)
Lesquerella (7+3?;3)	Acacia (2;2)

IV Unusual, hard-to-handle floral morphology;

unusually tiny pollen	pendant flowers
Cryptantha (24+2?;5)	Chamaedaphne (1?;1)
Mertensia (2;1)	Calochortus(albus+)(2;1)
Nama (8+2?;3)	Campanula (rot.+)(1;1)
Coldenia (15+2?;4)	Symphoricarpos (1;1)
	Erythronium (3;2)
unusually tiny flowers	Mertensia (2;1)
Croton (2;1)	Dicentra (1?;1?)
Euphorbia (28+10?;11)	Emmenanthe (2;2)
Eriogonum(16+3;2) (not fasciculatum)	Viola (1;1)
Tidestromia (3+2?;2+2?)	Vaccinium (1;1)
	Physalis/Chamaesaracha (16+6?;4)

TABLE 3
Classes of Plants with specialist-pollinators:
(# species; # independent lineages)

IV (cont.) Unusual, hard-to-handle floral morphology:

tubular flowers; with or without guard hairs
- Abronia (1;1)
- Amsinckia (1;1)
- Coldenia (15+2?;4)
- Cryptantha(24+2?;5)
- Eriastrum/Navarretia (10+3?;3)
- Heliotropium (5;4)
- Linanthus (6;3)
- Nemophila (7;4)
- Verbena (3+1?;1)
- Cirsium (4;2)
- Pontederia (3;2)
- Passiflora (1;1)
- Petalonyx (2;1)
- Menodora (1;1)
- Ipomopsis (1;1)
- Eriodictyon (4;4)
- Penstemon (7+5?;3)
- Nama (8+2?;3)
- Mimulus (1+1?;2)
- Lycium (2?;2?)
- Monardella (2;1)
- Salvia (2+1?;3)
- Monarda (5+1?;3)

unusually large pollen
- Callirhoe (2;2)
- Calystegia (1;1)
- Ipomoea (6;3)
- Hibiscus (1;1)
- Camissonia (35;4)
- Clarkia (11;9)
- Oenothera (25;11)
- Cirsium (4;2)
- Gayophytum (5;2)
- Malacothamnus (2;1)
- Sida/Sidalcea (1;1)
- Sphaeralcea(26+7?;10+1)
- Cactaceae (17+10?;8)

exclusion flowers
- Dalea(23+8?;12+1?)
- Lotus/Lupinus/Astragalus (36+14?;13+1?)
- Trifolium (8;4)
- Petalostemon+(12+2?;3)
- Melilotus (1?;1?)

V Flowers with oils but no nectar
- Steironema (4;1)

UNCATEGORIZED EXAMPLES
- total composites(416+74;38)
- Phacelia (39+7?;20)
- total Mentzelia(24+1?;8) (bees not nocturnal)
- total Potentilla(6;4)
- Capparidaceae (13+3?;9)
- Calochortus (16+3?;3) (not pendant)
- Stephanomeria (4;3)
- Lepidium (6+2?;2)
- Gilia (6;5)
- Campanula/Specularia(4;2) (not pendant)
- Heuchera (2;1)
- Nothoscordum (1;1)
- Polemonium (2+1?;1)
- Cornus (4+1?;1)
- Zizia/Taenidia/Thaspium (2+1?;1)
- Descurainia (3;1)
- Fallugia (3?;1?)
- Platystemon/Meconella (3+3?;1)
- Kalmia+(1+1?;1)
- Rhus (1;1)
- Hydrophyllum (1;1)
- Thelypodium (1;1)
- Arenaria (1;1)
- Barbarea (1;1)
- Argemone (1;1)

Lumping all papilionaceous specialist-feeders would yield about 40 separate specialist bee groups, but they are composed of only about 125 suspected specialist taxa. Many of the papilionaceous specialists are strongly genus-specific, and unlike the composite-feeders such a lumping on the familiar level may not be as meaningful a statistic.

All of the other groups of plants that have coevolved with specialist-feeding bees are of quantitatively a very different order of magnitude. Phacelia (Hydrophyllaceae) with at least 20 separate lineages comprising in excess of 40 species is exemplary. Camissonia (Onagraceae) and Sphaeralcea (Malvaceae) with about 35 specialist-feeders, Prosopis (Leguminosae), Cryptantha (Boraginaceae) and Salix (Salicaceae) with about 30, and Euphorbia (Euphorbiaceae), Oenothera (Onagraceae), Opuntia+ (Cactaceae) and Mentzelia (Loasaceae) with about 25 specialist-feeders each follow in that order. Of these groups however only Sphaeralcea (11), Salix (11), Oenothera (11), Prosopis (9), Euphorbia (8) and Mentzelia (8) are associated with more than 5 separate bee lineages each. Other specialist-feeding groups with 5-11 separate lineages but only 10-25 individual species are associated with Larrea (Zygophyllaceae), Ceanothus/Rhamnus (Rhamnaceae), Cleome/Cleomella/Wislizenia (Capparidaceae), Gilia (Polemoniaceae) and Eschscholzia (Papaveraceae). Plant groups with even fewer associated coevolved bee lineages but more than 10 individual species of obligate specialist-feeders are Penstemon (Scrophulariaceae), Physalis/Chamaesaracha (Solanaceae), Coldenia (Boraginaceae), Eriogonum (Polygonaceae), Cucurbita (Cucurbitaceae), Calochortus (Liliaceae) and Eriastrum/Navarretia (Polemoniaceae). All other plant genera with associated specialist feeders are associated with only 1-3 separate lineages and 10 or fewer bee species, so far as I am aware.

The plants utilized as resources by specialist-feeding bees are not a random sample of the North American flora, even though the wide range of bee sizes and energy requirements would not seem to preclude many possible non-anemophilous plants. Certain particular plant characteristics, however, seem most favorable to the coevolutionary relationships facilitating specialist-feeding habits (Table 3):

a) plants which bloom for a limited period very early in the morning or late at night generally represent the only available resource at that time and at the very least a facultative specialization by pollinators must result; continual competition from generalist-feeders on other resources during the

times when most floral resources are available might further restrict species pre-adapted to odd-time feeding and promote subsequent behavioral specialization. The majority of bees are associated with morning-blooming plants; the evening blooming plant-taxa are all primarily pollinated by moths and bee visits have probably not been major selective forces in evolving and maintaining the habit, though the bees associated with Camissonia are certainly locally important along the western edge of the Californian deserts and the southern Central Valley. On the other hand, the matinal Convolvulaceae, Cucurbitaceae, and Cichorieae are usually rather exclusively pollinated by these specialist bees. Though widespread throughout North America today, all such close co-associations are clearly arid southwest or Neotropical in origin.

b) plants which bloom at the very beginning or end of the blooming season within any community also force a restricted diet upon whatever pollinators are active contemporaneously. This temporally-induced restriction may be enhanced by selection for morphological specialization upon any short-lived bee species whose activity is completely restricted to these seasons. Such "odd-time blooming" specialists are present in all portions of North America, particularly so in the Eastern Deciduous Forests and mediterranean California. Desert regions are not particularly susceptible to this type of selective pressure, since in the majority of instances the entire blooming season is extremely short and keyed to relatively temporally unpredictable rains.

c) Dominant plants might be expected to support specialist herbivores even under conditions of heavy exploitation by generalist feeders, since the resource base is both predictable and sufficient to permit "table scrapping" by specialists. With the exception of the coniferous and deciduous forested regions of North America (the dominant species of which are nearly entirely anemophilous), dominants do support specialized pollinators throughout the year. Interestingly, in the Eastern Deciduous Forest, Cornus (Benthamidia) has not coevolved with any specialist bees, even though the less abundant Cornus (Svida) has coevolved with the abundant Andrena (Gonandrena). Dominant floral resources in the California grasslands and the Great Plains are semantic problems necessitating quantitative analysis, however, Eschscholzia, Lasthenia, Layia and Helianthus must certainly be analogous to dominant perennials in other ecosystems.

d) Plants with unusual tubular floral morphologies or species which produce pollen with exceptional dimensions can be partially exploited by

numerous strategies; however, bee species with morphological preadaptations increasing efficiency at utilizing such a resource will be favored. Should such a morphological specialization simultaneously decrease efficiency at exploiting more generalized floral syndromes, progressive positive selective feedback would be expected to result in the accentuation of both morphological adaptation and specialized-feeding habits. Bees collecting large pollen usually have long thick sparse transporting scopal hairs; bees collecting the small spikey pollen of the Compositae usually possess dense fine highly plumose scopal hairs; bees exploiting tubular morphologies generally have special setae on the mouthparts or front legs enabling extraction of pollen. This classification of floral hosts has by far the most component examples, especially plant genera with narrow tubular morphologies; frequently such plant genera are pollinated by many pollinators other than bees and hence such an adaptation should not be assumed to be a specialized morphological adaptation on the part of the plant resulting from the activity of specialist-feeding bees, indeed I believe the relation is not causal in the majority of cases. Nearly all plant genera in category (d) are arid adapted (or originally so); the only clear forest/moist associated taxa are Erythronium, Mertensia, Campanula and perhaps some leguminaceous groups.

The data presented in Table 3 indicate that these special circumstances are indeed often correlated with specialized-feeding tendencies. However, many plant genera with specialist pollinators cannot be included in these four categories. In cases (a), (b) and (d) the plants which are associated with specialist-feeders are generally even more frequently associated with generalists as well. Some plants evidencing strategy (d) and most of those which bloom at odd times of the day are the only species which rely upon specialists exclusively for their pollination.

These data on host-specialization are of course very preliminary; many taxa remain unknown and some of the associations extrapolated from known close relatives are probably incorrect. Thanks primarily to Professor Timberlake and the many apidologists associated with the University of California, California and west Sonoran Desert bee species are relatively well-known. Robertson in Illinois, Michener in Kansas, Bohart in Utah and Rozen and Neff in southern Arizona have also provided great amounts of floral data, but much of the country, particularly the eastern United States remains poorly known. In addition, very rare species, no matter

what their distribution, are always problematic. Lists of specialist-feeding (known or suspected with relative certainty) bees are presented in the appendix for each of 10 major subdivisions of North America. Not all species listed inhabit the entire region under consideration, and hence citations in the same list do not necessarily imply sympatry or occurrence at a particular locality. These lists are presented in their entirety so that: 1) future discoveries on host-associations can be incorporated easily into the conclusions presented herein; and 2) observations on pollination ecology of plant species in different parts of the country might be facilitated. Listings for the different regions of California are too voluminous to incorporate; interested persons may obtain them from the author directly.

The proportion of specialist-feeding bees (of total resident non-parasitic bee species) in all biotic regions of North America is correlated to species richness (Illus. 3). This positive correlation is observed within the geographic regions of California as well (Illus. 4). The percentage of specialist-feeders varies from a low of 15-22% in the forested and boreal regions of North America to 35-45% in the Great Plains and Great Basin, to a high of ca. 50% in mediterranean California and the desert. As documented in Moldenke (1976b) the percentages within subregions of California run much higher, clustering between 40-55% in most regions, with a low of 30% in the immediate maritime province to a high of 60% in the Mojave Desert. Within California, as noted from an entirely different point site viewpoint in Moldenke (1971), the alpine Sierra Nevada is noteworthy in supporting very few total bee species, a remarkably large 50% of which are specialized feeders (nearly all the specialist-feeding species are extremely rare however).

The total number of plant genera specialized upon within a region is also directly correlated to species richness. The number of plant genera with specialized feeders is highest in mediterranean California (55) and lowest in the Southern Mixed Forest (10) and tundra (6). The bee fauna of the forests of upper Austria falls on the low end of the curve (18 genera with coevolved specialist-feeding bees; 27 (12%) total specialist bee species -- Hamann & Koller, 1956), considerably below levels observed in the boreal forests of the United States (still poorly studied -- and probably will yield more cases of specialization upon subsequent analysis. No comparable data from other parts of the world are available.

