

Interspecific Mouthpart Length Variation and Floral Visitation in the Parasitic Wasp Genus *Agathirsia* (Braconidae: Agathidinae)

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ABSTRACT Carbohydrate energy sources are known to be important for many adult parasitic wasps. Floral visitation is commonly observed, and in many groups specialized mouthpart morphology is associated with deep nectar extraction. In parasitic wasps, there are few data examining the relationship between host plant use and the length of the mouthparts. In an effort to associate mouthpart length to nectar source, pollen was identified from museum specimens of selected species of *Agathirsia* (Hymenoptera: Braconidae). Despite drastic differences in glossa length, the pollen of several species of Asteraceae were commonly found on specimens of various species. We infer that increased feeding efficiency, as opposed to nectar access, is the adaptive value of elongate glossae in *Agathirsia*. Species with short mouthparts, however, exhibited a difference from both the medium and long mouthpart categories in pollen similarity. This suggests that members of *Agathirsia* with elongated mouthparts are more apt to visit certain flowers compared with short-tongued species. Males and females exhibited considerable overlap of their common nectar sources and displayed similar pollen richness. Pollen richness was higher in species in the medium length category compared with the short category, but these results are confounded by the fact that the medium-length specimens were on average larger bodied.

KEY WORDS mouthpart length, nectar feeding, parasitic wasps, Asteraceae

Parasitic wasps, including the generally smaller, non-aculeate taxa are common floral visitors (Jervis et al. 1993, 1996; Tooker and Hanks 2000). Mate- and host-searching behavior are seldom documented on flowers, and their occurrence on flowers is thought to be rare (Jervis et al. 1993). Likewise, documentation of active pollen consumption (i.e., not as a contaminant of liquid food) is exceptional for nonaculeate wasps (Jervis et al. 1993, Jervis 1998). Floral nectar feeding, however, has been observed regularly (Jervis et al. 1993, Patt et al. 1997) and is often associated with increased longevity and fecundity (Idris and Grafius 1995, 1997; reviewed in Jervis and Kidd 1986).

Most Hymenoptera possess short mouthparts that are capable of obtaining exposed liquid food. The most common feeding adaptation of parasitic wasps is the elongation of various mouthparts (Jervis 1998, Krenn et al. 2005). These are referred to as concealed nectar extraction apparatuses (CNEA) in Jervis (1998), wherein he describes seven functional types. Jervis (1998) also tabulates the taxonomic occurrence and independent appearance of parasitic wasp CNEA from the literature. A CNEA arose in several families but most often in the Ichneumonoidea (Ichneu-

monidae and Braconidae). At least one type of CNEA (usually at least three) occurs in five braconid subfamilies. Agathidine braconids are well represented in the number of CNEA types and species.

There are three mouthpart types in *Agathirsia* (Pucci and Sharkey 2004) based on the categories of Jervis (1998). Most species are characterized by similarly lengthened galea and glossa (Jervis type I), which range from 0.2 to 1.8 mm in *Agathirsia*. Four species possess galea that are much shorter than the long, exposed, tube-forming glossa (Jervis type IV), which range from 2.1 to 5.5 mm. The third type (Jervis type VI) has apomorphic (derived) labial palps. *Agathirsia* contains only one rarely collected species of this type and is not treated in this study.

Species of Agathidinae are solitary koinobiont endoparasitoids of larval Lepidoptera (Sharkey 1997). The natural history of *Agathirsia* species is available only from their morphology, collection data, and the biology of closely related groups (Pucci and Sharkey 2004). Most of the 32 described species are collected from August through November and seem to be restricted to the southwestern United States and arid regions of Mexico. Most members seem to have wasp or bee mimetic coloration and/or setal pattern. All species contain dense setae on the glossa, and most specimens contain visible pollen, which together indicate floral nectar feeding. Based on those species

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with large numbers of collected individuals, there seems to be no marked sexual dimorphism.

The correlation between mouthpart length and feeding on flowers with relatively long corollas has been documented in various insect groups (Kevan and Baker 1983, Graenicher 1909, Gilbert and Jervis 1998), particularly bees where the association between tongue and corolla length has been documented in the field (Morse 1978, Harder 1988) and shown to be related to feeding efficiency (Inouye 1980; Harder 1983, 1985; Graham and Jones 1996). Nectar feeding has been shown to be most efficient when glossa length is at least equal to feeder (simulated corolla) length (Harder 1983). Likewise, field studies support the hypothesis that shorter tongued bees are more efficient than longer tongued bees on flowers with shorter corollas (Plowright and Plowright 1977, Ranta and Lundberg 1980). However, due to a greater propensity to feed from flowers with differing corolla lengths, longer tongued bees use a greater diversity of plant species as compared with co-occurring bee species with shorter tongues (Ranta and Lundberg 1980, Harder 1985, Borrell 2005).

