

Studies of Halictinae
(Apoidea: Halictidae),
II: Revision of
Sphecodogastra Ashmead,
Floral Specialists of Onagraceae

RONALD J. MCGINLEY

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Ronald J. McGinley



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ABSTRACT

McGinley, Ronald J. Studies of Halictinae (Apoidea: Halictidae), II: Revision of *Sphecodogastra* Ashmead, Floral Specialists of Onagraceae. *Smithsonian Contributions to Zoology*, number 610, 55 pages, 151 figures, 3 tables, 2003.—The bee genus *Sphecodogastra* Ashmead is revised from the study of approximately 3200 specimens. Eight species are recognized with three described as new. All species are described and diagnosed. The systematic history of the genus, including questions concerning its monophyly, is presented. Flight records are summarized with histogram plots, distributions are indicated by dot maps, and illustrated keys are provided for species identification. Floral association data and daily flight activity records are summarized, and a literature review of nesting biology is presented for four species (*S. antiochensis*, *S. lusoria*, *S. oenotherae*, *S. texana*). The new species are *S. antiochensis* (a potentially endangered species), *S. danforthi*, and *S. potosi*. *Sphecodogastra lusoria* (Cresson) is elevated from junior synonymy under *S. aberrans* (Crawford), and *Halictus galpinisae* Cockerell is synonymized under *S. lusoria*. New combinations are *S. aberrans* (Crawford), *S. lusoria* (Cresson), and *S. oenotherae* (Stevens).

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Studies of Halictinae (Apoidea: Halictidae), II: Revision of *Sphecodogastra* Ashmead, Floral Specialists of Onagraceae

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Introduction

The eight known species of *Sphecodogastra* Ashmead are widely distributed throughout North America, ranging from southern Canada to Veracruz, Mexico (Figure 1). Females of this halictine genus collect pollen almost exclusively from evening primroses (Onagraceae). This specialized floral relationship and associated behavioral adaptations make *Sphecodogastra* of interest to bee biologists and pollination ecologists. The scopae (pollen collecting hairs on the hind legs of females) are reduced to a single, linear row of simple and apically curved hairs on the hind femora (Figures 2, 3). These relatively thick hairs apparently facilitate collection of the unusual pollen of their host plants (Thorp, 1979). The large pollen grains of Onagraceae are enveloped in what botanists refer to as viscin threads. These threads and associated pollen are "hooked" by the modified scopal hairs of these bees. As a result, females can accumulate extremely large pollen loads (Figure 4).

The dependence of *Sphecodogastra* on Onagraceae pollen affects their diurnal flight activity. Most species are both matinal and crepuscular, and two species (*S. noctivaga*, *S. texana*) are strictly crepuscular and nocturnal. The foraging activities of *Sphecodogastra texana* are correlated with lunar cycles, and

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TABLE 1.—Checklist of *Sphecodogastra* and numbers of specimens examined.

Species	Total	Females	Males
<i>S. aberrans</i> (Crawford)	426	327	99
<i>S. antiochensis</i> , new species	574	233	341
<i>S. danforthi</i> , new species	39	34	5
<i>S. lusoria</i> (Cresson)	918	633	285
<i>S. noctivaga</i> (Linsley and MacSwain)	225	201	24
<i>S. oenotherae</i> (Stevens)	170	104	66
<i>S. potosi</i> , new species	32	18	14
<i>S. texana</i> (Cresson)	903	847	56
Total	3287	2397	890

these bees apparently use their conspicuously enlarged ocelli (Figure 11) to navigate by moonlight (Kerfoot, 1967c).

The classification of *Sphecodogastra* has been fraught with questions concerning generic monophyly and with long-standing confusion surrounding the identity of two of the most common and widespread species, *S. aberrans* and *S. lusoria*. I hope this review will encourage additional systematic and biological work on this interesting group of bees.

MATERIAL AND METHODS.—This study was based on approximately 3200 specimens borrowed from 36 institutions. A summary of specimens examined of each species is presented in Table 1. Methods and terminology follow Harris (1979) and McGinley (1986). Following common convention, the terms "tergum" and "sternum" are abbreviated "T" and "S," respectively, in the "Systematics" and figure legends. Terminology associated with flight activity follows that of *The Torre-Bueno Glossary of Entomology* (Nichols, 1989:179, 423): crepuscular = "active or flying at dusk," and matinal = "of or in the morning, as in reference to activity patterns of insects." Flight data were recorded from labels for the specimens examined in this study.

ACKNOWLEDGMENTS.—I am grateful to the curators listed below who arranged the loan specimens for this study. The institution acronyms used follow those of Griffiths (1980) with minor modifications.

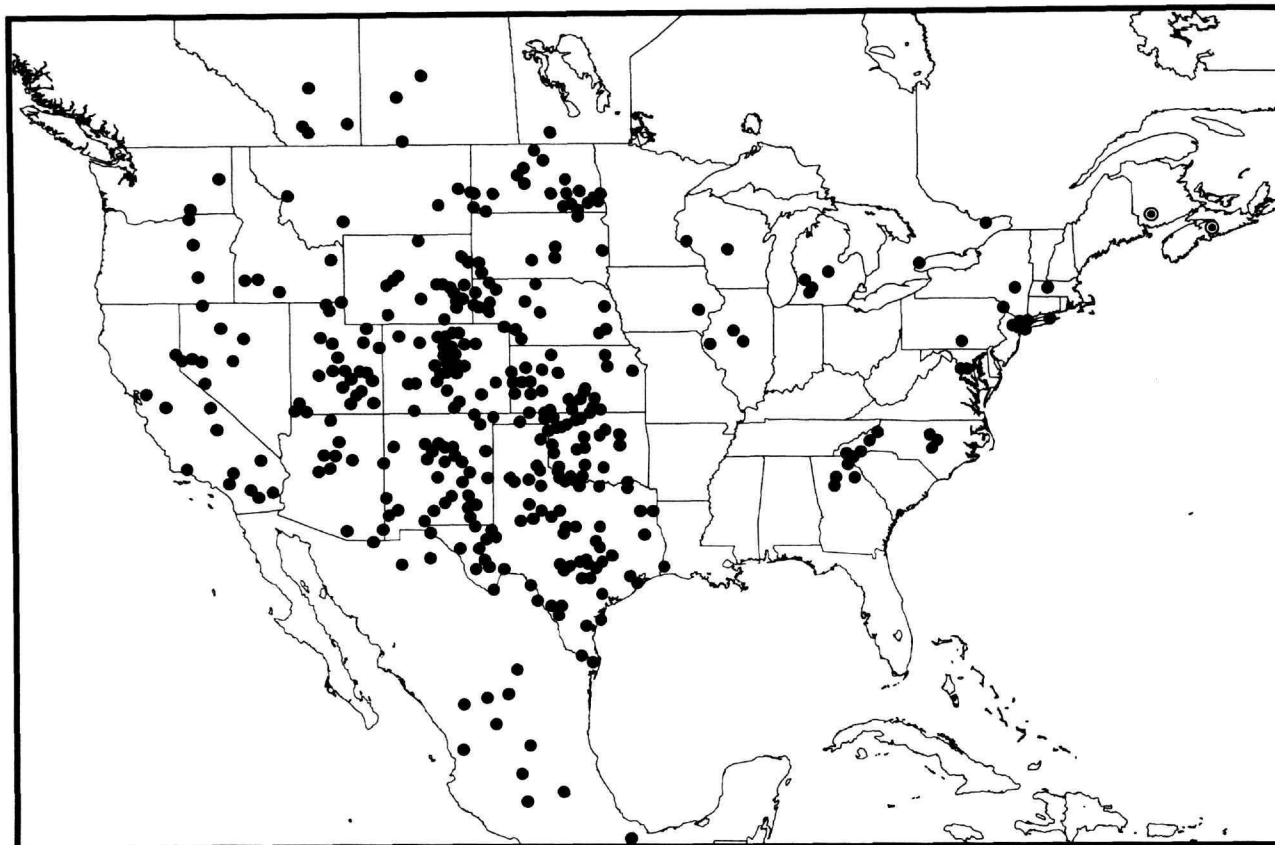
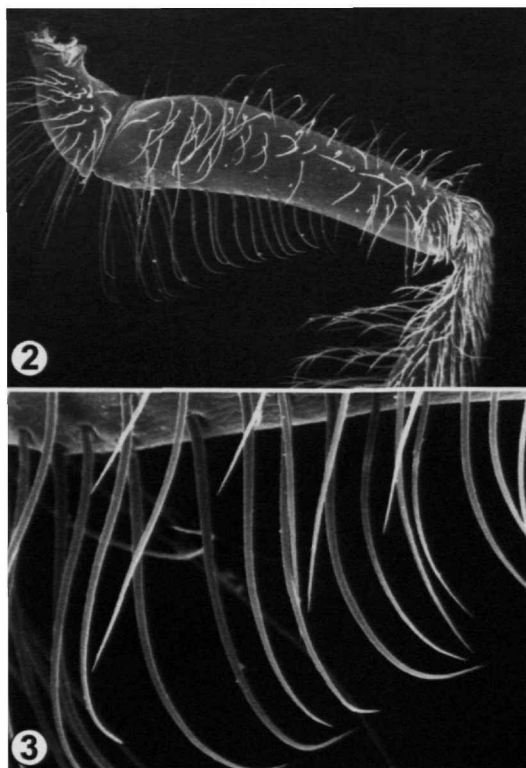


FIGURE 1.—*Sphecodogastra* distribution in North America (circled dots represent literature localities for *S. oenotherae*).