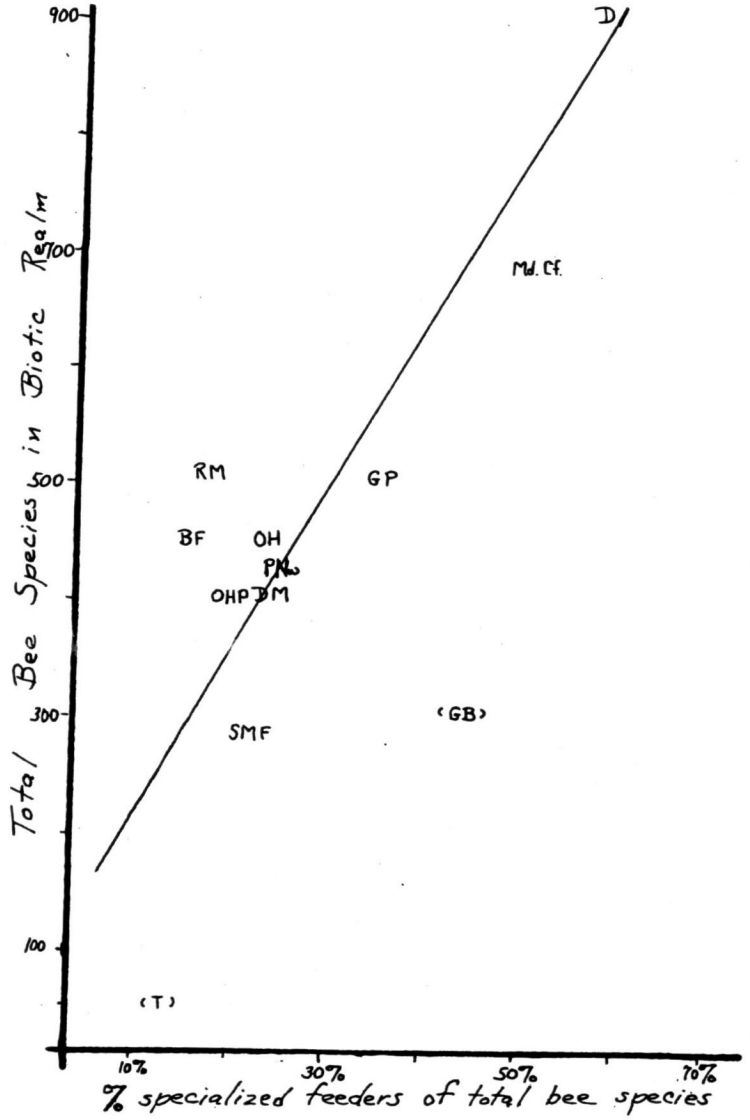


ILLUSTRATION 3

NORTH AMERICAN BEE DIVERSITY. Abbreviations as in Table 1. Faunal estimates of Great Basin and Tundra not considered robust enough to be considered in mathematical correlation. Slope significant at 99% certainty level.

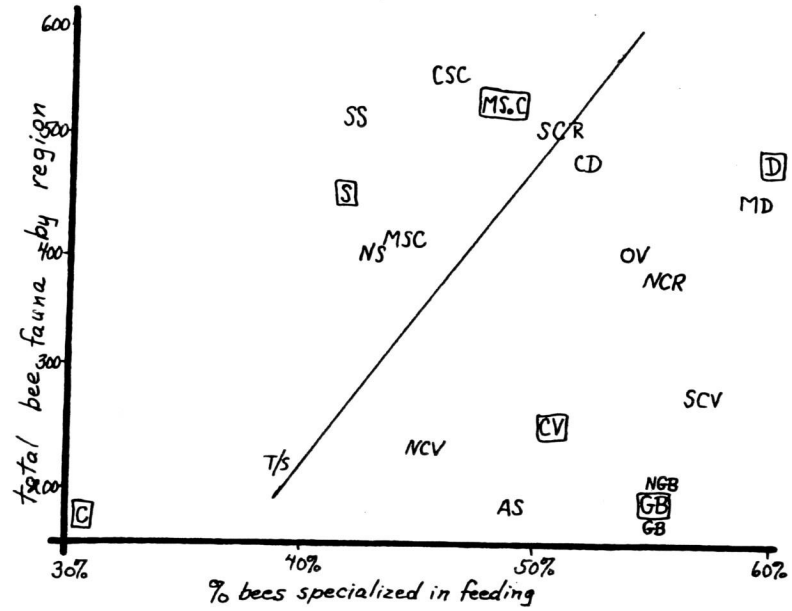


ILLUSTRATION 4

CALIFORNIA BEE DIVERSITY AND HOST-PLANT SPECIALIZATION. Abbreviations as in Table 2. Faunal estimates for AS, NGB & GB considered too tentative for mathematical analysis; slope significant at 90% certainty level. Average degree of specialization for compound regions indicated in squares: C=coastal; CV=central valley; GB; total Great Basin; D=desert; MSoC=montane southern California; S=Sierra/Cascade axis.

Within this group of specialist-feeding bees, the partial specialists "to the family level" (e.g., Compositae, Leguminosae) only increases as the total number of bee species and the percentage of total specialists decrease (Illus. 5). There is a semantic problem entailed in this analysis, however, since these type of "oligolectic" feeding patterns require extensive study, to determine whether such species in reality do utilize a number of unrelated confamilial plants throughout their range or whether there may be instances of true "generic specialists" included mistakenly within in the absence of more complete data. However, since this same trend is evident within the relatively better-studied subregions of California as well (Illus. 6), I presume it is not artifactual but reflects a reality of competition between specialists and generalists within constrained resource systems (ms. in prep.).

CONCLUSIONS

I. The host-association data base of North American bees is sufficient for tentative conclusions regarding many important aspects of host-plant specialization patterns.

II. There is only a 3-fold difference in bee species richness in the major phytogeographic realms of North America (excluding the depauperate tundra).
a) the high California bee diversity is in some ways an artifact of artificial political boundaries.
b) Great Basin and Southern Mixed Forest support fewest bee species; mediterranean California and desert support most bee species.

III. There is only a 3-fold difference in bee species richness between geographic regions of California.
a) cismontane southern California, southern Sierra Nevada and southern Coast Ranges are species rich; northern montane and coastal are species poor.

IV. There is not a clear species/area relationship underlying conclusion II. Bee species per area varies about 6-fold (excluding tundra), unrelated to possible simple causative correlations, but is an additional order of magnitude greater in mediterranean California.

V. True host specialization and host shifts have occurred about 250 times within the North American bee fauna.
a) nearly all ancestral stocks are primitively polylectic; nearly all diet changes are from polylectic ⟶ specialist. There are no known

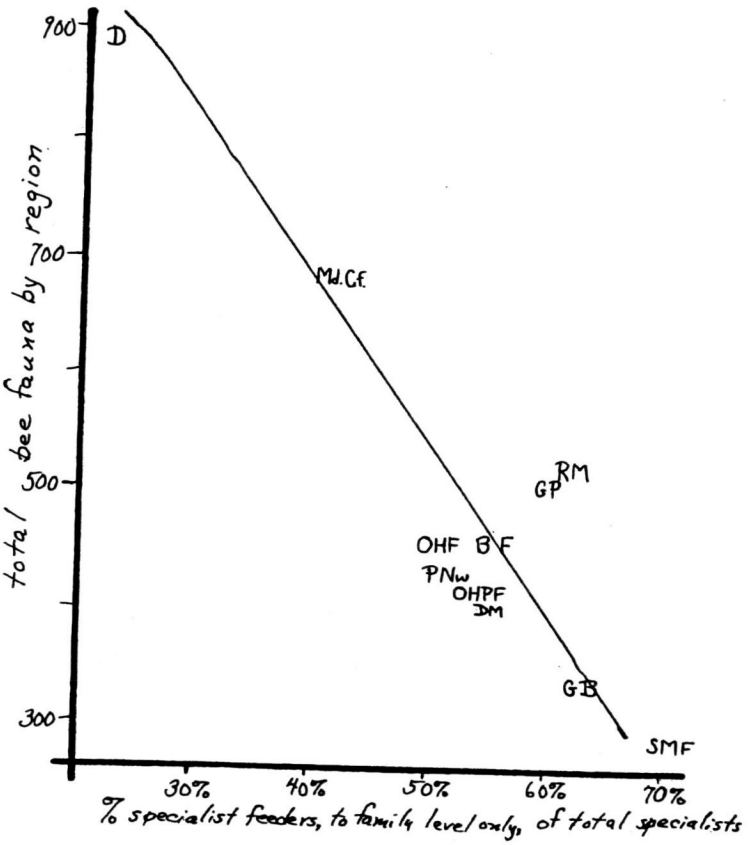


ILLUSTRATION 5

SPECIES RICHNESS OF "FAMILY-SPECIALIZED" BEES. Abbreviations as in Table 1. Correlation significant at 99% level.

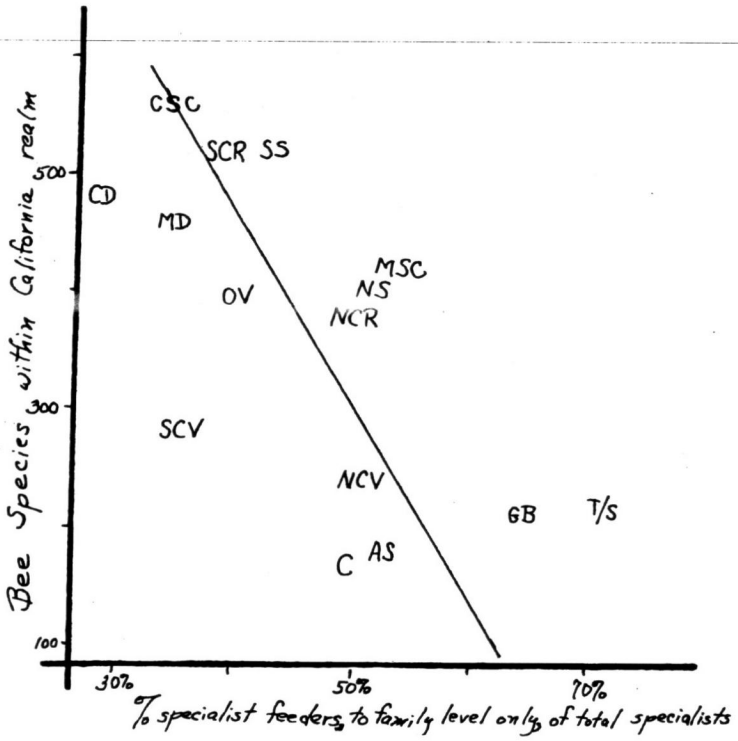


ILLUSTRATION 6

SPECIES RICHNESS OF "FAMILY-SPECIALIZED" BEES. Abbreviations as in Table 2. Correlation significant at 99% level.

specialist ⟶ polylectic switches; such switches are apparently therefore one-way changes only.

b) considering the diversity of the North American flora and North American bees in general, this is a surprisingly small number of host changes, relative to the number of common North American melittophilous plant genera not supporting specialist pollinators.

d) most such shifts onto a novel plant are not particularly successful, measured in subsequent adaptive radiation;

e) some immigrant phyletic lineages have entered the United States as specialists and have remained so on the same plants;

f) the two largest genera of North American bees are characterized by the highest levels of host-specialization; the third largest by perhaps none at all;

g) only 53 switches are known from $specialist_a \longrightarrow specialist_b$ (a not confamilial with b). Nearly all true host switches take place in the southwestern deserts or mediterranean California (equally); this type of host switch is characteristic primarily of Nomadopsis and Perdita (Pygoperdita);

h) few host switches are between visually similar taxonomically unrelated plants; few (except poorly documented Compositae) between very dissimilar but confamilial plants; most between groups without distinct characters in common -- sometimes the switch is to a dominant community member, sometimes to the only synchronous bloomer, many unexplicated.