The relationship between mouthpart variation and host plant use in parasitic wasps has not been investigated to the degree that it has in bees. The main purpose of our investigation was to establish whether glossa length in *Agathirsia* influences floral visitation. In particular, we sought to address the question, What is the benefit of possessing a long tongue for members of *Agathirsia*? Likely possibilities include 1) the ability to drink nectar from flowers with long corollas that would be otherwise inaccessible or 2) the ability to drink nectar faster than with short tongues. If only long-tongued *Agathirsia* are shown to visit flowers with relatively long corollas, the adaptive significance could be thought of in terms of access to nectar sources. Alternatively, if glossa length is not associated with corolla length, feeding efficiency is suggested as the driving force behind mouthpart evolution in *Agathirsia*.

Materials and Methods

Pollen was sampled from 122 museum specimens of 19 *Agathirsia* species. Specimens were chosen mainly to reflect a variety of species and glossal lengths as well as a variety of localities and dates (see *Appendix*). The long-glossa category refers to species with exposed, tube-forming glossae (Jervis type IV) in this article. Unfortunately, there were relatively few specimens available from this category ($n = 15$). The medium-glossa category consisted of species with glossae from 1 to 2 mm ($n = 59$), whereas the short-glossa category contained species with glossae < 1 mm ($n = 48$). Partitioning of these latter two groups was arbitrary. Pollen richness was calculated as the mean of plant species per wasp specimen.

Specimens were used from the following collections: American Entomological Institute, American Museum of Natural History, California Academy of Sciences, Canadian National Collection of Insects, Los Angeles County Museum, Cook Arthropod Collection

(Michigan State University), Snow Entomological Museum (University of Kansas), Texas A&M University Department of Entomology, U.S. National Museum, University of Arkansas Department of Entomology, Essig Museum of Entomology (University of California Berkley), and Bohart Museum of Entomology (University of California Davis).

A pin was used to transfer pollen from the specimens to 1.5-ml Eppendorf centrifuge tubes. Pollen was often attached to various body parts but was most abundant on the mouthparts. The pin was carefully cleaned after each use by rinsing with 95% ethanol and wiping with a clean paper towel. Part of each sample was placed onto a scanning electron microscope (SEM) stub for SEM analysis. The other portion of the sample was acetolyzed (Jones and Coppedge 1999) to remove the lipid layer surrounding the pollen grains. Acetolyzed pollen was viewed with light microscopy. Pollen was identified to the lowest taxonomic category possible. When identification to the species level was not feasible, a species code was designated so that pollen from conspecific plants could be recognized and tabulated for all wasp specimens. Pollen micrographs generated from this research are maintained as a part of the USDA-ARS, APMRU Pollen Reference Collection (College Station, TX).

The pollen assemblage between wasp groups was analyzed with PAST, version 1.94b (<http://folk.uio.no/ohammer/past/>). Analysis of similarity (ANOSIM) was used with the Jaccard similarity metric as the distance measure. ANOSIM is a multivariate, nonparametric test that compares distances between and within groups (Hammer et al. 2001). *P* values were based on 10,000 replicates of reconstructed group membership. A large number of uncommon pollen taxa have the potential to obscure our results. Therefore, ANOSIM was repeated several times with the rarest pollen taxa deleted each time.

Results

Approximately half of the 117 pollen taxa were members of Asteraceae (see *Appendix*). Furthermore, all but two of the 19 pollen taxa that were found on at least five wasp specimens are members of Asteraceae. In fact, wasps of all glossa lengths generally visited the same plant species (Table 1). Considering the pollen taxa that were counted from at least four wasp specimens, 11 of 24 were associated with all three mouthpart categories and accounted for 72% of the total pollen count. There were eight plant species that were associated only with the long tongue category, but these were based on only a single pollen grain.