AMNH	American Museum of Natural History, New York (J.G. Rozen, Jr.)	MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (M.K. Thayer)
ANSP	Academy of Natural Sciences, Philadelphia (D. Otte, D. Azuma)	NCSU	North Carolina State University, Raleigh (C. Parron)
ASU	Arizona State University, Tempe (F.F. Hasbrouck)	NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C. (P.D. Hurd, Jr., S. Shanks)
BYU	Brigham Young University, Provo, Utah (S.L. Wood)	NMW	Naturhistorisches Museum, Wien (Vienna), Austria (M. Fischer)
CAS	California Academy of Sciences, San Francisco (W.J. Pulawski)	NYSM	New York State Museum, Albany (T.L. McCabe)
CDA	California Department of Agriculture, Sacramento (M.S. Wasbauer)	OhS	Ohio State University, Columbus (C.A. Triplehorn)
CMP	Carnegie Museum, Pittsburgh, Pennsylvania (G. Etkis)	OrS	Oregon State University, Corvallis (W.P. Stephen, G.M. Stonedahl)
CNC	Canadian National Collection, Ottawa (L. Masner, M. Sharkey)	TOR	University of Toronto (G. Knerer, L. Packer)
CSUFC	Colorado State University, Fort Collins (H.E. Evans)	UAE	University of Alberta, Edmonton (G.E. Ball, D. Shpeley)
CTMI	Central Texas Melittological Institute (J.L. Neff)	UCB	University of California, Berkeley (H.V. Daly)
CU	Cornell University, Ithaca, New York (G.C. Eickwort)	UCoIB	University of Colorado, Boulder (U.N. Lanham)
FSCA	Florida State Collection of Arthropods, Gainesville (L.A. Stange)	UCR	University of California, Riverside (S.I. Frommer)
INHS	Illinois Natural History Survey, Champaign (W.E. LaBerge)	UGa	University of Georgia, Athens (C.L. Smith)
KSU	Kansas State University, Manhattan (H.D. Blocker)	UIM	University of Idaho, Moscow (J.B. Johnson)
KU	University of Kansas, Lawrence (R.W. Brooks, C.D. Michener)	UMSP	University of Minnesota, St. Paul (P.J. Clausen)
LACM	Los Angeles County Museum of Natural History, California (R.R. Snelling)	UND	University of North Dakota, Grand Forks (P.B. Kanowski)
MCPM	Milwaukee City Public Museum, Wisconsin (G.R. Noonan)	UNL	University of Nebraska, Lincoln (B.C. Ratcliffe)
		USU	Utah State University, Logan (T.L. Griswold)
		UWL	University of Wyoming, Laramie (R.J. Lavigne)
		UWM	University of Wisconsin, Madison (S. Krauth)



FIGURES 2, 3.—*Sphecodogastra* scopae, anterior views: 2, female *S. texana*; 3, closeup of *S. oenotherae* scopal hairs.

Many individuals contributed to the production of this monograph, and I would like to acknowledge their help. Elaine R.S. Hodges drew the male terminalia, Vichai Malikul took the habitus and head photographs, and George Venable was responsible for scanning these images and the SEM photos, for graphic enhancement, and for plate layout. Preliminary distribution maps were generated by Daniel Cole using Arc/Info software and were then enhanced for publication by George Venable in Adobe Illustrator. Maureen Mello handled the laborious return of borrowed specimens to 36 museums.

I am greatly indebted to my apoid colleagues Bryan Danforth (CU) and John Neff (CTMI) who provided critical specimens of the rarely collected new species *Sphecodogastra danforthi*. Warren Wagner (NMNH) contributed invaluable literature and advice on Onagraceae systematics and distribution. Michael Caterino (UCB) and Jerry Powell (UCB) contributed important information on the Antioch Dunes habitat, and Jerry Powell provided me with unpublished collection records for *S. antiochensis*.

Sphecodogastra Systematic History

The monophyly and generic limits of *Sphecodogastra* and the identity of two of its most commonly collected species, *S.*

aberrans and *S. lusoria*, have been subject to question and controversy for 131 years. *Sphecodogastra texana* was originally described by Cresson (1872) as a parasitic *Sphecodes* species, due to its orange abdomen and reduced scopa. In the same paper, Cresson described *Halictus lusorius*, a bee with a similarly reduced scopa but a dark abdomen. The monophyly of the Texana (orange species: *S. noctivaga*, *S. texana*, Figures 4, 5) and Lusoria groups (dark species, Figures 6, 7) and the problems associated with species identity within the Lusoria Group, will be explored below.

MONOPHYLY.—The following summary of systematic events relating to *Sphecodogastra* higher classification provides a chronological framework for the discussion that follows.

- 1872 Cresson described *Sphecodes texana* (mistaking this for a parasitic bee).
- 1898 Cockerell recognized *Sphecodes texana* as *Halictus (Parasphecodes) texanus*.
- 1899 Ashmead recognized *Sphecodogastra*. Although he incorrectly indicated "*Parasphecodes*" *texana* as the type species, he correctly noted that *P. texana* is not related to *Parasphecodes*.
- 1951 Michener recognized the monophyly of *Sphecodogastra* sensu lato as a subgenus of *Lasioglossum*, including *S. texana* and the dark-abdomened species originally described as *Halictus*.
- 1958 Linsley accepted Michener's inclusive concept of *Sphecodogastra* but cautioned that Hurd (in litt.) indicated [incorrectly] that several species of *Evyllaesus* have modified scopae similar to *Sphecodogastra*.
- 1960 Mitchell accepted Michener's inclusive concept of *Sphecodogastra*.
- 1962 Linsley and MacSwain, based on Hurd's comments (in litt.), resurrected the restricted concept of *Sphecodogastra* and recommended transfer of other species to the subgenus *Evyllaesus*.
- 1979 Hurd formalized the restricted concept of *Sphecodogastra* in his Hymenoptera catalog (restated by Moure and Hurd, 1987).
- 1994 Michener et al. restored Michener's (1951) inclusive concept of *Sphecodogastra*.

Sphecodogastra was established as a monobasic genus by Ashmead (1899) for *Sphecodes texana* Cresson (1872), a relatively large halictid having an orange abdomen, conspicuously enlarged ocelli, and highly modified scopae, apparently adapted for collecting pollen of Onagraceae. A related species, *Sphecodogastra noctivaga*, was later described by Linsley and MacSwain (1962). Other species (the Lusoria Group), herein included in *Sphecodogastra*, have similarly modified scopae, but being relatively small and darkly pigmented they were originally grouped with the other small, dark species of *Halictus*, and later, with *Evyllaesus*. Recognizing the monophyly of the then known species in question (*H. aberrans* Crawford, *H. lusorius* Cresson, *H. oenotherae* Stevens, *H. texanus*



FIGURES 4-7.—Figures 4, 5: *Sphecodogastra lusoria*: 4, female with full load of pollen from *Calylophus hartwegii* (length, 8.4 mm); 5, male (length, 7.2 mm). Figures 6, 7: *Sphecodogastra noctivaga*: 6, female (length, 10.2 mm); 7, male (length, 8.8 mm).

(Cresson)), Michener (1951) placed all of them in *Lasioglossum*, subgenus *Sphecodogastra*. Since that time the monophyly of this taxon has been disputed, largely because of classificatory changes made on the basis of literature review, not specimen examination. Linsley (1958:567) originally accepted Michener's inclusive concept of *Sphecodogastra* monophyly but noted that "the group is closely related to the subgenus *Evyllaesus*, which contains several species which gather pollen from diurnal Onagraceae and thus have the scopa similarly modified but have normal ocelli (Hurd, in litt.)." Hurd's statement that several *Evyllaesus* species not included in Michener's *Sphecodogastra* have *Sphecodogastra*-like characters was incorrect.