VI. Arctotertiary-and Neotropical-associated bee lineages have contributed about equally to pollination ecology relations in arid/semi-arid western plants. Range expansions into close association with a novel geoflora is usually by polyleges, or by specialists which are already associated with an invading plant genus, but occasionally by host shifts presumably onto a novel host in a region of parapatry. Nearly all such shifts have been from Arctotertiary to Madrotertiary floras; only two from Madrotertiary to Arctotertiary.

VII. Most specialist-feeding bees in North America are oligolectic on Compositae and legumes. More species are associated with Phacelia than any other genus. Most plant genera with obligate specialist pollinators have coevolved with only 1-3 lineages and less than 10 species.

VIII. Bees tend to coevolve specialist-feeding relationships with plants which:

a) tend to bloom only early in the morning or late in the evening;
b) those which bloom at the onset or close of the anthesis season for that particular community;
c) are community dominants;
d) plants with unusual floral morphologies (i.e., thin tubular corollas, extremely large or small pollen grains, pendant blossoms and unusually tiny flowers).

IX. The percentage of specialist-feeding bees on a faunistic basis varies from ca. 15-50%:
a) percentage of specialist-feeders is positively correlated to total bee diversity;
b) highest percentages occur in Mediterranean California and the desert, lowest in eastern deciduous forests;
c) the total number of plant genera with coevolved specialists in biotic realms of North America is also positively correlated to total bee diversity (but disproportionately highest in med. California);
d) oligolectic "specialists to the family level" are negatively correlated to total species diversity within the floristic provinces of North America and within geographic regions of California.

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(specific references not cited in the text but utilized in the construction of Illustration 2 are omitted for brevity sake; the author acknowledges that most of this information is not original)

APPENDIX:

The lists which follow represent an attempt to catalogue the specialist-feeding bees associated with particular host-plants throughout the major biotic provinces of North America. Following the entry of each bee species is a designation of the assurance I have in its host association: F = relatively certain fact based on considerable host collection data and perhaps pollen microscopic analysis in addition; IV = tentative assignment, relatively certain of validity but needs microscopic verification; ZO = uncertain host-association made in the absence of sufficient direct data, usually on the basis of the known behavior of close relatives.

Specialists in Mediterranean California

Compositae
Colletes angelicus F; annae disseptus F; fulgidus fulgidus F; fulgidus longiplumosus F; lutzi monticola IV; ochraceus IV; simulans simulans F.
Hesperapis semirudis IV; n. sp. IV.
Andrena citrinihirta F; isocomae F; pallidifovea F; scutellinitens F.
Heterosarus californicus; compactus F.
Calliopsis bernardinus F; pugionis F.
Perdita (octomaculata) ensenadensis F; hirticeps luteocincta F; scitula antiochensis F; (zonalis) colei F; ericameriae F; foleyi F; interserta interserta F; lepidosparti lepidosparti F; lepidosparti novella IV; lompocensis ZO; melanderi ZO; obispoensis ZO; pallidiventris ZO; polita F; punctifrons F; repens ZO; rivalis F; scotti F; similis similis F; sweezyi F; zonalis bernardina F; zonalis monticola F; zonalis zonalis F; (ventralis) colei F; (zonalis) ciliata.
Dufourea australis australis F; australis mexicana F.
Dianthidium parvum schwarzi F; pudicum consimile F(+?); singulare F; ulkei F.
Ashmeadiella bucconis denticulata F; cubiceps clypeata F.
Heriades cressoni IV.
Anthocopa hemizoniae F.
Osmia coloradensis F; texana F; californica F; grinnelli F; montana quadriceps F; subaustralis F.
Megachile alata F; nevadensis F; subnigra angelica F; parallela facunda F; perihirta F; fidelis F; inimica jacumbensis F; inimica sayi F; pugnata pomonae F; pugnata pugnata F.
Exomalopsis chionura IV.
Diadasia enavata F.
Anthophora exigua F.
Xenoglossodes davidsoni F; pomonae F.
Svastra obliqua expurgata F; sabinensis nubila F; texana eluta F.
Melissodes rivalis F-Cirsium; lupina F; lustra F; glenwoodensis F; agilis F; semilupina F; bimatris F; bicolorata F; expolita F; robustior F; hurdi F; pallidisignata F; lutulenta F; vernalis F; velutina F; saponellus F; apressa F; microsticta F; paulula F; personatella F; melanura F; moorei F; confusa F; micheneri F.

Lasthenia
Andrena baeriae F; duboisi F; lativentris ZO; dissimulans IV?; essigi ZO?; hermosa IV; orthocarpi IV?; pensilis ZO?; puthua F; submoesta F; vexabilis?
Dufourea californica F.

Blennosperma
Andrena blennospermatis F.

Stephanomeria
Perdita hirticeps hirticeps F; Melissodes nigricauda F.

Chaenactis/Eriophyllum
Micralictoides altadenae F.

Layia
Andrena sublayiae F; layiae F; lativentris ZO?; duboisi F; escondida ?.
Perdita aureovittata aureovittata F; layiae basalicola F; layiae exoisa F; layiae layiae F.

Dandelions/Malacothrix
Perdita vandykei IV; aureovittata aureovittata F; aureovittata stenozona F; aureovittata maderensis F.
Andrena malacothricis F.
Dufourea malacothricis F.

Dandelions/Agoseris
Andrena (Diandrena) ablegata F; agoseridis F; chlorosoma F; chalybioides F; evoluta F; gnaphalii F; olivacea F; subchalybaea F.

Legumes
Anthidium atripes F; clypeodentatum F; emarginatum F; mormonum F; palliventre F; tenuiflorae F; utahense F (e. m. p. & t with Phacelia too)
Osmia integra F; nigrifrons F; nigrobarbata F; obliqua F; physariae F; sedula ?; liogastra F; lupinicola F; latisulcata F; calla F; claresoens F; malina F; cyanopoda IV; kincaidii F; regulina IV; sanctae-rosae F; densa densa F; densa pogonifera F; gabrielis F; + many potential species ZO.
Megachile concinna IV; melanophoea submelanophoea F.
Synhalonia -- many potential species ZO.

Melilotus
Hylaeus bisinuatus IV.

Trifolium
Andrena plana F.
Nomadopsis anthidius anthidius F; anthidius lutea F; trifolii IV.

Specialists in Mediterranean California (cont.)

Lotus
Perdita pyrifera ZO; trisignata P.
Nomadopsis mellipes IV.
Ancylandrena atoposoma P.
Anthidium collectum P; pallidiclypeum P.
Osmia aglaia IV+Penstemon?.
Ashmeadiella timberlakei solida P + Phacelia; timberlakei timberlakei P +P.
Proteriades bunocephala P; howardi P.

Phacelia
Colletes californicus P; turgiventris P; consors pascoensis IV +?.
Andrena nigra P; viridissima P; nigroclypeata ?.
Nomadopsis barbata IV; phaceliae IV.
Conanthalictus bakeri P; macrops P; nigricans P.
Protodufourea parca P
Dufourea mulleri P; trochantera P.
Anthidium banningense P; tenuiflorae P; palmarum P; collectum P; emarginatum mormonum P; palliventre P; (o, e, m, t, & pall. on Lotus too) P;
Chelostoma californicum P; incisulum P; marginatum marginatum P; marginatum incisuloides P; minutum P; phaceliae P.
Ashmeadiella micheneri ?; timberlakei timberlakei P + Lotus; timberlakei solida P + Lotus too.
Hoplitis fulgida platyura - emphasis only.
Proteriades mohavensis ZO.
Anthocopa phaceliarum IV +?; copelandica albomarginata - emphasis only?

Emmenanthe
Conanthalictus seminiger P.
Protodufourea wasbaueri P.

Penstemon
Ashmeadiella australis P.
Anthocopa anthodyta anthodyta P; elongata P; hebitis P; pycnognatha pycnognatha P; pycnognatha solatus P; triodonta triodonta P; triodonta usingeri P.
Osmia -- several species perhaps IV.

Cryptantha
Andrena cryptanthae P; osmioides osmioides P; osmioides benitonis P; timberlakei P
Proteriades boharti ZO; jacintana P; caudex P; evansi P; incanescens tota IV; nanula sparsa P; nanula nanula P; seminigra seminigra P; seminigra yosemitensis P; semirubra P; tristis P; tricauda P; remotula P.

Camissonia
Hesperapis nitidula - emphasis only.
Andrena (Diandrena) anatolis P; apasta P; chalybaea P; cyanosoma P; eothina P; foxii P; macswaini P; parachalybaea P; sperryi P; (Onagandrena) blaisdelli P; chylismiae P; convallaria convallaria P; convallaria subhyalina P; flandersi P; furva P; oenotherae P; oraria actidis P; oraria oraria P; rozeni P; vespertina P.
Dufourea boregoensis P; oenotherae P; saundersi P; scintilla P +; truncata P; timberlakei P; tularensis P.

Oenothera
Evylaeus aberrans P.

Clarkia
Hesperapis regularis P; Andrena bernardina P; lewisorum P; omninigra clarkiae P; omninigra omninigra P; Dufourea macswainii P; Megachile gravita P; pascoensis P; Diadasia angusticeps P; Melissodes clarkiae P; Tetralonia venusta carinata P; Ceratina sequoiae P.

Eriogonum
Ashmeadiella rufitarsis P; altadenae ZO; Perdita claypolei australior P; claypolei claypolei P; claypolei limulata P; jucunda P; nevadensis nevadensis IV; nodoscornia P; rhois reduota - emphasis only; rhois rhois - emphasis only; timberlakei P; varleyi niveipennis P; yosemitensis P.

Sida
Diadasia consociata P.

Malacothamnus
Diadasia laticauda P; nitidifrons P.

Specialists in Mediterranean California (cont.)