The ANOSIM results, however, revealed some differences between mouthpart categories (Table 2). The pollen composition between the short and medium categories was significantly different regardless of the number of rare pollen taxa included. However, the composition between short versus long was significantly different only when the rarest pollen were excluded. There was not a significant difference between the me-

Table 1. Number of pollen grains of the most common taxa found on *Agathirsia* categorized by glossa length

Family	Scientific name/code	Short ^a	Medium	Long
Asteraceae	<i>Aster</i> sp. #1	12 (20)	30 (20)	3 (10)
Asteraceae	AST #60	4 (7)	21 (14)	4 (14)
Asteraceae	<i>Engelmannia pinnatifida</i>	3 (5)	20 (13)	5 (17)
Asteraceae	<i>Helenium</i> sp. #1	16 (27)	10 (7)	1 (3)
Asteraceae	AST #5	3 (5)	17 (11)	3 (10)
Asteraceae	AST #4	3 (5)	9 (6)	3 (10)
Asteraceae	<i>Helianthus</i> sp. #1	0 (0)	9 (6)	0 (0)
Asteraceae	<i>Viguieria</i> sp. #1	1 (2)	6 (4)	2 (7)
Asteraceae	AST #14	0 (0)	7 (5)	1 (3)
Asteraceae	AST #20	0 (0)	5 (3)	3 (10)
Asteraceae	AST #15	1 (2)	4 (3)	2 (7)
Malvaceae	cf. <i>Bastardia viscosa</i>	4 (7)	3 (2)	0 (0)
Asteraceae	AST #7	4 (7)	2 (1)	0 (0)
Asteraceae	<i>Ambrosia</i> sp. #1	2 (3)	2 (1)	2 (7)
Asteraceae	<i>Aster</i> sp. #2	1 (2)	5 (3)	0 (0)
Lamiaceae	<i>Lamium</i> sp. #1	6 (10)	0 (0)	0 (0)

^a Percentage (rounded) of the total number of grains listed here per category is in parentheses. Short glossa wasps, $n = 48$; medium glossa, $n = 59$; and long glossa, $n = 15$.

dium versus long categories except when at least four pollen grains were included in the analysis.

Pollen richness in all wasp categories failed the Shapiro-Wilk normality test. The only significant difference ($P \leq 0.05$) among glossa length categories was that the medium glossa length category exhibited a higher pollen taxa richness than the short glossa category according to a Kruskal-Wallis all-pairwise comparison test. Pollen richness (as the mean of each species with at least three specimens) increased with glossa length ($R^2 = 0.48$) and total wasp length ($R^2 = 0.31$) based on logarithmic regressions. However, these regressions were confounding, because the mean total length of the specimens in the medium-glossa category was 10.1 mm (SD 0.61), whereas the short-glossa and long-glossa categories measured only 8.1 mm (SD 1.0) and 8.2 mm (SD 0.43), respectively.

Commonly encountered pollen was generally similar between the sexes (Table 3). The most common pollen encountered was *Aster* sp. #1 for both sexes. For males, this was followed by AST #5 (Asteraceae) and AST #60. For females, it was followed by *Engelmannia pinnatifida* A. Gray ex T. Nuttall, and *Helenium* sp. #1. The ANOSIM comparisons between the sexes showed no significant differences, but they were often marginally significant

Table 2. P values of ANOSIM similarity tests of the pollen types found on *Agathirsia* wasps by glossa length categories

Min	SH vs. MD	SH vs. LG	MD vs. LG
1	<0.001	0.241	0.114
2	<0.001	0.164	0.288
3	<0.001	0.064	0.185
4	<0.001	0.015	0.026
5	<0.001	0.014	0.116
6	<0.001	0.003	0.110
7	<0.001	0.002	0.312
8	0.001	<0.001	0.299
9	<0.001	0.005	0.471
10	0.002	0.004	0.338

Min, minimum number of pollen grains to be included in the test; SH, short glossa (<1 mm); MD, medium glossa (1–2 mm); and LG, long glossa (>2 mm).

Table 3. Number of pollen grains of the most common pollen taxa (>5 occurrences) per sex

Family	Scientific name/code	Male ($n = 56$)	Female ($n = 67$)
Asteraceae	<i>Aster</i> sp. #1	21	23
Asteraceae	AST 60	15	13
Asteraceae	<i>Engelmannia pinnatifida</i>	10	17
Asteraceae	<i>Helenium</i> sp. #1	8	17
Asteraceae	AST 5	15	8
Asteraceae	AST 4	7	8
Asteraceae	<i>Helianthus</i> sp. #1	3	6
Asteraceae	<i>Viguieria</i> sp. #1	3	6
Asteraceae	AST 14	1	7
Asteraceae	AST 20	3	5
Malvaceae	cf. <i>Bastardia viscosa</i>	2	5
Asteraceae	AST 15	1	5
Asteraceae	<i>Ambrosia</i> sp. #1	3	3
Asteraceae	<i>Aster</i> sp. #2	1	5

(Table 4). In addition, there was no evidence of differing nectar source diversity between the sexes as males (mean rank = 56.5) and females (mean rank = 62.0) did not differ significantly in pollen richness (Kruskal-Wallis statistic = 0.803, $df = 117$, $P = 0.37$) according to a one-way analysis of variance.