Nevertheless, it highly influenced Linsley and MacSwain (1962:45):

Although Ashmead established *Sphecodogastra* as a monobasic genus, several other species have been subsequently added which share with *S. texana* one or more adaptive features associated with the collection of pollen from Onagraceae, including *Halictus aberrans* [sic] Crawford, *Halictus galpinsiae* Cockerell, *Halictus lusorius* Cresson, and *Halictus (Evyllaesus) oenotherae* Stevens. However, these added species are crepuscular or matinal bees, or both, not truly nocturnal, and as pointed out by Hurd (see Linsley 1958), they are closely related to species included in *Lasioglossum*, subgenus *Evyllaesus* by Michener (1951). We prefer to see them assigned to that group, since they agree with *Evyllaesus* in basic characters and in general facies. They also share with species in *Evyllaesus* and most of the other subgenera of *Lasioglossum* a distinct lateral

carina on the propodeum, which is lacking in the subgenus *Sphecodogastra* as here restricted.

This viewpoint was formalized by Hurd (1979) and Moure and Hurd (1987) who restricted the concept of *Sphecodogastra* to include only *S. noctivaga* and *S. texana* and transferred the smaller, darkly pigmented species to *Evylaeus*.

Aside from the misconception that several additional species of *Evylaeus* share *Sphecodogastra*-like characters, taxa should not be grouped on the basis of "basic characters" and "general facies" unless these similarities can be reasonably hypothesized or shown to be uniquely derived (i.e., synapomorphies). That the species of the Lusoria Group share the distinct lateral propodeal carina with most other *Lasioglossum* subgenera would suggest that the well-developed propodeal carina may be plesiomorphic and, therefore, of no value in estimating species relationships (to date, this character-state pattern remains unexplored, and polarities should be considered unknown).

There is little doubt that *S. noctivaga* and *S. texana* are sister species (details presented herein) and could logically be recognized at the generic, subgeneric, or informal species-group level; however, it appears these two species (the Texana Group) form a more inclusive monophyletic taxon with the Lusoria Group, which is recognized herein as *Sphecodogastra*, consistent with Michener's (1951) subgenus *Sphecodogastra*. The apparent synapomorphies supporting this grouping are as follows: (1) females have the femoral scopa reduced to a near linear row of stiff, apically recurved setae (Figures 2, 3; more diffused in *S. antiochensis*, Figure 25); (2) females are oligoleges of Onagraceae (a biological character correlated with the scopal modification); and (3) female foraging activity is matinal, crepuscular, and/or nocturnal (a behavioral modification also associated with phenology in Onagraceae). Ocellar size, also associated with foraging time, may be of interest for further study. Ocelli of *S. noctivaga* and *S. texana* are conspicuously large (the ratio of the lateral ocellar diameter to the ocellar-compound eye distance ranges from 0.33 to 0.35 in these species). Although not as large, ocelli in most other *Sphecodogastra* appear to be somewhat larger than in most *Evylaeus* species. The above ratio ranges from 1.18 to 1.44 in *S. aberrans*, *S. antiochensis*, *S. lusoria*, and *S. danforthi* and ranges from 1.78 to 2.00 in *S. oenotherae* and *S. potosi*. A preliminary survey of *Evylaeus* species for this character (*E. cinctipes* (Provancher), *E. nelumbonis* (Robertson), *E. pectinatus* (Smith), *E. pectoralis* (Smith), and *E. truncatus* (Robertson)) showed a ratio range of 1.90–2.25.

Male *Sphecodogastra* have monotonously similar genitalia with the exception of those of *S. aberrans* and *S. texana*. Unlike other species, *S. texana* has the membranous retrorse lobes very broad and twisted ventrally (Figures 31, 32). It is notable that these lobes in the closely related *S. noctivaga* are quite different (Figure 33) and are similar to those of the Lusoria Group (compare with *S. antiochensis*, Figure 78). The genitalia of *S. aberrans* differ significantly from those of other species in the Lusoria Group only in having the penis valves angulate and

concave dorsally (Figure 67). It should be emphasized that a comprehensive review of New World *Evylaeus* male genitalia remains to be documented, and so the cladistic significance of *Sphecodogastra* genitalic similarities remains to be determined; nevertheless, these similarities lend support for Lusoria plus Texana group monophyly. That the genitalia of *S. noctivaga* are so similar to those of the Lusoria Group is compelling evidence for monophyly.

Male *Sphecodogastra* also have conspicuous, elongate sternal vestiture (Figures 37, 38), and the male sternum 6 has a central, shallowly depressed area with an elevated longitudinal, subapical, rounded median ridge (Figures 66, 99). These characters, although characteristic of the males of this genus, should be carefully studied in other halictine taxa before they can be considered significant cladistic characters.

The most compelling evidence for the monophyly of *Sphecodogastra*, in the inclusive sense, is in the results of Bryan Danforth's (2002) molecular systematic studies of Halictinae. He analyzed a combined nuclear and mitochondrial data set for 54 species of *Lasioglossum* sensu lato (including 31 species of *Evylaeus*) and found the monophyly of *S. noctivaga* and *S. oenotherae* to be strongly supported by a 100% bootstrap value.

In summary, characters that would logically group any *Sphecodogastra* (sensu lato) species with other halictine taxa are unknown at present. The alternative position is to hypothesize, a priori, that the scopal modifications found in the Lusoria and Texana groups are the result of convergence associated with their use of Onagraceae pollen. As Thorp (1979:792) pointed out, such convergence is known to occur: "The scopal hairs of most oligolectic (pollen specialist) bees that collect pollen from the Onagraceae tend to be long and simple in contrast to those of their relatives." This is known in *Andrena* (*Onagrandrena*; most species of *Diandrena*), *Melissodes clarkiae* LaBerge, and *Diadasia angusticeps* Timberlake. However, the simple scopal hairs of *Sphecodogastra* are highly unusual in being extremely linear in their arrangement (except in *S. antiochensis*) and in having hooked apices (Figures 2, 3). Lacking evidence to the contrary, I consider the female scopa, suggestive male characters, and preliminary molecular data sufficient to recognize the Lusoria and Texana groups as being monophyletic (i.e., *Sphecodogastra*).

Sphecodogastra has been alternately recognized at the generic level (Hurd, 1979; Moure and Hurd, 1987) or as a subgenus of *Lasioglossum* (Michener et al., 1994; Michener, 2000). In this study, recognition of *Sphecodogastra* at the generic level is done merely to correspond with my generic treatment of *Lasioglossum* (McGinley, 1986). Decisions on the most useful categorical levels should await a better understanding of the relative rankings involved. The monophyly of many currently recognized halictine taxa is open to question, and a number of these taxa (e.g., *Dialictus*, *Evylaeus*) are possibly artificial as presently defined (Michener, 1974; McGinley, 1986).

SPECIES DESCRIPTIONS AND SYNONYMIES.—The following summary of systematic events relating to *Sphecodogastra* species descriptions and associated history provides a chronological framework for the discussion that follows.

- 1872 Cresson described *Halictus lusorius* and *Sphecodes texana*.
- 1897 Cockerell recorded one female of *H. lusorius* from New Mexico. (This is the last use of the name *lusorius* in the literature other than Crawford's 1907 note that he did not include *lusorius* in his key to *Halictus* species.)
- 1903 Crawford described *H. aberrans* but did not compare it with *lusorius*.
- 1903 Cockerell described *H. galpinsiae* but did not compare it with *lusorius*, which he apparently had forgotten about (*galpinsiae* is herein considered a junior synonym of *Sphecodogastra lusoria*).
- 1904 Vachal described *H. gelidus* (from a male specimen), later synonymized under *galpinsiae* by Crawford (1907).
- 1907 Cockerell maintained the distinctiveness of *galpinsiae* and *aberrans*.
- 1911 Graenicher contrasted *galpinsiae* with *aberrans*, supporting their separate identities.
- 1920 Stevens described *H. oenotherae*.
- 1920 Stevens synonymized *galpinsiae* under *aberrans*.
- 1951 Michener listed *galpinsiae* as a junior synonym of *aberrans*.
- 1952 Timberlake (in litt., Moure and Hurd, 1987) presented an inconclusive discussion of the identities of *aberrans*, *galpinsiae*, and an undescribed "Antioch species.
- 1962 Linsley and MacSwain described *Lasioglossum (Sphecodogastra) noctivaga*.
- 1976 Bohart and Youssef differentiated *galpinsiae* from *aberrans* and noted the existence of an undescribed species from Antioch, California.
- 1979 Hurd listed *galpinsiae* as a junior synonym of *aberrans* (agreeing with Stevens).
- 1987 Moure and Hurd listed *galpinsiae* as a junior synonym of *aberrans* and offered additional justification.
- Present paper McGinley synonymizes *H. galpinsiae* under *Sphecodogastra lusoria*; recognizes the distinctiveness of *S. aberrans* and *S. lusoria* (agreeing with Bohart and Youssef, Cockerell, Crawford, and Graenicher); and describes *Sphecodogastra antiochensis*, *S. danforthi*, and *S. potosi*.