Sidalcea
Diadasia nigrifrons F.
Eschscholzia
Hesperapis pellucida ZO; n. sp. F; Andrena haroldi ?; Nomadopsis obscurella F; Perdita coalingensis F; interrupta vernalis F; nitens IV; quadrisignata IV; distropica F; monterreyensis F; obtusa ? (d, m, & o on Calochortus too); Micralictoides ruficaudis F; Dufourea leachi F; Andrena coactipostica IV.
Platystemon/Meconella
Dufourea leachi F; Andrena angusticrus F; aquila IV; biareola ZO; buccata ZO; stipator F.
Ceanothus
Andrena ceanothifloris ?; candidiformis F +?; cleodora melanodora F; cleodora cleodora F +?; lupini IV +?; scurra scurra IV; Panurginus - several species possible; Perdita micheneri IV (emphasis only).
Ranunculus
Andrena coerulea F; suavis F; cuneilabris F; Panurginus melanocephalus IV; nigrihirtus IV.
Nemophila
Andrena crudeni F; subnigriceps F; torulosa F; viridissima F; nemophilae F; macrocephala macrocephala F; macrocephala tetleyi F; Panurginus spp. ZO.
Potentilla +
Andrena melanochroa F; Nomadopsis comptula F; edwardsii F.
Euphorbia
Nomadopsis helianthi F.
Calochortus
Perdita californica californica F; calochorti F; distropica F; macrostoma IV; monterreyensis F; obtusa ?; tularensis F (d & mon. on Eschscholzia too); Nomadopsis cincta hurdi F; edwardsii F(1 population only); Dufourea dentipes F-albus group.
Arctostaphylos
Andrena arctostaphyllae F; Tetralonia acerba F; Emphoropsis cineraria IV; dammersi IV.
Opuntia +
Ashmeadiella opuntiae F; Diadasia australis californica F; opuntiae F; rinconis mimetica F; rinconis rinconis F.
Lomatium/Sanicula
Andrena microchlora F; pallidiscopa pallidiscopa F; pallidiscopa trifasciata F.
Perideridia
Perdita nevadensis culbertsoni IV.
Ribes
Andrena caliginosa F; submaura F; n. spp. F.
Mimulus
Nomadopsis trifolii IV + (Trifolium); Dufourea pectinipes ZO; versatilis versatilis IV; versatilis rubriventris F.
Linanthus/Gilia
Andrena levipes F +?; Perdita propinqua IV; Dufourea brevicornis F; calientensis F; gilia F; linanthi F; tuolumne F; vanduzei F; Hesperapis rufipes F; Micralictoides n. sp. F; Dufourea femorata F; pectinipes ZO?; versatilis versatilis IV?;
Eriastrum/Navarretia
Perdita richardsi ZO; blaisdelli ZO; leucosticta F; navarretiae powelli IV; navarretiae angusticeps IV; navarretiae navarretiae F; pelargoides F; davidsoni ZO; eriastri eriastri F; eriastri fusciventris F.
Cucurbita
Peponapis pruinosa angelica F; Xenoglossa strenua F; angustior F.
Zigadenus
Andrena astragali F.
Salix
Andrena albihirta ?; perarmata ?; rhodotricha ?; thaspiiformis ?; annectens F; bucculenta F; concinnula F; gibberis IV; nevadensis F; cressoni infasciata ?; huardi ?; opacella ?; ishii F; subaustralis F; semipunctata F; Perdita salicis occidentalis F; salicis personata F; salicis tristis F; Colletes xerophilus oismontanus F.
Adenostoma
Hesperapis ilicifoliae F; Perdita fieldi F; rhois reducta F - emphasis only; rhois rhois F - emphasis only.
Salvia/Lepechinia/Trichostema
Ashmeadiella salviae F.

Specialists in Mediterranean California (cont.)

Lepidium
Andrena lepidii IV.
Monardella
Nomadopsis timberlakei F; zonalis sierrae F; zonalis zonalis F.
Amsinckia
Tetralonia amsinckiae F.
Calystegia
Diadasia bituberculata F.
Limnanthes
Andrena limnanthis F; Panurginus occidentalis F.
Heliotropium
Perdita heliotropii perducta F; Nomadopsis hesperia equina F; hesperia hesperia F; Anthophora flavocincta IV.
Arenaria ?
Andrena subapasta IV.
Eriodictyon
Chelostoma cockerelli F; Nomadopsis linsleyi F; fracta F; Hoplitis colei F.
Gayophytum
Dufourea davidsoni F; spilura F; subdavidsoni F.

Specialists in southwestern Deserts

Compositae
Colletes compactus compactus F; compactus hesperius F; annae annae F; annae disseptus F; rufocinctus F; laticinctus F; gypsicolens F; tectiventris IV.
Hesperapis fulvipes F - Geraea; arenicola F - Geraea; 2 n. spp. F - Geraea; 2 n. spp IV.
Andrena (Callandrena) isocomae F; balsamorhizae F; monticola F; accepta F; aliciarum F - Pectis: perpuncta F - Heterotheca; helianthi F; ofella IV; auripes ZO; vulpicolor F - Chrysothamnus; trimaculata IV; tegularis IV; pecosana F; ardis F; barberi ZO; calvata F; neomexicana IV; pectidis F - Pectis: simulata IV; sonorensis F - Gutierrezia F.
Calliopsis deserticola F; pectidis F; coloratipes F; timberlakei F; crypta F; rozeni F; unca F;
Protandrena pectidis F; verbesinae IV;
Pseudopanurgus fraterculus timberlakei F; fraterculus fraterculus F; aethiops F; perpunctatus F; dicksoni IV; pectidellus F; cazieri ZO; verticalis ZO;
Perdita (ventralis) snelling F; austini F; brevihirta F; semicrocea F; (martini) amicula ZO?; (sidae) ovaliceps ZO; (Cockerellia) albihirta albihirta F - Geraea; albihirta geraea F - Geraea; luculenta ZO; coreopsidis collaris F - Gaillardia; albipennis pasonis IV; beata beata F; incana ZO; lepachidis lepachidis F; perpulchra F; verbesinae verbesinae F - sunflowers; utahensis F - Pectis; (Xeromacrotera) cephalotes IV; (Pentaperdita) albovittata F; idahoensis F; mandibularis F - Geraea/Chaenactis; melanochlora F; amoena ZO; chrysophila F; megapyga F; (Hexaperdita) bebbiae - F Bebbia; callicerata F - Baileya; heterothecae heterothecae F - Heterotheca; asteris F; heterothecae trizonata F; compacta IV; ignota ignota F; xanthisma F; foveata persimilis IV; cambarella platyura F; (zonalis) ampla F; fraterna F; irregularis F - Chrysothamnus; baccharidis F - Baccharis; basinicola ZO; chrysothamni F; dicksoni F; ericameriae F; interserta F; isocomae F; lepidosparti lepidosparti F; nigrocincta ZO; pallescens F; zonalis zonalis F; taeniata F; townsendi F; placida ZO; primula ZO; proxima F; scocia ZO; scotti F - Chrysothamnus; similis similis F; sweezyi F - Erigeron; (octomaculata) abdominalis F - Pectis; elegans F - Palafoxia; apacheorum F; butleri F - Pectis; affinis F; flavifrons F; halli ZO; indioensis F - Haplopappus; media F; mimula F - Haplopappus; melanostoma albocincta F; aplopappi F; croceipes F - Gutierreza; fallax F; gutierreziae F; aperta F - Gutierrezia; biparticeps F; dalyi F - Haplopappus; lasiogastra F - Pectis; maculipes F - Haplopappus; mesillensis F; pluchea F; retusa F; scitula scitula F; trifida F; trimaculata F; xanthodes F; nuda F; pellucida F - Haplopappus; phymatae F - Gutierrezia; reperta F - Chrysothamnus; sedulosa F - Baccharis; sejuncta F - Gutierrezia; snowii F; translineata F; (subfasciata) subfasciata F;
Micralictoides arizonensis F - Chaenactis;
Dufourea australis australis F; dammersi F; oryx F;

Specialists in southwestern Deserts (cont.)

Compositae (cont.)
Heteranthidium autumnale ZO?;
Paranthidium jugatorium jugatorium F - sunflowers; jugatorium butleri F - sunflowers;
Dianthidium curvatum sayi F; desertorum ZO; heterulkei heterulkei F; heterulkei fraternum F+?; implicatum IV?; parvum parvum F; platyurum mohavense F; platyurum platyurum F; ulkei ulkei F; ulkei perterritum F; curvatum xerophilum F;
Heriades texana ZO +?; crucifera ZO +?;
Anthocopa mirifica F; viguierae F;
Ashmeadiella bucconis denticulata F; cubiceps clypeata F; difugita emarginata F;
Megachile alata F; subnigra angelica F - Chaenactis; townsendiana ZO; inimica sayi F; mellitarsis F; policaris F; subfortis ZO?; frugalis frugalis - emphasis only; frugalis pseudofrugalis - emphasis only; soledadensis IV?; parallela facunda F; rossi F; sabinensis F; manifesta F; mohavensis IV?; subparallela F; fidelis F;
Exomalopsis solidaginis IV; gutierreziae IV?; compactula IV?;
Diadasia enavata F - Helianthus;
Syntrichalonia exquisita F - Helianthus;
Anthophora exigua F - Chrysothamnus; maculifrons F - Chrysothamnus; petrophila F; curta F - emphasis only;
Svastra helianthelli F; obliqua expurgata F; pallidior F; texana texana F; texana eluta F; machaerantherae F; petulca suffusca F (all preceding species emphasize Helianthus); sabinensis nubila F; sabinensis laterufa IV; sabinensis sabinensis F; sila F;
Melissodes relucens F - Haplopappus/Chrysothamnus; agilis F - Helianthus; fasciatella F - Haplopappus; limbus F; montana F - Helianthus+; subagilis F - Grindelia; coreopsis F - Helianthus/Aster/Solidago; exilis F; humilior F - Aster/Solidago/Haplopappus; pallidisignata F; rivalis F - Cirsium; submenuacha F - Helianthus+; plumosa F - Helianthus; menuachus F - Solidago/Grindelia; ochraea F - Haplopappus/Chrysothamnus; cerussata F; expolita F; lutulenta F; utahensis F; brevipyga F - Haplopappus/Chrysothamnus; vernalis F - Erigeron+; appressa - Helianthus/Grindelia+; velutina F; personatella F; verbesinarum IV;

Stephanomeria
Perdita albonotata F; hirticeps apicata F; stephanomeriae F.

Pyrrhopappus
Andrena tonkaworum ZO?(-Engelmannia)

Encelia
Anthocopa enceliae enceliae F; enceliae mortua F.

Malacothrix
Andrena agoseridis F+; olivacea F; malacothricidis F; Dufourea malacothricis F; Nomadopsis puellae F; Perdita dammersi F; malacothricis malacothricis F; malacothricis unica F.

Legumes
Anthidium atripes F; clypeodentatum IV; dammersi IV; palliventre F + Phacelia; emarginatum F + Phacelia; utahense IV - emphasis only; Ashmeadiella cazieri F; Anthocopa nitidivitta F; robustula F - Dalea; segregata ZO; timberlakei IV; Osmia titusi F; liogastra F; latisulcata F; clarescens F; Chelostomoides chilopsidis F; browni IV; lobatifrons F; occidentalis F (b, c, l & o emphasis tree legumes); subexilis F.

Lotus
Anthidium pallidiclypeum IV; Ancylandrena atoposoma F; Ashmeadiella aridula aridula - emphasis only.

Astragalus?
Anthophora porterae IV?; Nomadopsis zebrata IV?

Petalostemon
Colletes gilensis ZO; Perdita perpallida IV.

Dalea
Colletes petalostemonis IV; Hesperapis leucura F; n. sp. F; Nomadopsis melliloti IV?; Ancylandrena koelbelei F; Perdita amplipennis IV; hirsuta F; chloris F; eremica IV - emphasis only?; erythropyga F; paroselae F; Heteranthidium bequaerti F; Ashmeadiella inyoensis F; erema IV; eurynorhyncha IV; cazieri IV +?; rhodognatha F; xenomastax F; Hoplitis elongaticeps ZO; paroselae IV; Anthophora hololeuca F; Anthocopa daleae F; hypostomalis F; hurdiana F; rubrella rubrella ZO; rubrella rubrior F; rubrella macswaini F.

Specialists in southwestern Deserts (cont.)

Phacelia
Colletes californicus F; turgiventris F; Andrena nigra F; palpalis F; Nomadopsis phaceliae IV; Perdita cuspidata F + Nama; dentata IV; eremophila IV; nigrella IV; Conanthalictus bakeri F; caerulescens F; cockerelli F; macrops F; minor F; wilmattae F; Michenerula beameri F; Protodufourea n. spp. F; Dufourea mulleri F; trochantera F; Anthidium palliventre F + Lotus; palmarum F; emarginatum F + Lotus; Chelostoma marginatum marginatum F; Proteriades bullifacies F; mohavensis IV + Nama; Anthocopa beameri F + Nama; rupestris F; copelandica arefacta F.

Mentzelia/Eucnide
Hesperapis laticeps F + Eucnide; Megandrena mentzeliae F; Perdita atrata F; adustiventris F + Eucnide; bicuspidariae F (involucrata only); koelbelei concinna F (involucrata only); koelbelei koelbelei F (involucrata only)(+ Eucnide); mentzeliae F; mentzeliarum F; viridinotata ZO?; perplexa F; nigridia F; punctifera F; falcata F; Conanthalictus mentzeliae F; Xeralictus timberlakei F; bicuspidariae F; n. sp. F (all 3 involucrata only); Ashmeadiella leachi F.