Discussion

Mouthpart Length and Flower Visitation. The majority of the pollen found on *Agathirsia* was from Asteraceae. In the literature, flowers of Asteraceae and Apiaceae are most commonly associated with parasitic wasp feeding (Graenicher 1909, van Emden 1963, Jervis et al. 1993, Tooker and Hanks 2000). The scattered accounts of flower visitation by wasps with CNEA consist mainly of Asteraceae (Jervis 1998).

The corollas of nectar bearing Asteraceae flowers are by and large short and tubular (Cronquist 1981). There is no indication that members of *Agathirsia* visit complex flowers that might require learning to access. However, *Lamium* pollen was collected from some specimens. The only species of *Lamium* that occurs in the area where these specimens were collected is *L. amplexicaule* L. (Calflora 2008). The flowers of this mint have an enlarged opening and a narrowing corolla that extends ≈ 9.5 –16 mm (Kirkpatrick 1992). This suggests that at least a few species of *Agathirsia* are occasionally either nectar thieves or crawl into constricted areas for nectar feeding.

Table 4. P values of ANOSIM similarity tests of the pollen types found on *Agathirsia* wasps by sex

Min	Male vs. female
1	0.119
2	0.075
3	0.066
4	0.053
5	0.074
6	0.161
7	0.155
8	0.191
9	0.281
10	0.262

Min, minimum number of pollen grains to be included in the test.

Despite probable differences of feeding efficiency based on differing corolla length to glossa length ratios (see Introduction), members of each mouthpart category commonly visited flowers of the same species. Regardless of this overlap in resource use, there was a difference in the pattern of plant use, i.e., the composition of the most favored host plants. The short-tongued group possessed pollen whose composition differed significantly from both the medium- and long-tongued groups. The occurrence of the single significant *P* value in the medium versus long comparison (Table 2) is not considered to be indicative of a real difference between the groups. Indeed, randomization tests of our data sporadically produced significant *P* values in ANOSIM, but never like the patterns associated with the short-tongued category (Table 2).

The methods used here did not measure the number of visits to each nectar source per wasp—resource partitioning therefore might further be reflected in the degree to which certain flowers are visited as has been noted for bees (Ranta and Lundberg 1980, Harder 1988, Borrell 2005). Also, the interaction of glossa length with other aspects of wasp morphology might be responsible for differences in flower choice. Harder (1985) found that the combination of several aspects of bumble bee (*Bombus* spp.) morphology were better at predicting flower use than any one (including mouthpart length) alone. Similarly, Inoue and Kato (1992) found the length and width of bumble bee glossae are associated with flower visitation. Nevertheless, the hypothesis that species with short glossae are excluded from at least some of the common nectar sources of those with long glossae is not supported. Feeding efficiency is suggested as the adaptive value of elongated glossae. Although nectar source utilization in *Agathirsia* needs to be confirmed in situ, these results indicate that caution should be used if morphology is used to ascribe nectivores to nectar source.

Not all species of *Agathirsia* were well represented in this study—there could very well be cases of diet specialization by some species or populations in certain habitats. Indeed, Harder (1985) found flower choice to be related to local nectar source richness and flower abundance for several species of bumble bees. Documentation of flower use for all species of *Agathirsia* at specific localities is necessary to better understand their feeding ranges.

Mouthpart Length and Diversity of Nectar Sources.

Unlike results from the bee literature (Ranta and Lundberg 1980, Harder 1985, Borrell 2005), *Agathirsia* with the longest glossae did not have the highest diversity of pollen sources. The medium-length category had significantly higher pollen diversity than the short category, but this is confounded by a size difference between the groups. In bees, body size has been shown to be associated with flower choice (Harder 1985) and positively correlated with foraging efficiency (Harder 1983). Furthermore, larger bee species have been shown to forage over greater areas (Gathmann and Tscharrntke 2002, Greenleaf et al. 2007). It should be stressed that our sampling method was not well suited for diversity measurement. These

results are tentative, because the amount of pollen sampled from each specimen was not equal.