The confusion surrounding the identities of *Sphecodogastra aberrans* and *S. lusoria* (= *H. galpinsiae*) was reviewed by Moure and Hurd (1987:68):

Stevens (1920) has discussed the identity of this species [*S. aberrans*] and concluded that *galpinsiae* is a synonym of *aberrans*. Bohart and Youssef (1976) consider these to be distinct, citing ecological criteria, and comment that a species closely related to *galpinsiae* from Antioch, California is an undescribed species. Years ago, Timberlake (in litt.) looked into the identity of the Antioch species and wrote the following on 10 July 1952: ["]The species of *Halictus*

that you sent from Antioch is, I think, *H. galpinsiae* Ckll. The males agree closely with Colorado males that I collected in June, 1939. The fact that I had determined females from Antioch previously as *H. aberrans* Cwfd. might indicate that the two names refer to one species, but against this is the fact that Crawford considered the two distinct.["] Cockerell [1906b:427] reports "Mr. Crawford writes that *H. galpinsiae* and *aberrans*, so similar in the female, are widely different in the male." In another place Cockerell states that *aberrans* is a diurnal species. The male of *aberrans* which I presume is correctly placed has slightly smaller ocelli, much less white tomentose hair on head and thorax, abdomen less banded and the genitalia very distinctive. Timberlake further comments that "Stevens' bee from North Dakota may or may not have been the true *aberrans*, although presumably it was, as some of his material was determined by Crawford (but these specimens were diurnal ones from *Helianthus*)." Until a critical systematic study is made of the nominal forms throughout the range in North America, we have elected to consider that only one species [*S. aberrans*] is represented in this area.

Much of the above confusion might have been avoided had Cockerell recalled that he was aware of Cresson's (1872) description of *Halictus lusorius*. Cockerell (1897:167) identified one female from New Mexico as *Halictus lusorius* and wrote, "it is possible that the specimen represents a species distinct from *lusorius*, but Cresson's description so nearly fits it that the identity may be assumed until the contrary is proven." As soon as 1901, Cockerell referred to specimens of this same species as *Halictus amicus*, "var. a," and later in 1903 he described additional specimens as *Halictus galpinsiae*. Cockerell contrasted *H. galpinsiae* with *H. amicus*, which is an entirely different *Evyllaesus* species, but did not mention *H. lusorius*, a species he had previously recognized. Other than the problem of synonymy, the identity of *H. galpinsiae* and *H. aberrans* should have been resolved in 1906 with the above quotation by Cockerell in which he reported Crawford's note on the similarity of the females but extreme difference of males; Crawford also noted the distinctive genitalia of *H. aberrans*. In his key to North American *Halictus* species, however, Crawford (1907) unfortunately chose to differentiate the males on the basis of pubescence characters (correct, but subtle without illustrations) with no mention of genitalic characters, and he separated the females by differences in first metasomal tergal and mesoscutal punctation (virtually useless without definition or illustration, both of which were lacking in Crawford's treatment). Cockerell (1907b) also differentiated *H. aberrans* and *H. galpinsiae* on the basis of color differences of the wing stigma—another difficult character to use with unidentified material. By this time, the synonymy question concerning *H. lusorius* and *H. galpinsiae* could have been settled, but Crawford, who mentioned that he knew of Cresson's *H. lusorius*, excluded it from his key (probably for lack of specimens).

As noted by Moure and Hurd (1987), Stevens (1920:37) was the first worker to critically address the identity problem relating to *H. aberrans* and *H. galpinsiae*. He mentioned "2 females and 9 males taken at Dickinson [North Dakota], by Mr. C.H. Waldron [that] were determined by Mr. Crawford as *H. aberrans*." Two of these males are in the collection of the National Museum of Natural History (Smithsonian Institution) and are indeed *aberrans*, as determined by Crawford. Unfortunately,

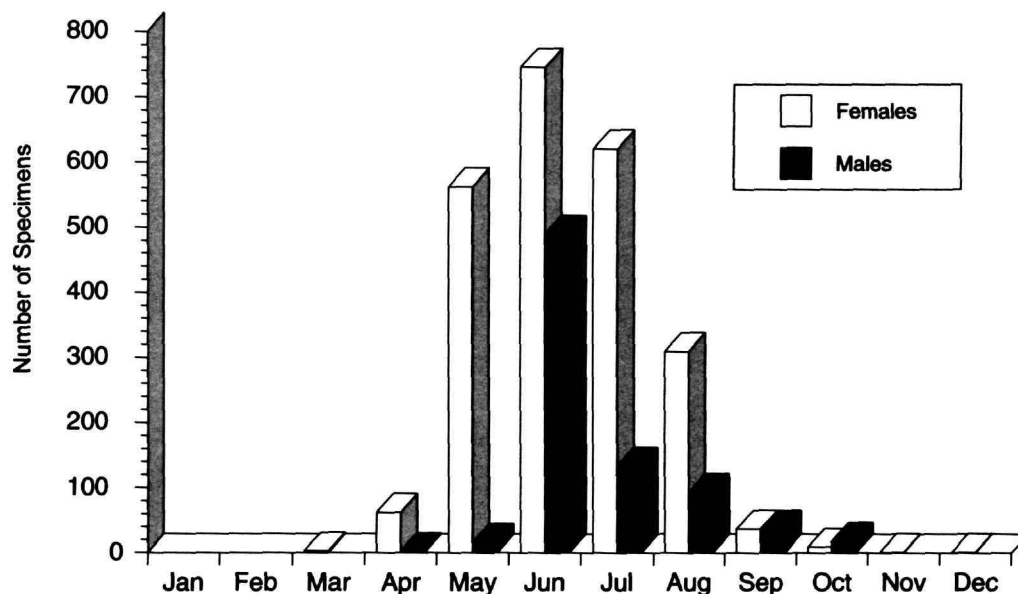


FIGURE 8.—*Sphecodogastra* flight records, by month of collection.

Stevens went on to say that these specimens “agree well with Cockerell’s description of *galpinsiae* [and that] a paratype female of *galpinsiae* sent by Prof. Cockerell agrees with the North Dakota specimens.” Although Stevens was mistaken on both counts, his opinion apparently had a major influence on Moure and Hurd’s (1987) decision to recognize the synonymy of *aberrans* and *galpinsiae*. Timberlake’s cautious remarks (in litt., Moure and Hurd, 1987) reflected the fact that the females of *S. antiochensis* are similar to those of *aberrans* whereas the males of *S. antiochensis* resemble those of *galpinsiae*. As recently as 1976, Bohart and Youssef emphasized the distinctiveness of *aberrans* and *galpinsiae* and, contrary to the above quote by Moure and Hurd (1987), supported this on the basis of morphological characters: “It [*galpinsiae*] differs from *E. aberrans* Crawford (the only other species in the Intermountain Region of the USA) in being smaller (average 8 mm in length) and having more numerous minute appressed pale hairs on the thorax” (Bohart and Youssef, 1976:185).

I herein synonymize *H. galpinsiae* under *Sphecodogastra lusoria*, describe as a new species the Antioch *Sphecodogastra* long known to Bohart and Timberlake (*S. antiochensis*), and recognize the distinctiveness of *S. aberrans* and *S. lusoria* (agreeing with Bohart and Youssef, Cockerell, Crawford, and Graenicher). Diagnoses for all species are provided in the species treatments below.

Flight Activity

GENERAL FLIGHT RECORDS.—*Sphecodogastra* specimens examined in this study were collected from March through December (Figure 8). Most females (82%) were collected during

May through July and most males (79%) were collected slightly later, in June and July. Given the lack of standardization in collecting methods and the broad geographic ranges summarized, little should be concluded from these data. Variations in yearly patterns as well as subtleties of generational patterns cannot be determined from these data; for example, Bohart and Youssef (1976) reported *S. lusoria* to usually have in most years two full generations and a partial third at Cornish, Utah. The only valid comments might be that *Sphecodogastra* species have been collected primarily during the late spring and summer months, males emerge later than females, and that unlike other species, *S. antiochensis* and *S. oenotherae* have been primarily collected in late spring (Figures 82, 128). However, in the northern area of its distribution in Ontario, Canada, Knerer and MacKay (1969) observed *S. oenotherae* to be most active in June and July. Data for individual species are presented in the species accounts that follow.

DAILY FLIGHT ACTIVITY RECORDS.—Most species of the Lusoria Group (*S. aberrans*, *S. antiochensis*, *S. lusoria*, *S. oenotherae*) have long been known to be both crepuscular and matinal in flight activity (Stevens, 1920; Linsley et al., 1963, 1973; Turner, 1966; Knerer and MacKay, 1969; Bohart and Youssef, 1976). I am not aware of time data for the two other rarely collected species of this group, *S. danforthi* and *S. potosi*, but one might assume they have activity patterns similar to the above species, which would, in conjunction with their known distributions, explain their relative lack of representation in museum collections.