Petalonyx
Perdita exilis F; crandalli F.

Eriogonum
Perdita clypeata clypeata F; clypeata immaculata F; distans F; jucunda F; labrata F; lucens F; nasuta nasuta F; nasuta galacticoptera F; nasuta obscurescens F; pectoralis IV; semilutea F; thermophila thermophila F; thermophila trilobata F; timberlakei F; varleyi varleyi F; xerophila fuscicornis F; xerophila xerophila F;

Larrea
Colletes clypeonitens F; covilleae F; larreae F; salicola F; stepheni F; Megandrena enceliae F +?; Hesperapis arida F; larreae F; Nomadopsis foleyi F; larreae F; Ancylandrena larreae F; Perdita covilleae F; flavipes IV; larreae F; punctulata IV; semicaerulea F; lateralis lateralis F - emphasis only; marcialis F - emphasis only; Hoplitis biscutellae F; Heteranthidium larreae F; Emphoropsis pallida F.

Penstemon
Anthocopa abjecta abjecta IV; anthodyta anthodyta F; arizonensis ZO?; elongata F; panamintensis ZO; pycnognatha pycnognatha F; triodonta triodonta F.

Sida
Exomalopsis sidae IV; Diadasia consociata IV; afflictula ZO.

Sphaeralcea
Hesperapis n. sp. F; Protandrena sphaeralceae IV?; Andrena sphaeralceae F; Calliopsis rhodophila IV?; Colletes sphaeralceae F; Hypomacrotera subalpinus subalpinus F; subalpinus andradensis F; Dufourea vandykei F; Perdita arcuata dinognatha F; bridwelli F; latior F; portalis F; sphaeralceae sphaeralceae F; sphaeralceae alticola F; magniceps IV; haplura IV; Tetralonia albescens ZO?; mohavensis ZO?; Diadasia lutzi F; diminuta F; martialis F; sphaeralcearum sphaeralcearum F; sphaeralcearum affinis F; tuberculifrons F; vallicola F; megamorpha F; olivacea F+; palmarum F+.

Argemone
Perdita argemonis F; Andrena argemonis - emphasis only.

Eschscholzia
Nomadopsis obscurella F; Perdita inflexa F; interrupta interrupta F; mohavensis F; mucronata F; robustella F; duplonotata F; mohavensis pimana ZO?

Abronia
Anthophora abroniae F.

Salvia
Ashmeadiella salviae F; Perdita salviae IV.

Cryptantha
Andrena cryptanthae F; Proteriades basingeri F; bidenticulata F; cryptanthae F; deserticola F; hamulicornis F; incanescens incanescens IV; incanescens nevadensis IV; nanula nanula F; nigrella attonita F; nigrella nigrella F; pygmaea F; reducta F; similis F; palmarum F; xerophila F.

Camissonia
Andrena (Diandrena) sperryi F; (Onagandrena) boronensis F; chylismiae F; convallaria convallaria F; convallaria subhyalina F; deserticola F; flandersi F; anograe F; mojavensis F; oenotherae F; rozeni F; rubrotincta IV; vespertina F; Dufourea boregoensis F; nudicornis F + Oenothera; latifrons F; scintilla F+.

Specialists in southwestern Deserts (cont.)

Oenothera
Hesperapis wilmattae - emphasis only; Andrena linsleyi F; Perdita pallida F; bequaertiana F; Evylaeus aberrans F; Sphecodogastra noctivaga F; Anthedonia nevadensis F; compta F; Tetralonia venusta venusta F; Anthophora affabilis F; aterrima F.

Nama
Conanthalictus deserticola F; minor F + Phacelia; namatophilus F; rufiventris F; conanthi F; cotullensis F; Sphecodosoma dicksoni F; pratti F; Protodufourea n. sp. F + Phacelia; Proteriades mojavensis F + Phacelia; Anthocopa rupestris F; beameri F (both + Phacelia); Perdita cuspidata F + Phacelia; namatophila F.

Tidestromia
Protandrena tidestromiae ZO?; Nomadopsis callosa ZO; Exomalopsis rufiventris F; Perdita cladothricis F; drymariae ZO?

Verbena
Calliopsis verbenae F; hirsutifrons F.

Acacia
Colletes platycnema IV; Eulonchopria punctatissima F.

Ipomopsis
Perdita giliae F.

Menodora
Simanthedon linsleyi F.

Euphorbia
Calliopsis squamifera F; anomoptera F; rogeri F; limbus F; gilva F; fulgida F; Nomadopsis nigromaculata F; Protandrena euphorbiae ZO?; Pterosarus nanulus IV; Exomalopsis euphorbiae F; Perdita euphorbiae F; mellea F; minima F; polycarpae F; helianthi F; biguttata F; cochiseana IV; crassula ZO; crotonis crotonis F + Croton; nanula F; obscurella F;

Prosopis
Colletes algarobiae F; deserticola IV?; perileucus ZO?; prosopidis F; Hylaeus sejunctus IV?; Perdita ashmeadi simulans F; ashmeadi vierecki F; difficilis F; discors ZO; exclamans F; genalis genalis F + Acacia; genalis panamintensis F; innotata F; luciae luciae F; luciae decora F; numerata numerata F + Salix; numerata hesperia F; nigricornis F; pallidipes F; prosopidis F; punctosignata punctosignata F; punctosignata flava F; punctosignata sulphurea F; mimosae F + Mimosa; sonorensis F; stathamae stathamae F; stathamae eluta IV; triangulifera F; Ashmeadiella prosopidis IV?; Megachile newberryae F + Acacia; Chelostomoides odontostoma F + Acacia; browni IV + Acacia.

Coldenia
Perdita arenaria F + Heliotropium; bellula F; coldeniae F; frontalis F; maculosa F; optiva F; rhodogastra F + Heliotropium; scutellaris F; sexfasciata F; wasbaueri F; trifasciata ZO?; vesca ZO?; diversa ?; Conanthalictus n. sp. F.

Calochortus
Nomadopsis cincta cincta F; Perdita bilobata F; bispinata F; calochorti F; californica inopina F; leucozona F; arizonica F; digressa IV?

Arctostaphylos
Andrena cristata F; Emphoropsis cineraria IV.

Cactaceae
Perdita carinata IV; texana texana F; texana ablusa F; Lithurgus apicalis apicalis F; apicalis opuntiae F; arizonensis ZO?; socorroensis ZO?; Melissodes opuntiella IV?; paucipuncta F; Exomalopsis cerei ZO?; Diadasia australis australis F; australis californica F; opuntiae F; piercei ZO?; rinconis rinconis F.

Echinocactus
Dufourea echinocacti F; Lithurgus echinocacti F; Idiomelissodes duplocincta F

Cucurbita
Peponapis pruinosa F; timberlakei F; crassidentata F; michelbacherorum F; utahensis F; Xenoglossa strenua F; kansensis F; angustior F; patricia F; gabbii F.

Heliotropium
Perdita heliotropii heliotropii F.

Proboscidea
Perdita hurdi F.

Specialists in southwestern Deserts (cont.)

Salix
Colletes xerophilus xerophilus F; xerophilus sonoranus F; Andrena cressoni infasciata IV; papagorum IV; concinnula F; Perdita salicis hirsutior F; salicis imperialis F; salicis laeta F; maculigera maculigera F + Prosopis.

Croton
Perdita crotonis leucoptera F; cucullata F; titusi F; crotonis F; undecimalis F.

Capparidaceae
Anthophora cockerelli IV; Centris californica IV; Perdita wilmattae stanleyae F.

Cleome +
Perdita vittata tricolor F + Wislizenia; zebrata flavens F; zebrata zebrata F; cleomellae F; thelypodii F; wislizeniae F (Wislizenia); Exomalopsis eriogoni ZO?; Nomadopsis scitula lawae F; macswaini IV - Wislizenia.

Descurainia
Andrena piperi F.

Lepidium
Andrena lepidii F; Perdita tortifoliae tortifoliae F; tortifoliae fremontii F; confusa F; geminata IV; greggiae F; Nomadopsis australior F.

Lesquerella
Andrena prima F; mohavensis ZO?; capricornis F; jessicae F; mesillae F; primulifrons F; alamonis F; Dufourea pulchricornis F; Perdita trinotata

Lycium
Anthophora phenax IV?; perdita lycii F; Anthophora coptognatha IV?.

Eriastrum
Hesperapis n. sp. F; Perdita compta IV; eriastri fusciventris F; richardsi ZO.

Physalis/Chamaesaracha
Hypomacrotera callops callops F; callops persimilis F; Perdita binotata ZO; physalidis F; rozeni ZO; lenis F; munita F; chamaesarachae F; sexmaculata IV +?; Colletes scopiventer F; chamaesarachae IV.

Ipomoea
Ancyloscelis sejunctus F.

Cercidium
Colletes cercidii ZO?; Chelostomoides discorhina F (+?); Ashmeadiella clypeodentata clypeodentata - emphasis only.

Dasylirion/Nolina
Perdita dasylirii - emphasis only; rehni - emphasis only.

Specialists in Great Basin

Compositae
Colletes compactus hesperius F; gypsicolens F; laticinctus F; rufocinctus F; simulans simulans F;
Andrena (Callandrena) ardis F; pecosana F; helianthi F - Helianthus; simulata IV; utahensis IV; vulpicolor F - Chrysothamnus; (Cnemidandrena) nubecula F; colletina F; ramaleyi F; chromotricha F; xanthigera F; costillensis F; canadensis F; sulcata F; bendensis F;
Calliopsis chlorops F; coloratipes F; timberlakei F;
Perdita (Cockerellia) albipennis F-Helianthus; hilaris F; (subfasciata) subfasciata F; (Hexaperdita) ignota ignota F; (Xeromacrotera) cephalotes ZO; (ventralis) brevihirta F; semirosea F; (zonalis) aemula aemula F; adjuncta F-Chrysothamnus; zonalis aequalis F-Chrysothamnus; aemula quadrifasciata F-Chrysothamnus; oregonensis oregonensis F; lepidosparti lepidosparti F; confinis ZO; affecta ZO; fraterna F; townsendi F; albopicta F; dubia parilis F; festiva ZO; vestita F; haigi ZO; munda ZO; similis similis F; similis pascoensis IV; subvestita F; toschiae ZO; stottleri stottleri F; (ootomaculata) affinis F; aplopappi F; aridella F; electa F; hirticeps candidipennis F; idonea F; knowltoni F; nuda F; percincta F; reperta F; phymatae F; rectangulata F; rhodura F; sejuncta F; snowii F; gutierreziae F; imbellis ?; luteola F; mesillensis F.
Dufourea marginata halictella F; oryx F.
Ashmeadiella bucconis denticulata F.
Osmia texana F; coloradensis F; californica F; grinnelli F; montana montana F; subaustralis F.

(cont. over)

Specialists in Great Basin (cont.)

Compositae (cont.)
Megachile agustini F-Helianthus; manifesta F; nevadensis IV?; parallela facunda F; asterae ZO?; nebraskana IV?; perihirta F.
Dianthidium curvatum sayi F +?; heterulkei heterulkei +?; parvum parvum F; cressoni ZO?; singulare F; subparvum F; ulkei ulkei F.
Anthophora exigua F; maculifrons F (both Haplopappus/Chrysothamnus).
Svastra obliqua expurgata F.
Melissodes rivalis F-Cirsium; lupina F; plumosa F-Helianthus; metenua IV; coreopsidis F; snowi F; coloradensis F-Helianthus; lustra F-Haplopappus/Chrysothamnus; agilis F-Helianthus; bimatris F-Chrysothamnus; menuachus F-Solidago/Grindelia; semilupina F; bicolorata F-Chrysothamnus; perpolita F; confusa F; robustior F-Helianthus; pallidisignata F-Haplopappus/Chrysothamnus; rustica F; grindeliae F; hymenoxidis F; subagilis F-Grindelia; brevipyga F-Haplopappus/Chrysothamnus; lutulenta F; utahensis F; vernalis F; saponellus F; monoensis F-Chrysothamnus; microsticta F.