Sex and Flower Visitation. *Agathirsia* males and females seem to have similar nectar-feeding behavior based on similar pollen richness and pollen taxa found for each sex. This suggests that males are not restricted to the emergence site as they are in some species of parasitic wasps (Hardy et al. 2007). This is consistent with the apparent lack of size-related sexual dimorphism in the genus. The ANOSIM results, however, are ambiguous due to the group of marginally significant results (Table 4). Further research at the species level is needed to establish whether there are differences of host use associated with sex.

The apparent similarity in feeding between the sexes is consistent with the view that nectar nourishment is used mainly for locomotion as opposed to egg production. This is contrary to some results in the literature. Based on the field observations of Jervis et al. (1993), most flower-visiting parasitic wasps exhibited nectar-feeding behavior, and female parasitic wasps were more common and diverse than males. Furthermore, Pollard (1967) (cited in Jervis et al. 1993) and van Emden (1963) found female ichneumonoid wasps were more likely to possess immature ovaries when collected near flowers as opposed to areas without flowers. Jervis et al. (1993), however, dissected several species of ichneumonoid females ($n = 44$) taken from flowers, and only one specimen was deemed relatively immature. The rest contained either a large proportion of mature eggs or had atrophied ovaries.

Morphological feeding specializations tend not to be sexually dimorphic in parasitoids despite differing ecological and physiological factors associated with sex (Gilbert and Jervis 1998). This contradiction may be explained by mouthpart morphology being coded principally by autosomal alleles (Gilbert and Jervis 1998).

In conclusion, we conclude that the advantage of elongate mouthparts in *Agathirsia* is increased feeding efficiency on nectar from flowers with typical Asteraceae morphology, i.e., deep-lying nectar beneath tubular corollas. This may be realized by either feeding faster and/or attaining more nectar, on average, for each floral visit. Visitors with short mouthparts may only gain access to concealed nectar when it has accumulated to a relatively high level, whereas long-tongued visitors may attain nectar regardless of nectar level. This can be important for water and caloric intake. In fact, Gilbert and Jervis (1998) point out that many of the parasitic wasps with CNEA are from arid regions.

In addition to a decreased investment in mouthpart tissue, short mouthparts are advantageous by way of increased efficiency on food sources, such as honeydew, host blood, and extra floral nectaries. This may result in a greater diversity of food sources being used. For example, tachinid flies with long mouthparts have been shown to concentrate on floral nectar, whereas those with shorter mouthparts generally used honeydew and extra floral nectar in addition to floral nectar (Gilbert and Jervis 1998, analyzing data from Allen 1929). In fact, Bernstein and Jervis (2008) consider

exposed sources of sugar-rich food to be more common than concealed sources.

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Appendix. Collection data and pollen list for the specimens used in this study