The two species of the Lusoria Group with the most time data associated with known specimens, *S. aberrans* (236 records) and *S. lusoria* (230 records), have flight times equally

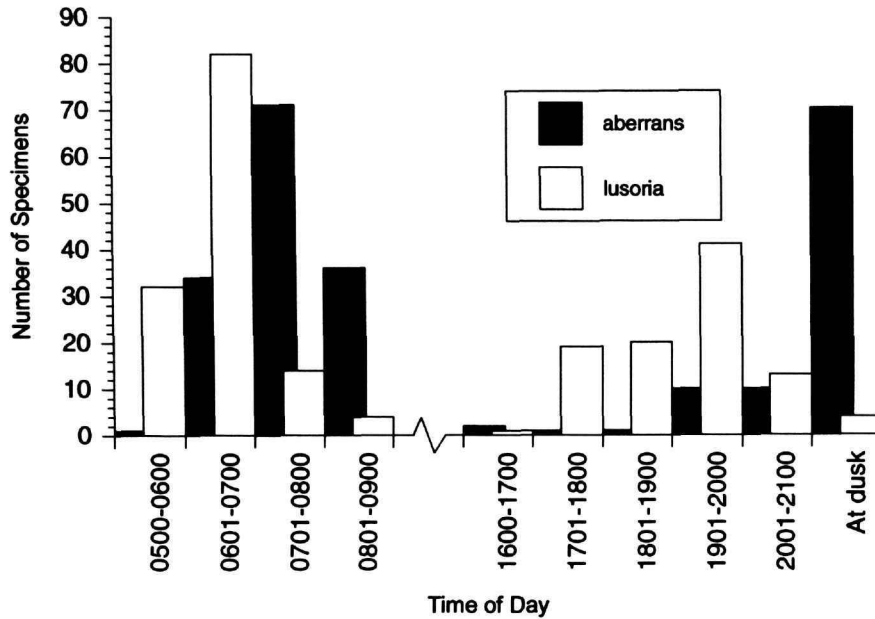


FIGURE 9.—Flight-time records, by hour of day, for *Sphecodogastra aberrans* ($n = 236$) and *S. lusoria* ($n = 230$) (data from specimen labels examined in this study).

distributed between the early morning and the late afternoon to early evening hours (Figure 9). For *S. lusoria* at Cornish, Utah, Bohart and Youssef (1976) reported the earliest recorded inception of foraging during its morning activity period was 0558 hours and the latest was 0810 hours. Flights started after dawn but usually before the sun directly illuminated the nest sites. Morning flights usually ended between 0800 and 0840 hours in late August. Bohart and Youssef concluded that initiation and termination of morning foraging were primarily dependent on temperature and increasing light levels. Foraging activity in the evening period was apparently controlled by decreasing light levels and the opening and availability of new *Oenothera* flowers. Evening foraging began around 2000 hours, which was shortly after sunset or about 40 minutes before dusk (this schedule was maintained throughout the season). Flights ended around 2100 hours, at which time illumination was extremely low. No bees were observed to fly in the dark, even during full moon periods, and bees were never collected at lights.

In this study I examined only nine specimens of *S. oenotherae* associated with time data, and all were collected between 1930 and 2030 hours. Knerer and MacKay (1969) observed a population of *S. oenotherae* in Toronto, Canada, to be initially both matinal and crepuscular; however, when pollen resources became unavailable in the evening, the bees at this site learned to restrict their activity to morning hours. During their morning foraging periods, females were observed to leave nests as early as 0600 hours. Nest plugging usually started around 0800 hours and all nests were closed by 0900 hours.

Turner (1966) observed a similar switch in foraging activity periods for *S. antiochensis*. Early in the season this species collected pollen and nectar from *Oenothera* both in the early morning and early evening. Later in the season, apparently associated with pollen competition from *Agapostemon texanus* Cresson (Halictidae), *S. antiochensis* foraged for pollen primarily in the morning. Evening activity became less intense, and females then foraged primarily for nectar. Although pollen competition from *A. texanus* may be involved, Turner emphasized that, as the season progressed, new flowers of the *Oenothera* host plant opened later in the evening, possibly when the illumination levels were insufficient for flight activity by *S. antiochensis*.

Turner reported that in the morning, *S. antiochensis* opened their nests 45–60 minutes before they initiated foraging. During his study the mean time of flight initiation was approximately two minutes before sunrise; however, some individuals left their nests for the first time as late as 48 minutes after sunrise. Evening flight began around 47 minutes before sunset and usually ended about 30 minutes after sunset. This could extend as much as 79 minutes after sunset late in the season.

Unlike the Lusoria Group, examined specimens of the two species of the Texana Group (*S. noctivaga*, *S. texana*) were crepuscular and nocturnal, being active exclusively in the evening hours (Figure 10), as reported by Kerfoot (1967c). Of the 187 specimens of *S. texana* associated with time data, 175 were simply labeled "at light." Only four specimens of *S. noctivaga* had time data, but all were collected between 1901 and 2100 hours or "at light."

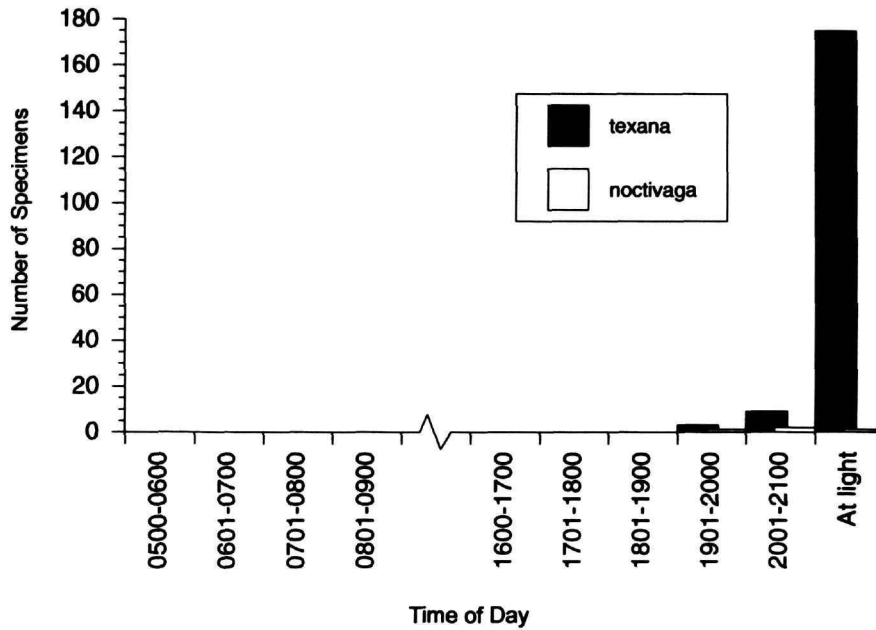


FIGURE 10.—Flight-time records, by hour of day, for *Sphecodogastra noctivaga* (n = 4) and *S. texana* (n = 187) (data from specimen labels examined in this study).

Kerfoot (1967c) reported that nests were usually unplugged just before sunset (about 1930 hours during midsummer in Kingman County, Kansas). When the moon was visible by 2130 hours, foraging then continued long into the night until moonset or until pollen resources were depleted. Kerfoot termed this the “moonlight period” of the month. The latest reported flight record for *S. texana* was 0030 hours. If the moon was not visible after sunset, foraging activity continued until approximately 2100 hours. During this lunar period, females were poised at their nest entrances, and if the moon remained down, they closed their nest by approximately 2130 hours. If the moon rose after this time, the nests remained closed and foraging was not resumed. Kerfoot termed this the “crepuscular period” for *S. texana*.

Floral Associations

Female *Sphecodogastra* collect pollen almost exclusively from Onagraceae (Table 2) but are known to visit flowers of other plant families for nectar; they are rarely known to collect non-onagraceous pollen, which apparently occurs only under duress when evening primrose resources are unavailable (Bohart and Youssef, 1976). Males, however, commonly visit several plant families for nectar.

Onagraceae pollen is apparently not required for *Sphecodogastra* larval development. Bohart and Youssef (1976) reported rearing larvae on alfalfa (*Medicago sativa* L.) pollen. Development time was somewhat longer, but eggs were successfully reared to adults. They speculated that the advantage of Ona-

graceae specialization to *Sphecodogastra* was pollen harvesting efficiency (e.g., *S. lusoria* often requires less than one minute to gather a full pollen load; see Table 2) and the precise timing of their foraging activity with the unusual opening periods of primrose flowers, which reduces competition from other bees. An additional benefit may be avoidance of nest parasites by having nests closed during the day, when most potential cleptoparasites are active. The only report of a possible cleptoparasitic bee association with *Sphecodogastra* is Bohart and Youssef’s (1976) observation of an overwintering adult *Sphecodes* female in a nest of *Sphecodogastra lusoria* (see “Nest Architecture and Parasites,” below).

ONAGRACEAE FLORAL ASSOCIATIONS.—Table 3 lists the Onagraceae floral records for the 826 female *Sphecodogastra* specimens associated with floral data that were examined in this study as well as a few reliable literature records. These

TABLE 2.—Numbers of *Sphecodogastra aberrans* and *S. lusoria* collected from *Oenothera pallida*, Maryhill Ferry, 3 miles east of Briggs, Sherman County, Oregon, 3 June 1963 (P.H. Raven, collector). Only two of the nine *S. aberrans* had pollen; all *S. lusoria* had pollen except the female collected at 0845 hours.