Nothocalais
Andrena nothocalaidis F.

Malacothrix
Nomadopsis puellae F.

Agoseris
Andrena ablegata F; evoluta F.

Stephanomeria
Perdita albonotata F.

Penstemon
Anthocopa abjecta abjecta IV; abjecta alta F; anthodyta anthodyta F; elongata F; pycnognatha pycnognatha F; triodonta triodonta F; Osmia penstemonis F; spp. IV; Ashmeadiella australis F.

Phacelia
Chelostoma phaceliae F; Dufourea trochantera F.

Legumes
Nomadopsis zebrata bobbae IV?; Tetralonia chrysophila IV; spp. IV; Osmia integra F; physariae IV?; sedula F; clarescens F; gaudiosa IV?; kincaidii F; densa densa F; spp. IV; Megachile rohweri IV; Anthophora porterae IV?; Anthidium mormonum F +Phacelia; atripes F; clypeodentatum F.

Trifolium
Nomadopsis filiorum ZO?; anthidius lutea F.

Salix
Perdita salicis monoensis F; subtristis F; salicis euxantha IV; salicis sublaeta IV; Andrena erythrogaster F; subaustralis F; illinoiensis F; labergei F; salictaria F; ishii F; mariae F; sigmundi F; striatifrons F; wellesleyaea F; gibberis IV; andrenoides F.

Croton
Perdita crotonis caerulea F; crotonis juabensis F; crotonis dilucida F.

Gayophytum
Dufourea scabricornis F.

Sphaeralcea
Perdita beatula F; latior F; xanthochroa F; Diadasia lutzi F; olivacea F +; nitidifrons F; Calliopsis rhodophila IV?; Colletes sphaeralceae F; Hesperapis sphaeralceae IV; Protandrena sphaeralceae ?

Camissonia
Dufourea orovata F; Andrena nevadae F.

Oenothera
Andrena anograe knowltoni F; thorpi F; raveni F; chylismae F; rozeni F; Tetralonia speciosa IV?; Anthophora affabilis F; Megachile umatillensis F; anograe IV?; Anthedonia nevadensis F; Sphecodogastra noctivaga F; Evylaeus aberrans F.

Mentzelia
Andrena mentzeliae F; Perdita holoxantha IV; lunulata F; albata F; Conanthalictus mentzeliae F.

Eriogonum
Perdita xerophila discrepans F; pectoralis ZO?; gentilis F; jucunda F.

Petalostemon/Amorpha
Colletes gilensis ZO; petalostemonis IV; robertsonii F; albescens IV.

Argemone
Andrena argemonis - emphasis only.

Wislizenia
Perdita vittata confinis F.

Cleome/Cleomella
Perdita depressa F; zebrata zebrata F; Nomadopsis scitula F; personata F.

Specialists in Great Basin (cont.)

Stanleya
Perdita wilmattae wilmattae F; wilmattae miricornis F; Andrena hallii IV.
Lepidium
Perdita florissantella F; Nomadopsis australior F.
Ceanothus
Andrena oleodora F; candidiformis F (+?).
Calochortus
Perdita sculleni sculleni ?; sculleni segona ?; Nomadopsis cincta cincta F.
Arctostaphylos
Andrena obscuripostica F; cristata F.
Lomatium
Andrena microchlora F.
Cryptantha
Proteriades remotula F; incanescens incanescens F; Andrena chapmanae F.
Crucifers
Perdita cruciferarum F; Andrena piperi F; scurra F.
Cucurbita
Peponapis pruinosa F; utahensis F; Xenoglossa strenua F.
Thelypodium
Andrena winnemuccana IV?
Potentilla
Nomadopsis edwardsii F.

Specialists in Montane Western U.S.A.

Compositae
Colletes fulgidus F; laticinctus F; compactus compactus F; rufocinctus F; simulans simulans F; lutzi monticola F;
Hesperapis dispar F; carinata rodecki F;
Protandrena pectidis F;
Pseudopanurgis fraterculus timberlakei F;
Calliopsis chlorops F; coloratipes F;
Perdita ciliata IV; (Hexaperdita) ignota ignota F; (zonalis) dubia dubia F; dubia parilis F; stottleri stottleri F; oregonensis expleta F; rivalis F-Erigeron; sweezyi F-Erigeron; (octomaculata) fallax F; snowii F; solidaginis F; affinis F; aperta F; aplopappi F; luteola F; gutierreziae F; melanostoma F; phymatae F; rhodura F;
Andrena (Callandrena) accepta F; calvata F; helianthi F; neomexicana IV; ofella F; pecosana F; simulata IV; sonorensis F; vulpicolor F; (Stenandrena) pallidifovea IV; (Cnemidandrena) columbiana F; surda F; scutellinitens F; nubecula F; apacheorum IV; colletina F; sulcata F; hirticincta F; costillensis F; canadensis F; bocensis F; robervalensis IV (all Cnemidandrena emphasis Aster/Solidago).
Dufourea marginata marginata F; marginata halictella F (both Helianthus+);
Ashmeadiella bucconis denticulata F;
Heriades cressoni IV;
Dianthidium curvatum sayi F; ulkei ulkei F;
Osmia texana F; coloradensis F; californica F; marginipennis F; montana montana F; montana quadriceps F; subaustralis F;
Megachile agustini F; wheeleri F; parallela facunda F; perihirta F; fidelis F; frugalis frugalis F; inimica sayi F; mellitarsis F; pugnata pugnata F; pugnata pomonae F; subnigra angelica F; frugalis pseudofrugalis F;
Anthophora curta F (+?);
Svastra obliqua expurgata F;
Melissodes rivalis F-Cirsium; lupina F; composita F; glenwoodensis F; coloradensis F-Helianthus; agilis F-Helianthus; perlusa F-Helianthus; montana F-Helianthus; confusa F; pallidisignata F-Haplopappus/Chrysothamnus; grindeliae F; subagilis F-Grindelia; lutulenta F; microsticta F; lustra F; bimatris F-Chrysothamnus; robustior F-Helianthus; pullatella F; wheeleri F; rustica F; snowi F;
Phacelia
Dufourea trochantera F; Proteriades laevibullata ZO?; plagiostoma ZO?; rufina ZO?; Chelostoma phaceliae F; minutum F; Anthocopa copelandica albomarginata F; copelandica copelandica F.
Polemonium
Andrena ribblei ZO?; segregans F.
Zigadenus
Andrena astragali F.

Specialists in Montane Western U.S.A.

Fragaria
Andrena melanochroa F.

Prunus/Pyrus
Andrena miserabilis F (+?).

Cornus
Andrena persimulata IV; flocculosa ZO? Andrena hallii IV.

Campanula
Dufourea campanulae F; maura F; dilatipes F.

Symphoricarpos
Dufourea holocyanea F.

Potentilla +
Colletes nigrifrons F; Andrena birtwelli F; Nomadopsis edwardsii F; Dufourea fimbriata fimbriata F; fimbriata sierrae F; Panurginus bakeri F; cressoniellus F.

Calochortus
Perdita sculleni segona ZO?; leucostoma IV?; pulliventris ZO?; tularensis F; Dufourea calochorti F; dentipes F.

Mertensia
Colletes paniscus paniscus F; paniscus sculleni F; consors consors F(+?); consors pascoensis F (+?).

Petalostemon
Colletes gilensis ZO; petalostemonis IV; robertsonii IV.

Steironema
Macropis nuda F; steironematis opaca IV.

Arctostaphylos
Andrena cristata F; obscuripostica F; arctostaphyllae F; Emphoropsis cineraria IV; Tetralonia acerba F.

Gayophytum
Dufourea scabricornis F; spilura F; subdavidsoni F.

Legumes
Andrena lupinorum F; Tetralonia aragalli IV; spp. IV; Nomadopsis zebrata IV?; Megachile melanophoea calogaster F; melanophoea melanophoea F; melanophoea submelanophoea F; melanophoea wootoni/rohweri IV; Osmia integra F; longula F; nifoata F; nigrifrons F; physariae IV?; sedula F; trifoliama F; gaudiosa IV?; kincaidii F; malina F; densa F; calcarata F; nigrobarbata F; obliqua F; calla F; cyanopoda IV?; regulina IV?; gabrielis IV?; spp. IV.

Salix
Andrena semipunctata F; striatifrons F; sigmundi F; salicifloris F; mariae F; subaustralis F; erythrogaster F; nevadensis F; wellesleyana F; andrenoides F; concinnula F; trizonata F; labergei F; nigrae F; salictaria F; illinoiensis F; Perdita maculigera maculigera F; numerata numerata F; salicis coloradensis F; salicis subtristis F; werneri ZO?

Mimulus
Dufourea versatilis rubriventris F.

Ceanothus
Andrena cleodora F; mackiae F; scurra F; candidiformis F.

Ranunculus
Andrena suavis F; caerulea F; cuneilabris F.

Penstemon
Ashmeadiella australis F; Osmia penstemonis F; spp. IV; Anthocopa triodonta shastensis F; triodonta triodonta F; oregona ZO; hebitis F; abjecta abjecta IV; abjecta alta F; elongata F; anthodyta anthodyta F.

Clarkia
Melissodes clarkiae F; Ceratina sequoiae F; Diadasia angusticeps F; Megachile gravita F; pascoensis F; Andrena lewisorum F.

Trifolium
Andrena plana F; Dufourea afasciata F; spinifera F; Nomadopsis trifolii IV (+Mimulus); anthidius anthidius F; micheneri F.

Lomatium/Sanicula
Andrena microchlora F.

Agoseris
Andrena chalybioides F.

Sidalcea
Diadasia nigrifrons F.

Crucifers
Andrena scurra F.

Hydrophyllum
Andrena geranii F.

Heuchera
Colletes aestivalis F.

Ribes
Andrena (Dactylandrena) spp. F.

Stanleya
Andrena hallii IV.

Specialists in Great Plains & Prairies

Compositae

Colletes compactus F; simulans F-Solidago/Aster/Bidens; rufocinctus F-Solidago/Aster/Heterotheca; birkmanni ZO?; laticinctus F-Pectis/Gutierrezia; americanus F-Aster/Solidago; mandibularis ZO?; lutzi IV?;

Andrena(Callandrena) accepta F-Helianthus; aliciae F-Helianthus; melliventris F-Gaillardia; rudbeckiae F-Rudbeckia/Ratibida; helianthi F-Helianthus; helianthiformis F-Echinacea; irrasus F-Amphiachrys; beameri IV; simplex F-Solidago; asteris F-Aster; bullata F-Heterotheca; Haynesi F-Helianthus; gardineri F-Senecio; ardis F; berkeleyi ZO?; biscutellata ZO; tonkaworum - Engelmannia F.