Species and measurements ^a /collection site		Sex/collection date/pollen taxa ^b
Short-glossa species (<1 mm)		
<i>Agathirsia armandi</i> Pucci & Sharkey – glossa length = 0.87 mm; body length = 6.9 mm		
Puebla, nr. Petalcingo	m	21-viii-1963
		AST #56, <i>Aster</i> sp. #1
<i>Agathirsia asterophila</i> Pucci & Sharkey – glossa length = 0.59 mm; body length = 9.3 mm		
Guerrero, nr. Iguala	m	23-vii-1981
		AST #50, <i>Helonium</i> sp. #1, <i>Aster</i> sp. #1
Jalisco, 28 mi. E Guadalajara	f	15-viii-1962
		AST #60, <i>Helonium</i> sp. #1
Jalisco, nr. Autlan	m	1-viii-1978
		AST <i>Aster</i> sp. #1, <i>Helonium</i> sp. #1,
Morelos, nr. Zacatepec	f	28-viii-1967
		AST <i>Aster</i> sp. #1, <i>Helonium</i> sp. #1; MAL cf. Bast. vis.
Morelos, Cuernavaca	m	15-viii-1954
		AST <i>Helonium</i> sp. #1
Morelos, nr. Cuernavaca	m	12-viii-1954
		AST #7, #11, <i>Aster</i> sp. #1
Morelos, nr. Yautepec	f	17-viii-1962
		AST #5
<i>Agathirsia capillata</i> Pucci & Sharkey – glossa length = 0.57 mm; body length = 7.6 mm		
Morelos, nr. Tequesquitengo	f	16-viii-1962
		AST #47, <i>Cirsium</i> sp. #1
Morelos, 45 mi. S Cuernavaca	f	12-ix-1957
		AST <i>Helonium</i> sp. #1
Morelos, nr. Cuernavaca	f	14-viii-1954
		AST #11, <i>Aster</i> sp. #1; ? #44
Morelos, nr. Cuernavaca	?	14-viii-1954
		AST #7, <i>Helonium</i> sp. #1; ? #36
<i>Agathirsia collini</i> Pucci & Sharkey – glossa length = 0.53 mm; body length = 6.7 mm		
Puebla, Matamoros	f	8/9-ix-1948
		AST #4, #28, <i>Helonium</i> sp. #1
Puebla, Petalcingo	m	3-viii-1963
		AST Eng. pinn.
<i>Agathirsia davidi</i> Pucci & Sharkey – glossa length = 0.70 mm; body length = 8.2 mm		
AZ, Cochise Co, Apache	f	20-viii-1972
		AST <i>Eupatorium</i> sp. #1; POL <i>Eriogonum</i> sp. #1
AZ, San Cruz Co., nr. Lochiel	m	6-ix-1971
		AST <i>Aster</i> sp. #1, Eng. pinn., <i>Viguiera</i> sp. #1; OLE <i>Ligustrum</i> sp. #1
AZ, Pima Co., Canelo	f	22-viii-1974
		AST #59; SCR #1.;? #38
AZ, Pima Co., Sonoita	m	21-viii-1974
		CAP #4; NYC #8; ? #41
Chihuahua, 118km N Chihuahua	m	29-viii-1991
		AST <i>Ambrosia</i> sp. #1; PIN <i>Pinus</i> sp. #1
AZ, San Cruz Co., nr. Lochiel	f	6-ix-1971
		AST <i>Aster</i> sp. #2; FAB <i>Amorpha</i> sp. #1; POL <i>Eriogonum</i> sp. #1; ? #31
TX, Jeff Davis Co., Davis Mtns. S.P.	m	19-viii-1974
		AST #4; API #1.; LAM <i>Lamium</i> sp. #1; ROS <i>Prunus</i> sp. #1
<i>Agathirsia heleni</i> Pucci & Sharkey – glossa length ≈ 0.50 mm; body length = 6.1 mm		
San Luis Potosi, Matehuala	m	25-x-1962
		AST #4, #60, <i>Aster</i> sp. #1
<i>Agathirsia papotii</i> Pucci & Sharkey – glossa length = 0.70 mm; body length = 8.2 mm		
Guanajuato, nr. Leon	m	19-viii-1954
		AST #28, #33
Hidalgo, nr. Tizayuca	m	28-viii-1962
		AST #5, #36, <i>Helonium</i> sp. #1; VER #20
<i>Agathirsia rostrata</i> Pucci & Sharkey – glossa length = 0.50 mm; body length = 6.3 mm		
Puebla, 30 mi. SW Tehuacan	f	13-x-1968
		AST #61, #46, <i>Helonium</i> sp. #1
<i>Agathirsia testacea</i> Muesebeck – glossa length = 0.48 mm; body length = 7.6 mm		
CA, Fresno Co., nr. Firebaugh	?	9-ix-1948
		AST <i>Xanthisma</i> sp. #1; POL <i>Polygonum</i> sp. #1
TX, Kinney Co., 16 mi. SE Del Rio	f	10-iv-1950
		MAL <i>Abutilon</i> cf. <i>abutiloides</i> ; SOL <i>Nicotiana</i> sp. #1
CA, Riverside Co., 18 mi. W Blythe	m	8-iv-1979
		AST #63, <i>Helonium</i> sp. #1; ? #23
TX, Brewster Co., Rio Grande Vill.	m	12-viii-1976
		AST <i>Ambrosia</i> sp. #1, <i>Aster</i> sp. #1
CA, Imperial Co., Indian Pass Sum.	m	5/6-iii-1994
		LAM <i>Lamium</i> sp. #1; POA #25; RUB #2; SCR #1; ? #24
CA, Riverside Co., Palm Springs	f	26-iii-1955
		POL cf. <i>Antigonon</i> sp. #1; Ros <i>Crataegus</i> sp. #1
CA, Riverside Co., Palm Springs	m	27-iii-1916
		AST <i>Artemisia</i> sp. #1; RUB #1
TX, Bexar Co, Bexar	m	5-xi-1930
		AST <i>Aster</i> sp. #1
NM, Hidalgo Co., Rodeo	f	19-viii-1958
		NYC <i>Boerhaavia</i> cf. <i>diffusa</i>
CA, San Diego Co., Borrego	f	3-v-1956
		EUP #22; ? #33
CA, San Diego Co., Borrego	m	3-v-1956
		EUP #22
NM, Dona Ana Co., nr. Las Cruces	m	8-ix-1961
		MAL cf. Bast. vis.
CA, Riverside Co., Palm Springs	?	11-iv-1955
		AST #15, <i>Helonium</i> sp. #1; LAM <i>Lamium</i> sp. #1
Nuevo Leon, 13 mi. N Cienaga de Flores	f	23-vii-1976
		EUP #22
CA, Imperial Co., Indian Pass Sum.	m	5/6-iii-1994
		LAM #12, <i>Lamium</i> sp. #1
NM, Hidalgo Co., nr. Cotton City	m	14-viii-1986
		AST #5, #60, <i>Eupatorium</i> sp. #1, <i>Helonium</i> sp. #1; PNT <i>Platanus</i> sp. #1
CA, Riverside Co., Palm Springs	f	30-iii-1977
		AST <i>Helonium</i> sp. #1; LAM <i>Lamium</i> sp. #1, <i>Physotegia</i> cf. <i>intermedia</i> ; MAL cf. Bast. vis.
CA, Riverside Co., 18 mi. W Blythe	m	11-v-1978
		CLU <i>Hypericum</i> sp. #1; HYD #2; SAL <i>Salix nigra</i> ; MAL cf. Bast. vis.
CA, San Diego Co., Borrego Springs	m	14-iv-1954
		LAM <i>Lamium</i> sp. #1