Hours	<i>S. aberrans</i>	<i>S. lusoria</i>
0530–0559	0	14
0600–0629	0	26
0630–0659	0	10
0700–0729	0	3
0730–0759	9	1
0800–0829	0	0
0830–0859	0	1

TABLE 3.—Records of female *Sphecodogastra* associated with Onagraceae flora as well as associations indicated in the literature by other researchers: A = Gregory (1964); B = Stevens (1920); C = Knerer and MacKay (1969); D = Kerfoot (1967a); M&H = Moure and Hurd (1987; this catalog data should be considered with reservation).

Associated flora	<i>S. aberrans</i>	<i>S. antiochensis</i>	<i>S. danforthi</i>	<i>S. lusoria</i>	<i>S. noctivaga</i>	<i>S. oenotherae</i>	<i>S. potosi</i>	<i>S. texana</i>
<i>Calylophus hartwegii</i>	—	—	22	10, A	1, A	—	—	1
<i>Camissonia claviformis</i>	—	—	—	20	—	—	—	—
<i>Camissonia tanacetifolia</i>	88	—	—	—	—	—	—	—
<i>Clarkia pulchella</i>	2	—	—	—	—	—	—	—
<i>Gaura coccinea</i>	10	—	—	56	—	—	12	—
<i>Gaura suffulta</i>	—	—	—	16	—	—	—	—
<i>Gaura</i> sp.	—	—	—	2	—	—	—	—
<i>Oenothera albicaulis</i>	—	—	—	1	—	—	—	—
<i>Oenothera biennis</i>	—	—	—	—	—	M&H	—	2
<i>Oenothera caespitosa</i>	4	—	—	32	—	—	—	1
<i>Oenothera deltoides</i>	—	135	—	40	—	—	—	—
<i>Oenothera drummondii</i>	—	—	—	—	—	—	—	17
<i>Oenothera elata</i>	70	—	—	—	—	—	—	—
<i>Oenothera engelmannii</i>	—	—	—	—	—	—	—	A
<i>Oenothera fruticosa</i>	—	—	—	—	—	C	—	—
<i>Oenothera grandis</i>	—	—	—	21	—	—	—	—
<i>Oenothera laciniata</i>	—	—	—	—	—	1	—	A
<i>Oenothera latifolia</i>	—	—	—	18	—	—	—	—
<i>Oenothera macrocarpa</i>	—	—	—	2	3	B	—	9
<i>Oenothera nuttallii</i>	—	—	—	—	—	—	—	M&H
<i>Oenothera pallida</i>	—	—	—	99	—	—	—	2
<i>Oenothera pilosella</i>	—	—	—	—	—	C	—	—
<i>Oenothera rhombipetala</i>	—	—	—	—	—	—	—	D
<i>Oenothera villosa</i>	1	—	—	—	—	—	—	M&H
<i>Oenothera</i> sp.	5	3	—	62	58	—	—	—

data indicate that *Sphecodogastra* species are broad oligoleges of Onagraceae, with individual species visiting a variety of *Oenothera* species and other onagraceous genera.

Among the *Lusoria* Group species, *Sphecodogastra lusoria* had the greatest number of floral records (379) in this study and was recorded from eight species of *Oenothera* and two species of *Gaura* as well as *Calylophus hartwegii* and *Camissonia claviformis*. The preponderance of floral records for *S. aberrans* associated with *Camissonia tanacetifolia* (49%) and *Oenothera elata* (39%) is interesting but will have to await further study before this pattern can be considered meaningful. The rarely collected *S. danforthi* and *S. potosi* are only known to be associated with *Calylophus hartwegii* and *Gaura coccinea*, respectively, but it would be surprising to not find these species associated with *Oenothera* given additional study. *Sphecodogastra antiochensis*, known only from Antioch, California, is associated almost exclusively with the similarly restricted *Oenothera deltoides howellii*.

Within the crepuscular/nocturnal *Texana* Group (*S. noctivaga*, *S. texana*), 92 of the 94 recorded floral associations were with *Oenothera* species.

The more popular Onagraceae species among *Sphecodogastra* species appear to be the widespread and common *Calylophus hartwegii*, *Gaura coccinea*, *Oenothera caespitosa*, and the somewhat less common *Oenothera macrocarpa*. All four species are known to be associated with three or more *Sphecodogastra* species. However, given the vagaries associated with

limited, nonsystematic collecting, not much should be concluded from these preliminary data.

SIGNIFICANCE OF *Sphecodogastra* IN ONAGRACEAE REPRODUCTIVE BIOLOGY.—*Sphecodogastra* is a highly specialized oligolege of Onagraceae and has evolved morphological and behavioral characters to efficiently harvest the resources of its host plants. However, at least from the literature, these bees often appear to be at best ineffectual pollinators and at worst, from the plant's perspective, skilled pollen thieves capable of "stealing" large amounts of Onagraceae pollen (see Figure 4), with little or no benefit to the plant's reproductive biology. A similar relationship has been reported by Barrows et al. (1976) for the andrenid bee *Perdita texana*, an oligolege of prickly pear cactus (*Opuntia phaeacantha*). The cactus flowers are large and so configured that the relatively small bees can collect large amounts of pollen without normally contacting the plant's stigmas.

Evidence for this nonmutualistic type of relationship between *Sphecodogastra* and its host plants initially came from Gregory's (1963, 1964) excellent studies of *Oenothera* reproductive biology. He concluded that the most effective pollinators of the plant species he studied were hawkmoths (Sphingidae). "At two colonies [of *Calylophus hartwegii*], [at] Monahans and Ector County, over 50% of the flowers had been pollinated, most lightly, before any hawkmoths were seen. At Monahans four species of bees were collecting pollen before sunset and were responsible for most of the pollen transfer"

(Gregory, 1964:394). He suspected that most of this was "single flower self-pollination" in a self-incompatible species and that most cross-pollination was effected by hawkmoths. For *Oenothera drummondii*, he concluded that there was certainly some pollination by *Celerio* [= *Hyles*, Sphingidae] at Aransas Pass [San Patricio County, Texas] but *Lasioglossum* (*Sphecodogastra*) *texanum* (Cresson) took so much pollen during the hour or more before dark that pollination by *Celerio* was greatly reduced. In this case the addition of a regular and abundant visitor species seriously decreased the amount of pollination rather than supplementing it.

The most compelling support for thinking of *Sphecodogastra* species as pollen thieves is from Wagner et al. (1985:8), who reported that *S. aberrans* and *S. lusoria* [as *galpinisae*] were both observed at a locality in Larimer County, Colorado, to "collect pollen from *Oenothera caespitosa* subsp. *macroglottis*, primarily in the early mornings." They reviewed Stockhouse's (1973) study in which, on six successive evenings, he bagged half the flowers of a population of this *Oenothera* species to exclude hawkmoths at night and then removed the bags in the morning so the two *Sphecodogastra* species could visit the flowers. The exposed flowers were visited by hawkmoths in the evenings. Later, marked capsules were collected and analyzed. Approximately 70% of the flowers visited by hawkmoths produced capsules, whereas only one out of the 150 flowers visited by bees produced capsules. This is strong evidence that *Sphecodogastra*, at that one locality and time, played no significant role in the pollination of *Oenothera*.

Countering the above conclusions is a three-year study of *S. texana* by Kerfoot (1967c). He concluded that whereas *Oenothera rhombipetala* is probably adapted for pollination by moths, *Sphecodogastra texana*—although clumsy pollen collectors—were apparently responsible for cross-fertilization of plants of this species at his study sites. This was because he saw only one moth during his study.

In summarizing their six-year study of *Oenothera pallida* and *S. lusoria*, Bohart and Youssef (1976) also concluded that the hawkmoth *Hyles lineata* (Fabricius) was probably the most important pollinator. However, unlike *S. texana*, *S. lusoria* females were not clumsy at *Oenothera* flowers but were very efficient pollen foragers that only rarely made contact with plant stigmas. However, similar to Kerfoot's (1967a) findings, they observed no hawkmoths at their study site at Cornish, Utah, until 1973, the last year of their study.

During his two-year study of *S. antiochensis*, Turner (1966) observed no hawkmoths at flowers or at electric lights and concluded the moths were either rare or absent. As Turner pointed out, this raises interesting questions concerning the pollination of the self-incompatible host plant, *Oenothera deltooides howellii*, which is confined to the Antioch dune area. Turner observed a shift in foraging activity of *S. antiochensis* females during the year. Early in the season, when there was no competition from *Agapostemon texanus* (and apparently none from hawkmoths), pollen was plentiful and females harvested *Oeno-*

thera pollen with alacrity (Turner, 1966), visiting only one flower during each foraging trip (of no use for cross-pollination). Later in the season, with floral resource competition from *A. texanus*, foraging *Sphecodogastra* females appeared rather frantic and needed to visit seven or more flowers to obtain a full pollen load. During this period, Turner frequently observed females with partial pollen loads land on several different stigmas and was of the opinion that they easily could have effected pollination. He concluded that the assumption that only hawkmoths pollinated hawkmoth flowers was not necessarily true.