Calliopsis coloradensis F-Solidago/Bidens;

Pseudopanurgus aethiops F-Helianthus; albitarsis F-Helianthus; rugosus F-Helianthus;

?Pterosarus labrosifrons distractus F; nebraskensis nebraskensis F; compositarum ?; innuptus F-Helianthus;

Perdita (Cockerellia) shinnersi F; purpurascens F-Gaillardia; perpulchra flavidior F; perpulchra punctatissima F-Heterotheca; lacteipennis lacteipennis F; lepachidis lepachidis F-Gaillardia; lepachidis pallidipennis F; lepachidis canadensis F; coreopsidis kansensis F; (Hexaperdita) pratti F-Helianthus/Heterotheca; cambarella cambarella F-Heterotheca; cambarella platyura F-Heterotheca; xanthismae F; fedorensis ZO; bishoppi planorum F-Heterotheca; ignota crawfordi F-Heterotheca; ignota ignota F-Heterotheca; foveata foveata ZO; foveata brachycephala F; alexi F-Helianthus/Heterotheca; (zonalis) stottleri F; (Pygoperdita) nebraskensis ZO; (?) albipennis F-Helianthus; (octomaculata) luteola F; rhodura F-Haplopappus; gutierreziae F-Gutierrezia/Haplopappus; laticincta F-Haplopappus; melanostoma F-Gutierrezia; lasiogastra F-Pectis; microsticta ZO; bruneri F-Solidago/Grindelia; swenki F-Solidago/Grindelia; prionopsidis F; tridentata F-Helianthus; fallax F-Helianthus; dolichocephala F-Helianthus; octomaculata terminata F-Solidago/Aster; atriventris F-Heterotheca;

Dufourea marginata F; oryx F (both Helianthus);

Nomia heteropoda kirbii F-Helianthus;

Paranthidium jugatorium jugatorium F; jugatorium perpictum F (both Helianthus);

Dianthidium curvatum sayi F; curvatum curvatum F; ulkei ulkei F;

Ashmeadiella bucconis bucconis F;

Osmia subaustralis F; texana F;

Megachile townsendiana F; fortis F; parallela F; pugnata pugnata F; fidelis F; policaris F; inimica sayi F; perihirta F; frugalis F; nebraskana F; manifesta F; nevadensis F; wheeleri F;

Diadasia enavata F-Helianthus;

Svastra obliqua obliqua F; petulca F-Helianthus; brevicornis F-Helianthus; comanche IV?;

Melissodes trinodis F-Helianthus; vernoniae F-Vernonia; wheeleri F-Helianthus; elegans F; snowi F; grindeliae F; subagilis F-Grindelia; agilis F-Helianthus; bidentis F-Helianthus/Rudbeckia; boltoniae F; coreopsidis F; denticulata F-Vernonia; fumosa F-Solidago; illata F; menuachus F-Grindelia/Solidago; rustica F-Aster/Solidago; desponsa F-Cirsium; coloradensis F-Helianthus; tuckeri F-Aster/Heterotheca; dentiventris F; perlusa F; nivea F; confusa F; pallidisignata F-Haplopappus/Chrysothamnus; gelida F-Helianthus; microsticta F;

Legumes

Chelostomoides suberilis F; Megachile melanophoea melanophoea F; Osmia dakotensis IV?; spp. IV; Anthidium maculifrons IV (emphasis?); psoraleae IV (emphasis?); atriventre astragali IV (emphasis?); Tetralonia belfragei IV?; illinoiensis IV?; chrysobothrys IV?; spp. IV; Calliopsis andreniformis F.

Petalostemon /Amorpha

Colletes robertsoni IV (+Amorpha); metzi ZO?; kansensis ZO?; aberrans IV; albescens IV (+Amorpha); susannae IV; wilmattae F; petalostemonis IV; Andrena cragini (Amorpha) F; Perdita perpallida F; Hoplitis micheneri (Amorpha) IV; Xenoglossodes albata ZO?

Salix

Perdita maculigera maculipennis F; maculigera bilineata F; Andrena illinoiensis F; salictaria F; nigrae; erythrogaster F; mariae F; trizonata F; bisalicis F; arenicola F; wellesleyana F; andrenoides F; nida IV.

Specialists in Great Plains & Prairies (cont.)

Monarda
Perdita gerhardi gerhardi F; gerhardi dallasiana F; variegata pura F; variegata variegata F; Metapsaenythia abdominalis abdominalis F; Dufourea monardae F.
Pyrrhopappus
Hemihalictus lustrans F; Andrena verecunda F; afimbriata IV; crawfordi F (+Serinia); sitilliae IV; senticulosa IV (+Serinia).
Croton
Perdita crotonis crotonis F; crotonis dilucida F; crotonis subnitens F.
Steironema
Macropis clypeata F; nuda F; patellata F; steironematis F.
Ipomoea
Melitoma taurea F; grisella F; Cemolobus ipomoea F; Ancyloscelis sejunctus F.
Opuntia
Lithurgus bruesi F; apicalis apicalis F; Perdita opuntiae F.
Euphorbia
Nomadopsis helianthi F; Perdita labergi F.
Lesquerella
Andrena trapezoidea F; primulifrons F.
Physalis/Chamaesaracha
Colletes wickhami ZO?; swenki ZO?; Perdita maura F; halictoides F.
Stanleya
Perdita wilmattae wilmattae F; Andrena halli IV.
Oenothera
Tetralonia speciosa IV?; Melissodes fimbriata F; Anthophora aterrima F?; Sphecodogastra texana F; oenotherae F; Megachile amica ZO; anograe F; oenotherae F;
Callirhoe
Diadasia afflicta perafflicta F; Melissodes intorta F.
Sphaeralcea +?
Diadasia diminuta F.
Phacelia
Andrena lamelliterga F.
Fragaria
Andrena melanochroa F.
Zizia
Andrena ziziae F.
Cleome
Perdita zebrata zebrata F.
Mentzelia
Perdita wootonae F.
Verbena
Calliopsis nebraskensis F.
Melilotus?
Hylaeus bisinuatus IV.
Heuchera
Colletes andrewsi F.
Specularia
Colletes brevicornis F.
Rhus
Andrena brevipalpis F.
Zigadenus
Andrena astragali IV.
Hydrophyllum
Andrena geranii F.
Prunus/Pyrus +
Andrena miserabilis F+.
Lepidium
Nomadopsis australior F.
Hibiscus
Ptilothrix bombiformis IV (+?).

Specialists in Northern Boreal Forests

Compositae
Colletes compactus F; simulans F-Solidago/Aster; americanus F-Solidago/Aster; mandibularis ZO?; solidaginis ZO?;
Andrena (Callandrena) helianthi F-Helianthus; aliciae F-Helianthus; simplex F-Solidago; placata F-Solidago; asteris F-Aster; asteroides F-Aster; (Cnemidandrena) canadensis F-Aster/Solidago; hirticincta F-Aster/Solidago; nubecula F-Solidago/Aster; peckhami ZO; chromotricha F-Solidago/Aster; robervalensis IV;
Paranthidium jugatorium jugatorium F-Helianthus;
Dianthidium simile IV;
Osmia subaustralis F;
Megachile pugnata pugnata F;
Svastra obliqua obliqua F;
Melissodes desponsa F-Cirsium; agilis F-Helianthus; denticulata F-Vernonia; dentiventris F-Aster; illata F; rustica F; subillata F; trinodis F-Helianthus;
?Pseudopanurgus albitarsis F-Helianthus; labrosus F-Helianthus;
?Pterosarus aestivalis IV; andrenoides IV; illinoiensis IV; nebraskensis nebraskensis IV; solidaginis IV;

Specialists in Northern Boreal Forests (cont.)

Salix
Andrena (Andrena) frigida IV; clarkella IV+; (Micrandrena) salictaria F; nigrae F; (Thysandrena) bisalicis F; (Parandrena) andrenoides F; nida IV; wellesleyana F; (Trachandrena) sigmundi F; mariae F; (Tylandrena) erythrogaster F.

Ericaceae
Colletes productus ZO?; impunctatus ZO?; Andrena kalmiae (Kalmia) F; bradleyi (Chamaedaphne) IV; carolina (Ledum) IV; Osmia inermis IV?

Legumes
Megachile melanophoea F; Osmia integra IV; spp. IV.

Cornus
Andrena persimulata IV; nigrifrons F; integra IV; fragilis F.

Pontederia
Melissodes apicata F; Dufourea nova-angliae F.

Steironema
Macropis longiligua F; ciliata F; nuda F; patellata F.

Penstemon
Osmia spp. IV.

Claytonia
Andrena erigeniae F.

Fragaria/Waldsteinia
Andrena ziziaeformis F; melanochroa F.

Thaspium/Taenidia
Andrena ziziae F.

Heuchera
Colletes andrewsi F; aestivalis F.

Mertensia
Colletes consors IV?

Melilotus ?
Hylaeus bisinuatus IV.

Rhus
Andrena brevipalpis IV.

Hydrophyllum
Andrena geranii IV.

Prunus/Pyrus +
Andrena miserabilis F.

Cucurbita
Peponapis pruinosa F.

Oenothera
Sphecodogastra oenotherae F.

Echium
Hoplitis anthocopoides F.

Bees of Boreal America (Tundra & Muskeg)

Mertensia
Colletes consors mesoscopus ZO.

Potentilla
Colletes nigrifrons F; Dufourea fimbriata F.

Aster/Solidago +
Andrena (Cnemidandrena) nubecula F; canadensis F; hirticincta F; columbiana IV; robervalensis ZO.

Salix
Andrena frigida IV; mariae F; salicifloris F; sigmundi F.

Ericaceae
Andrena bradleyi (Chamaedaphne) IV.

Legumes
Anthidium psoraleae zo?; Osmia longula ZO; (Acanthosmoides) spp. IV; Megachile melanophaea melanophoea F.

Specialists in Oak/Hickory & Mixed-Mesophytic Forests

Compositae
Colletes solidaginis F; mandibularis ZO?; compactus F; simulans F-Aster/Solidago; americanus F.
Andrena (Callandrena) accepta F-Helianthus; aliciae F-Helianthus; rudbeckiae F-Rudbeckia/Ratibida; helianthi F-Helianthus; simplex F-Solidago; placata F-Solidago; asteris F-Aster; duplicata F-Helianthus; gardineri F-Senecio; fulvipennis F; asteroides F-Aster; (Cnemidandrena) hirticincta F-Aster/Solidago; nubecula F-Aster/Solidago; robervalensis IV; canadensis F-Aster/Solidago.
Pseudopanurgus rudbeckiae IV; pauper ZO?; solidaginis IV; rugosus F-Helianthus; labrosus F-Helianthus?; helianthi F-Helianthus? albitarsis F-Helianthus?
Pseudopanurgus rugosus F-Helianthus.
?Pterosarus albitarsis IV-Helianthus?; helianthi IV-Helianthus?; labrosus IV-Helianthus?; andrenoides IV; compositarum IV; rudbeckiae IV; solidaginis IV; labrosiformis labrosiformis IV; nebraskensis nebraskensis IV.
Heterosarus illinoiensis F.
Perdita (Cockerellia) bequaerti indianensis F; (Hexaperdita) boltoniae boltoniae F-Chrysopsis; (octomaculata) swenki F-Solidago/Grindelia; octomaculata octomaculata F-Solidago/Aster.
Nomia heteropoda heteropoda F-Helianthus.
Osmia texana F.

Specialists in Oak/Hickory & Mixed Mesophytic Forests (cont.)

Compositae
Megachile inimica sayi F; frugalis frugalis F; pugnata pugnata F; parallela F.
Ashmeadiella bucconis bucconis - emphasis only?
Dianthidium simile IV.
Paranthidium jugatorium jugatorium F; jugatorium lepidum F (both Helianthus).
Svastra obliqua obliqua F; petulca F.
Melissodes desponsa F-Cirsium; coloradensis F; agilis F-Helianthus; bidentis F; boltoniae F; denticulata F-Vernonia; dentiventris F-Aster; fumosa F-Solidago; illata F; nivea F; rustica F-Solidago/Aster; subillata F; tincta F; trinodis F-Helianthus.

Monarda
Perdita gerhardi gerhardi F; Metapsaenythia abdominalis tricolor F; Dufourea monardae F.

Steironema
Macropis ciliata F; nuda F; patellata F; steironematis F.

Cucurbita
Peponapis pruinosa F; Xenoglossa kansensis F.