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Appendix. Continued

Species and measurements ^a /collection site		Sex/collection date/pollen taxa ^b
<i>Agathirsia trichosoma</i> (Cameron) – glossa length = 0.73 mm; body length = 10.3 mm		
Morelos, nr. Cuernavaca	f	1-ix-1974
Michoacan, Cotija	f	7/8-ix-1972
Michoacan, Cotija	m	14-ix-1975
Guerrero, nr. Ixcateopan	m	13-ix-1982
Medium-glossa species (>1 mm<2 mm)		
<i>Agathirsia cressoni</i> (Mues. & Walkley) – glossa length = 1.2 mm; body length = 10.5 mm		
Nuevo Leon, 32 km W Linares	m	5-x-1962
TX	m	?
Nuevo Leon, 32 km W Linares	f	5-x-1962
TX	m	?
Nuevo Leon, 32 km W Linares	f	5-x-1962
TX, Uvalde Co., Garner St. Park	m	22-ix-1979
TX, McLennan Co., Waco	m	x-?
TX, Brazos Co., College Station	f	1-x-1923
Nuevo Leon, 32 km W Linares	f	6-x-1962
TX, Travis Co., Austin	f	8-x-1983
TX, Travis Co., Austin, Aldrich Farm	f	17-x-1951
TX, Plassal?	f	30-ix-1931
TX, Travis Co., Austin, Plase Park	f	21-ix-1979
TX, Uvalde Co., Garner St. Park	m	22-ix-1979
TX, Plassal?	f	30-ix-1936
TX, Brazos Co., Koppe's Bridge	f	12-x-1968
<i>Agathirsia nigricauda</i> (Viereck) – glossa length = 1.4 mm; body length = 9.8 mm		
NM, Grant Co., Hachita	f	31-viii-1974
TX, Atascosa Co.	f	23-x-1934
AZ, Conchise Co., nr. Portal	m	13-viii-1958
AZ, Conchise Co., nr. Portal	f	18-viii-1957
AZ, Conchise Co., nr. Ft. Huachuca	m	26-viii-1952
AZ, Conchise Co., nr. Ft. Huachuca	f	26-viii-1952
AZ, Conchise Co., nr. Portal	m	13-viii-1958
AZ, Conchise Co., nr. Portal	f	13-viii-1958
AZ, Conchise Co., nr. Portal	f	1-ix-1957
AZ, Cochise Co., Douglas	m	8-viii-1955
AZ, Conchise Co., nr. Portal	f	6-ix-1957
AZ, Conchise Co., nr. Portal	f	7-viii-1958
AZ, Pima Co., nr. Tucson	m	7-viii-1940
TX, Big Bend N.P., nr. Persimmon Cap	f	24-ix-1984
Chihuahua, Camargo	f	5-x-1966
NM, Hidalgo Co., Rodeo	m	13-viii-1959
TX, Culberson Co., Van Horn	?	10-ix-1976
NM, Lincoln Co., 17mi. N Carrizozo	f	?
TX, Terrell Co., nr. Dryden	m	28-ix-1973
TX, Culberson Co., Van Horn	f	10-ix-1976
NM, Grant Co., Hachita	f	31-viii-1974
AZ, Conchise Co., nr. Portal	m	14-viii-1957
NM, Grant Co., Hachita	m	29-viii-1974
AZ, Cochise Co., Douglas	m	11-viii-1940
TX, Jeff Davis Co., up. Limpia Cyn.	f	30-viii-1986
TX, Bexar Co.	m	16-x-1920
TX, Atascosa Co., Pleasanton	f	13-xi-1937
TX, Brewster Co., Big Bend N.P., N Posillos Mts.	m	4-x-1991
TX, Plassal?	f	5-x-1936
NM, San Miguel Co., Las Vegas	f	?
Durango, 36 mi. SW Cd. Lerdo	f	16-viii-1963