As documented by Gregory (1963, 1964), Stockhouse (1973), and Wagner et al. (1985), hawkmoths (especially *Hyles lineata*), when present, are undoubtedly the most effective pollinators of *Oenothera* and related genera. However, as reviewed above, three long-term studies of Onagraceae pollination ecology (Turner, 1966; Kerfoot, 1967a; Bohart and Youssef, 1976) reported situations where hawkmoths were found to be rare or apparently absent. Turner addressed this issue of erratic sphingid faunal representation and mentioned their migratory capabilities, citing Williams (1957:168), who (without providing references) wrote strongly concerning *Hyles lineata* migration: "The insects breed during the winter somewhere in Central or South America, almost certainly in the semiarid climate of the western coast. Thence they move north in the spring into the southern states where, as in Europe [the subspecies *H. lineata livornica* (Esper)], they become a minor pest of vines." Williams cited Grant (1937) as demonstrating statistically significant evidence supporting correlations for heavy migration years between the New and Old World subspecies. In her paper, Grant documented the apparent erratic representation of *H. lineata* in North America but made no mention of long distance overwintering migration; however, she indicated that *H. lineata* might migrate gregariously after the larvae completely destroyed their host plants (many hosts but especially vineyard vines). Whether *Hyles* migration involves travel to distant overwintering sites or more local movements prompted by resource depletion is apparently unresolved (D. Ferguson, pers. comm., 1993). Whatever the cause, local representation of these moths is erratic and undoubtedly has implications for Onagraceae pollination. These observations suggest that additional studies similar to those of Stockhouse (1973) should be pursued for other *Sphecodogastra*-Onagraceae relationships before it can be concluded that these bees never play a significant role in the cross-pollination of their host plants, especially in situations where hawkmoth populations are at low densities or are absent.

NON-ONAGRACEAE FLORAL ASSOCIATIONS.—Associations with plant genera from 19 non-Onagraceae families are listed below, as recorded from *Sphecodogastra* specimens examined in this study. The mostly commonly visited family is Asteraceae (43% of female records; 65% of male records). Bohart and Youssef (1976) reported *S. lusoria* collecting pollen of *Lygodesmia grandiflora* (Asteraceae): one female had a mixed load of pollen (90% *Oenothera* and 10% *Lygodesmia*). They

also noted P.F. Torchio's observation of a female attempting to collect pollen from *Cleome serrulata* (Capparidaceae).

Sphecodogastra aberrans: *Allionia* (3♂), *Arnica* (1♀), *Chrysothamnus* (4♀), *Coreopsis* (1♂), *Cucurbita* (1♂), *Geranium* (1♀), *Grindelia* (2♂), *Gutierrezia* (1♂), *Helianthus* (1♂), *Heterotheca* (1♂), *Iris* (1♀), *Melilotus* (1♂), *Taraxacum* (1♀), *Verbesina* (1♀), *Viguiera* (1♂).

Sphecodogastra antiochensis: *Layia* (1♀).

Sphecodogastra lusoria: *Arenaria* (1♀), *Argemone* (1♀), *Asclepias* (1♂), *Barbarea* (2♀), *Brassica* (1♂), *Callirhoe* (1♀), *Chrysothamnus* (3♂), *Cirsium* (2♂), *Cleome* (1♀, 9♂), *Coreopsis* (1♀), *Cucurbita* (10♀), *Descurainia* (1♀), *Engelmannia* (2♂), *Eriogonum* (1♂), *Galpinsia* (1♀), *Geranium* (1♀), *Grindelia* (1♀), *Gutierrezia* (1♀), *Helianthus* (3♀, 12♂), *Iris* (1♂), *Lactuca* (1♀), *Lupinus* (2♂), *Malacothrix* (2♀), *Malvastrum* (1♀), *Medicago* (1♀), *Melilotus* (3♀, 2♂), *Monarda* (3♂), *Poliomintha* (3♂), *Potentilla* (4♂), *Prunus* (3♀), *Pyrrhopappus* (2♀, 1♂), *Salsola* (1♀), *Senecio* (1♀), *Sitilias* (2♀), *Solidago* (5♀), *Sphaeralcea* (1♀), *Tamarix* (3♀), *Taraxacum* (1♀), *Thelesperma* (1♀), *Xanthisma* (5♂).

Sphecodogastra noctivaga: *Chrysothamnus* (1♀).

Sphecodogastra oenotherae: *Carduus* (3♂), *Cichorium* (2♂), *Coreopsis* (1♀, 2♂), *Eupatorium* (1♂), *Salix* (1♂), *Taraxacum* (1♂), *Tragopogon* (2♀, 22♂).

Sphecodogastra potosi: *Asclepias* (1♂).

Sphecodogastra texana: *Allionia* (10♀), *Bidens* (1♀), *Mentzelia* (1♀).

Nesting Biology

The nesting biologies of four *Sphecodogastra* species have been studied: *S. antiochensis* (Turner, 1966; two-year study, Antioch, Contra Costa County, California; details of nest architecture were not reported); *S. lusoria* (as *galpinsiae*, Bohart and Youssef, 1976; six-year study, Cornish, Cache County, Utah); *S. oenotherae* (Knerer and MacKay, 1969; one-year study, Toronto, Canada); and *S. texana* (Kerfoot, 1967a; three-year study, Kingman County, Kansas). Bohart (in Bohart and Youssef, 1976) indicated he had unpublished data for *S. aberrans* and included some information on this species in his paper on *S. lusoria*. The following review is based on the papers cited above.

SOCIAL BEHAVIOR.—*Sphecodogastra* species are primarily solitary bees but show several tendencies towards limited social behavior. Females of all species studied return to their natal nests for overwintering. For *S. oenotherae* this can involve as few as one but usually three to four females and sometimes as many as 10 individuals. Inseminated females of *S. lusoria* have been reported to number from one to nine in overwintered nests, resulting in an early-season transitional period during which more than one active female can be found in a single nest. Of 33 nests of *S. texana* examined by Kerfoot (1967a), 12 contained more than one female; however, among all the fe-

males in these 12 nests, only one female appeared to be fertilized, with the other females showing no mandibular wear or ovarial development. As for other species, only one female reuses the natal nest for brood rearing, and eventually surplus females leave to establish their own nests. However, one nest of *S. texana* was found to contain two fertilized and two unfertilized females.

Bohart and Youssef (1976) reported a similar situation for *S. lusoria* in the early season of 1970 in which a few nests contained up to three females, but later in the same year, when provisioning had begun, all nests appeared to be occupied by a single female. Under exceptional conditions *S. lusoria* appeared to be truly communal. There was no *Oenothera* bloom at the Cornish, Utah, site in 1972. The bees that year emerged but finding no host flowers returned to their shared natal nests with undeveloped ovaries and resumed their dormancy. These bees emerged in 1973 as two-year-old sisters. Up to 30 percent of the nests examined that year were communal, with more than one female sharing a common opening burrow and apparently maintaining their own burrow beneath this (the number of females in a nest always corresponded with the number of sub-burrows). Bohart and Youssef (1976) speculated that this communal behavior was possibly the result of increased tolerance between these unusually old sisters who had shared their natal nests.

Turner (1966) provided strong indications that *S. antiochensis* may be communal. He observed "guard" bees at nest entrances as well as several long-established nests that contained many females. The nature of this social behavior needs further investigation and clarification.

NEST ARCHITECTURE.—Most *Sphecodogastra* species are known to nest in stabilized sand in open xeric areas (*S. antiochensis*, *S. lusoria*, *S. texana*). One observation was made of *S. lusoria* nesting in vertical banks (Bohart and Youssef, 1976). This occurred only among bees of the 1968 second generation brood of *S. lusoria* at Cornish, Utah. However, the third (overwintering) generation of this population reverted to nesting in flat ground. Bohart indicated that unlike *S. lusoria*, *S. aberrans* "is generally found in more mesic and highland surroundings, on brush-covered slopes or open woodlands" (Bohart and Youssef, 1976:186). *Sphecodogastra oenotherae* was reported to nest on gently sloping ground in patches of dirt between well-cared-for lawns and gardens (Stevens, 1920).