Taenidia/Thaspium
Andrena personata F; ziziae F; neonana ZO?

Phacelia
Andrena lamelliterga F; phaceliae F.

Oenothera
Sphecodogastra texana F; Anthedonia compta F.

Cornus
Andrena nigrifrons F; integra IV; fragilis F.

Salix
Andrena erythrogaster F; illinoiensis F; salictaria F; nigrae F; mariae F; bisalicis F; andrenoides F; wellesleyana F; nida IV.

Legumes
Megachile ingenua IV; melanophoea melanophoea F; mucida F; Tetralonia atriventris IV; spp. IV; Anthidium maculifrons IV; Osmia spp. IV;

Cruciferae
Andrena arabis F.

Ericaceae
Colletes validus IV?; productus ZO?

Fragaria/Waldsteinia
Andrena ziziaeformis F.

Pyrrhopappus
Hemihalictus lustrans F.

Krigia
Andrena krigiana F.

Prunus/Pyrus +
Andrena miserabilis F+.

Specularia/Campanula
Colletes brevicornis F.

Heuchera
Colletes aestivalis F.

Hibiscus
Ptilothrix bombiformis IV?

Melilotus ?
Hylaeus bisinuatus IV.

Rhus Calliopsis andreniformis F

Polemonium
Andrena polemonii F.

Hydrophyllum
Andrena geranii F.

Viola
Andrena violae F.

Penstemon
Osmia spp. IV.

Physalis
Perdita halictoides F.

Pontederia
Dufourea nova-angliae F.

Passiflora
Anthemurgus passiflorae F.

Ipomoea
Melitoma taurea F.

Ceanothus ?
Heterosarus pauper IV; virginicus IV

Specialists restricted to Pine Barrens & Coastal Sandy E. U.S.A.

Compositae
Colletes mitchelli F; thysanellae ZO?; Andrena braccata F; placata F; fulvipennis F; Perdita (Hexaperdita) bishoppi bishoppi F; bishoppi isopappi F; boltoniae chrysopina F; nubila F; (octomaculata) discreta F; consobrina consobrina F; consobrina lepida F; Megachile inimica inimica F; townsendiana F; Melissodes pilleata F; manipularis F.

Physalis
Perdita halictoides F.

Monarda
Perdita gerhardi monardae F.

Euphorbiaceae
Perdita picturata ZO?

Opuntia
Lithurgus gibbosus F; Melissodes mitchelli IV.

Kuhnistera
Colletes howardi IV.

Pontederia
Melissodes apicata F.

Hibiscus
Ptilothrix bombiformis IV (+?)

Specialists restricted to Pine Barrens & Coastal Sandy E. U.S.A.

Ipomoea
Melitoma taurea F; Cemolobus ipomoea F.
Ericaceae
Colletes validus IV?; Andrena daecki IV.
Oenothera
Megachile oenotherae F; Melissodes fimbriata IV; Anthedonia compta F.

Specialists in Oak/Hickory/Pine Forests

Compositae
Andrena (Callandrena) accepta F-Helianthus; aliciae F-Helianthus; ignota ZO; (Cnemidandrena) hirticincta F-Aster/Solidago; nubecula F-Aster/Solidago;
Colletes compactus F; simulans F-Solidago/Aster; americanus F-Aster/Solidago; mandibularis ZO?; solidaginis ZO?;
Perdita (Cockerellia) bequaerti bequaerti F; (Hexaperdita) georgica F-Chrysopsis/Aster; boltoniae boltoniae F-Chrysopsis; boltoniae chrysopina F-Chrysopsis; (octomaculata) consobrina consobrina F-Chrysopsis; octomaculata octomaculata F-Solidago/Aster;
Paranthidium jugatorium jugatorium F; jugatorium lepidum F (both on Helianthus);
Dianthidium simile F; curvatum curvatum F;
Ashmeadiella bucconis bucconis F;
Megachile townsendiana F; parallela paralella F; pugnata pugnata F; frugalis frugalis F; inimica sayi F; policaris F;
Svastra aegis F; obliqua caliginosa F; petulca F;
Melissodes desponsa F-Cirsium; coloradensis F; agilis F-Helianthus; boltoniae F; denticulata F-Vernonia; dentiventris F-Aster; fumosa F-Solidago; illata F; nivea F; rustica F-Aster/Solidago; tincta F-Aster/Chrysopsis; trinodis F-Helianthus;
Nomia heteropoda heteropoda F-Helianthus;
Pseudopanurgus rugosus F-Helianthus.
Heterosarus illinoiensis F.
?Pterosarus albitarsis F-Helianthus; compositarum IV; labrosiformis labrosiformis IV; solidaginis IV; nebraskensis meusebecki IV.
Legumes
Anthidium maculifrons IV (emphasis only?); Tetralonia atriventris IV; spp. IV; Megachile mucida IV: ingenua IV?: Chelostomoides spp. IV; Osmia spp. IV; Calliopsis andreniformis F.
Cucurbita
Peponapis pruinosa F; Xenoglossa strenua F; kansensis F.
Salix
Andrena mariae F; bisalicis F; andrenoides F; nida IV; nigrae F; erythrogaster F.
Taenidium/Thaspium
Andrena personata F; neonana ZO?; ziziae F.
Opuntia
Melissodes mitchelli IV; Lithurgus gibbosus F.
Oenothera
Megachile oenotherae F; Anthedonia compta F; Sphecodogastra oenotherae F.
Ericaceae
Colletes productus ZO?; validus IV?
Ipomoea
Melitoma taurea F.
Prunus/Pyrus +
Andrena miserabilis F (+?)
Cornus
Andrena fragilis F.
Pontederia
Melissodes apicata F.
Steironema
Macropis ciliata F; steironematis F.
Passiflora
Anthemurgus passiflorae F.
Ceanothus ?
Heterosarus pauper IV; virginicus IV
Krigia
Andrena krigiana F.
Fragaria/Waldsteinia
Andrena ziziaeformis F.
Specularia
Colletes brevicornis F.
Gerardia
Perdita gerardiae IV.
Melilotus ?
Hylaeus bisinuatus IV?
Potentilla
Panurginus potentillae IV.
Monarda
Metapsaenythia abdominalis F.

Specialists in Southern Mixed Forests

Compositae
Colletes simulans F-Solidago/Aster/Bidens; mandibularis ZO?; solidaginis ZO?;
Andrena (Callandrena) aliciae F-Helianthus; asteroides F-Aster; fulvipennis F;
Perdita (octomaculata) consobrina lepida F-Chrysopsis; (Cockerellia) bequaerti bequaerti F; lepachidis levifrons F; (Hexaperdita) georgica F-Chrysopsis/Aster; blatchleyi F; bishoppi bishoppi F-Heterotheca; graenicheri F-Chrysopsis; boltoniae chrysopina F-Chrysopsis; nubila F-Erigeron;
Pseudopanurgus rugosus F-Helianthus;
Heterosarus illinoiensis F;
?Pterosarus nebraskensis meusebecki IV; solidaginis IV;
Dufourea marginata F-Helianthus;
Nomia heteropoda kirbii F-Helianthus;
Megachile parallela F; townsendiana F; pugnata pugnata F;
Svastra aegis F; petulca F;
Melissodes desponsa F; agilis F-Helianthus; boltoniae F; denticulata F-Vernonia; dentiventris F-Aster; fumosa F-Solidago; nivea F; rustica F-Aster/Solidago; tincta F-Aster/Chrysopsis; trinodis F-Helianthus.

Legumes
Anthidium maculatum IV (emphasis only?); Osmia spp. IV; Tetralonia spp. IV; Chelostomoides spp. IV; Megachile ingenua IV.

Salix
Andrena nigrae F; bisalicis F; andrenoides F.

Ipomoea
Melitoma taurea F; Cemolobus ipomoea F.

Cucurbita
Peponapis pruinosa F; Xenoglossa kansensis F; strenua F.

Oenothera
Anthedonia compta F; Melissodes fimbriata F; Sphecodogastra oenotherae F; Megachile oenotherae F.

Opuntia
Lithurgus gibbosus F.

Prunus/Pyrus +
Larandrena miserabilis F (+?)

Pyrrhopappus
Hemihalictus lustrans F.

Gerardia
Perdita gerardiae IV.

Specularia
Colletes brevicornis F.

Ericaceae
Colletes productus ZO?

Thaspium/Taenidia
Andrena ziziae F; neonana ZO?

ADDITIONAL NOTES ON THE GENUS PRIVA. VII

Harold N. Moldenke

PRIVA Adans.

Additional & emended bibliography: Spreng. in L., Syst. Veg., ed. 16, 2: 753 & 754. 1825; Mold., Phytologia 43: 297 & 324—334. 1979.

PRIVA ARMATA S. Wats.

Additional bibliography: Kobuski, Ann. Mo. Bot. Gard. 13: 2, 3, 7, 16, 23, & 32—[35], pl. 4, fig. 11, & pl. 5, fig. 20. 1926; Mold., Phytologia 43: 332. 1979.

Illustrations: Kobuski, Ann. Mo. Bot. Gard. 13: [33] & [35], pl. 4, fig. 11, & pl. 5, fig. 20. 1926.

PRIVA ASPERA H.B.K.

Additional & emended synonymy: Priva aspera Humb. & Bonpl. ex Steud., Nom. Bot., ed. 1, 651 & 873. 1821. Priva aspera Kunth ex Spreng. in L., Syst. Veg., ed. 16, 2: 753. 1825.

Additional bibliography: Steud., Nom. Bot., ed. 1, 651 & 873. 1821; Spreng. in L., Syst. Veg., ed. 16, 2: 753. 1825; Steud., Nom. Bot., ed. 2, 2: 397. 1841; Kobuski, Ann. Mo. Bot. Gard. 13: 1, 3, 4, 7, 18—20, 23, & 32—[35], pl. 4, fig. 14, & pl. 5, fig. 23. 1926; Mold., Phytologia 43: 332—334. 1979.

Illustrations: Kobuski, Ann. Mo. Bot. Gard. 13: [33] & [35], pl. 4, fig. 14, & pl. 5, fig. 23. 1926.

PRIVA BAHIENSIS P. DC.

Additional bibliography: Kobuski, Ann. Mo. Bot. Gard. 13: 2, 4, 6, 10, 23, & 32—[35], pl. 4 & 5, fig. 9 & 18. 1926; Mold., Known Geogr. Distrib. Verbenac., ed. 1, 38, 41, & 99. 1942; Jacks. in Hook. f. & Jacks., Ind. Kew., imp. 2, 2: 628. 1946; Mold., Known Geogr. Distrib. Verbenac., ed. 2, 89, 99, & 195. 1949; Jacks. in Hook. f. & Jacks., Ind. Kew., imp. 3, 2: 628. 1960; D. de Andrade Lima, Anais XV Cong. Soc. Bot. Bras. 348. 1964; Mold., Phytologia 14: 343—344. 1967; Mold., Fifth Summ. 1: 169 & 187 (1971) and 2: 612 & 905. 1971; Troncoso, Darwiniana 18: 360, 408, & 411. 1974; Mold., Phytologia 43: 334. 1978.

Illustrations: Kobuski, Ann. Mo. Bot. Gard. 13: [33] & [35], pl. 4 & 5, fig. 9 & 18. 1926.

Recent collectors describe this species as a lank, perennial, branched herb, 0.5—1 m. tall, or an "arbusto" [Pareira 9713, mixed label?], the leaves pale- or dark-green and rugose, the flowers very small, and the calyx [in fruit] inflated, pale-green. They have encountered it in disturbed ground by cutover woodland, in waste ground with scattered shrubs and marshy lake margins, in cacao plantations "in coastal rainforest with small rivers and clearings with disturbed ground", "in disturbed roadsides near