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Appendix. Continued

Species and measurements ^a /collection site		Sex/collection date/pollen taxa ^b
Nuevo Leon, 41 mi. S Saltillo	f	7-ix-1962
Nuevo Leon, 41 mi. S Saltillo	f	7-ix-1962
<i>Agathirsia michelei</i> Pucci & Sharkey – glossa length = 1.4 mm; body length = 8.2 mm	f	18-viii-1953
Jalisco, nr. Encarnacion de Diaz	f	3-x-1966
<i>Agathirsia parkeningi</i> Pucci & Sharkey – glossa length = 1.4 mm; body length = 7.1 mm	f	3-x-1966
Jalisco, Zapotlanejo	f	3-x-1966
<i>Agathirsia sericans</i> (Westwood) – glossa length = 1.7 mm; body length = 10.8 mm	f	3-x-1966
Nayarit, Chapalille	m	1-x-1966
Nayarit, Ixtlan	f	14-x-1968
Nayarit, Abuacatlan	m	14-ix-1970
Jalisco, nr. Magdalena	f	10-x-1975
Guerrero, nr. Taxco	m	16-ix-1976
Mexico, nr. Toluca	m	17-viii-1954
Mexico, nr. Toluca	f	17-viii-1954
Michoacan, El Cangrejo	f	30-x-1987
Long-glossa species (>2 mm)		
<i>Agathirsia longigladia</i> Pucci & Sharkey – glossa length = 3.5 mm; body length = 7.4 mm		
Morelos, Cuernavaca	m	19/21-xi-1987
<i>Agathirsia longilingua</i> Pucci & Sharkey – glossa Length = 4.6 mm; body length = 8.7 mm		
Queretaro, nr. Queretaro	f	21-ix-1977
Queretaro, nr. Queretaro	f	21-ix-1977
Zacatecas, nr. Rio Grande	f	27-ix-1975
Jalisco, San Fandia	f	24-ix-1963
<i>Agathirsia proxima</i> Westwood – glossa length = 3.5 mm; body length = 8.2 mm		
Morelos, Cuernavaca	f	8/10-xi-1987
Morelos, Cuernavaca	m	8/10-xi-1987
Morelos, Cuernavaca	f	8/10-xi-1987
Puebla, Chapulco	m	4-xi-1991
Jalisco, Teocaltiche	f	25-ix-1975
Morelos, Cuernavaca	f	13/14-xi-1987
Morelos, Cuernavaca	m	13/14-xi-1987
Zacatecas, nr. Rio Grande	f	27-ix-1975
<i>Agathirsia rufula</i> Westwood – glossa length = 2.4 mm; body length = 7.5 mm		
Morelos, nr. Thayacapan	m	28-x-1991
Distrito Federal	m	11-x-1962

^a Measurements are medians for the species and are calculated from a more extensive set of specimens than what is presently listed.

^b API, Apiaceae; APO, Apocynaceae; AST, Asteraceae; CAP, Caprifoliaceae; Cheno-Am, Chenopodiaceae-Amaranthus; CLU, Clusiaceae; COM, Commelinaceae; EUP, Euphorbiaceae; FAB, Fabaceae; HAM, Hamamelidaceae; HYD, Hydrangeaceae; LAM, Lamiaceae; MAL, Malvaceae; NYC, Nyctaginaceae; OLE, Oleaceae; PLA, Plantaginaceae; PNT, Platanaceae; PIN, Pinaceae; POA, Poaceae; POL, Polygonaceae; ROS, Rosaceae; RUB, Rubiaceae; RUT, Rutaceae; SAL, Salicaceae; SCR, Scrophulariaceae; SOL, Solanaceae; VER, Verbenaceae; ?, unknown; Eng. pinn., *Engelmannia pinnatifida*; Bast. vis., *Bastardia viscosa*.