All species studied showed slight to conspicuous tendencies toward nesting gregariously and forming distinct aggregations. Kerfoot (1967a) observed *S. texana* to be gregarious at times, with 100 or more nests found within a small area, and at other times having nests widely scattered. Bohart and Youssef (1976) reported for *S. lusoria* that 15 to 20 nests per square meter were observed in years of high population density, but only 10 nests in a few square meters were seen during low-density years even though similar, empty areas surrounded these aggregations. *Sphecodogastra oenotherae* formed aggregations with a maximum density of about 25 nests per square meter, with a

minimum internidal distance of 2 cm. Turner (1966) indicated that *S. antiochensis* aggregations never surpassed seven burrows per square meter.

Nests were always, at least initially, associated with conspicuous tumuli (3.0–5.5 cm in diameter for *S. texana*; usually 5.0 cm in diameter for *S. lusoria*). Main nest burrows are usually vertical and straight—remarkably so as reported by Kerfoot (1967a) for *S. texana*. He reported that nest depths ranged from 20.0 cm (mean for *S. oenotherae* during provisioning period; hibernacular cells averaged 30.0 cm deep) to 55.0–75.0 cm (*S. lusoria*) and 45.5–145.0 cm (*S. texana*; mean = 102.0 cm). This range possibly represents increased depths in drier soils (L. Packer, pers. comm., 1994).

The main burrow of all *Sphecodogastra* nests studied was usually plugged during nonforaging periods. For *S. antiochensis*, Turner (1966) said these plugs consisted of 5 or 6 distinct and compact sand pellets. Oddly, nests of this species were often plugged before all females returned. In most cases these females made unsuccessful attempts at entry but eventually flew away to await reopening of the nests during the next foraging period. Kerfoot (1967a) observed that *S. texana* closed their nests with sand plugs that mutillids could not penetrate (even after concerted effort), but that bees easily passed through. He speculated that when the bees were ready to exit the nests they moistened the plugs (presumably with nectar).

Brood cells of *Sphecodogastra* are horizontal (*S. lusoria*) or slope slightly downward (*S. oenotherae*, *S. texana*). The cells are unusual for halictines in that they are only partially lined with a waxy secretion. This is reported as being over the distal three-fourths of the cell for *S. oenotherae*; the distal two-thirds for *S. lusoria* (with the lining being thickest under a depression for the pollen ball); and only partially covering just the bottom of the cell for *S. texana*. Cells were sessile (*S. oenotherae*), connected to the main burrow by extremely short lateral tunnels (1–3 mm, *S. lusoria*), or connected by distinct laterals (average length = 2.6 cm, *S. texana*; see “Nest Architecture and Social Behavior,” below). The number of cells found per nest were 12–20 for *S. oenotherae* (6–20 cm below the surface) and varied for *S. lusoria*, with the greatest number being 31 (20–43 cm deep). The number of cells per nest appeared to be unusually low for *S. texana*, but numbers increased throughout the season (cell depth ranged from 20 to 110 cm below the surface). Kerfoot (1967a) reported that 16 nests excavated in June averaged 1.1 old cells and 1.0 occupied cells; 8 nests in July averaged 3.6 old and 1.9 occupied cells; 5 nests in August averaged 11.2 old and 3.2 occupied cells. This apparent low number of brood cells may be associated with Kerfoot’s (1967c) observation that *S. texana* actively provisions cells primarily during its “moonlight period” of the month and does little provisioning and egg laying during the “crepuscular period” of the month (see “Daily Flight Activity Records”).

NEST ARCHITECTURE AND SOCIAL BEHAVIOR.—The nest architecture of *Sphecodogastra* species studied includes characteristics typical of solitary halictines as well as some character-

istics correlated with primitively eusocial species. The brood cells of most solitary halictines are not clustered and are connected to the main burrow by elongate lateral tunnels. However, Packer (1991) pointed out that there are some solitary halictines with brood-cell clusters and cavities that may represent a reversal to solitary behavior. Some primitively eusocial species (e.g., *Evylaeus malachurus*) construct clustered cells that have the surrounding soil excavated, are left open during the early stages of larval development, and are sessile, i.e., not connected to the main burrow by lateral tunnels (Packer, 1991). The brood cells of *S. texana* were connected to the main burrow by distinct lateral burrows. Cells were loosely “clumped” at different depths, but Kerfoot (1967c) thought this might be correlated with the different foraging activity periods observed for this species (i.e., the crepuscular versus the moonlight periods; see “Daily Flight Activity Records”).

Sphecodogastra oenotherae at Toronto, Canada, is apparently univoltine, and Knerer and MacKay (1969:293) reported that the species “lacks even the most rudimentary social behavior.” Nevertheless, the nests of this species have some eusocial characteristics: sessile, clustered cells with cell closures consisting of a porous layer of loose soil particles. Knerer and MacKay also observed that formation of the pollen ball was not immediately followed by oviposition and that this delay may exceed 24 hours. They concluded that these characteristics may represent a preadaptation towards social behavior that might have been arrested because of the species’ specialized association with *Oenothera*. It would be interesting to study the nesting biology of *S. oenotherae* in southern areas of its range where the possibility of multivoltinism is likely.

Bohart and Youssef (1976) observed that *S. lusoria* females shape more than one pollen ball in advance of egg laying and leave the cells (which are closely positioned but not clustered) and short lateral burrows (1–3 mm in length) initially unplugged—characteristics of social halictines. These researchers wondered whether this could be a step leading to social behavior or if it represented a habit retained from a more social ancestor. A large part of this question may be answered after the phylogenetic relationships of *Sphecodogastra* to related halictines are resolved. Much biological work, however, remains to be pursued—in particular, clarification of the “social” behavior of *S. antiochensis*, study of *S. aberrans*, and observation of *S. oenotherae* in the southern latitudes of its range. Nothing is currently known about the nesting biologies of the newly described *S. danforthi* and *S. potosi*.

NEST ARCHITECTURE AND PARASITES.—The maternal, crepuscular, and nocturnal periods of foraging activities of *Sphecodogastra* combined with nest plugging during nonforaging periods most likely contribute to the paucity of nest parasites reported for this genus. The cleptoparasitic bees of the genus *Sphecodes*, commonly associated with halictine nests, have only tenuously been associated with *Sphecodogastra*. In their six-year study of *S. lusoria*, Bohart and Youssef (1976) reported only one observation of *Sphecodes* in a host nest. This was a

single, adult female found in a hibernacular (nonbrood) cell. Presumably, this female made her way into the hibernaculum of this one nest and managed to overwinter there. No other cleptoparasitic bee associations with *Sphecodogastra* have been reported.

Kerfoot (1967a) occasionally found mutillids (*Myrmillodes grandiceps* Blake) in nests of *S. texana* that had been left open, but none of these were in brood cells. He speculated that these wasps simply might have been trying to avoid the hot sand of the ground surface. Turner (1966) observed the nest sites of *S. antiochensis* also to be associated with mutillids (*Photopsis* spp., *Pseudomethoca anthracina* (Fox)). Mutillids inspecting nest openings of this species were always deterred from entering by brief encounters with "guard" bees. One female of *P. anthracina* was artificially introduced into a guarded *S. antiochensis* nest and was repeatedly repelled by the bee at the nest entrance. Of 14 nests excavated at Antioch, Turner found no evidence of parasites or predators or evidence of cell entry.

Knerer and MacKay (1969) reported finding one dying *S. oenotherae* female at the bottom of her nest with a third instar larva of the conopid fly (*Thecophora*) completely filling her abdomen. Bohart and Youssef (1976) found adult phorid flies in the main burrows of two nests of *S. lusoria*, and larval phorids in a few cells, but did not believe these flies were responsible for the absence of bee larvae in the infested cells. Kerfoot (1967a) dissected 62 adult *S. texana* (57 females; five males) and found none to have internal parasites.

Miscellaneous associates reported in *Sphecodogastra* nests include nematodes in fecal material (*S. lusoria*) and mites in cells and on pollen of *S. lusoria* (anoetids [*Histiogaster*], pyemotids [*Parapygmephorus*], and scutacarids). Kerfoot (1967a) reported an unidentified fungus from the cells of *S. texana*.

General predator reports are confined to Bohart and Youssef (1976) finding three nest cells of the bee-storing sphecic wasp, *Philanthus gibbosus* (Fabricius), with several intact *S. lusoria* of both sexes.

Systematics

Sphecodogastra Ashmead

Sphecodogastra Ashmead, 1899. [Type species: *Parasphecodes texana* (Cresson). Monotypic and original designation. (= *Sphecodes texana* Cresson, 1872).]

DIAGNOSIS.—Female *Sphecodogastra* can be distinguished from other Halictidae by their distinctively reduced scopae composed of simple, apically hooked, and linearly arranged setae on the ventral surface of the hind femora (Figures 2, 3, 26). These setae are surrounded by conspicuously nonsetose areas on the anterior and posterior femoral surfaces (this pattern is somewhat diffused in *S. antiochensis*, Figure 25). The orange abdomens and extremely enlarged ocelli of males and females of *S. noctivaga* and *S. texana* make both species highly distinctive (Figures 11, 29). Males of the Lusoria Group (dark species) are more problematic to diagnose. Most helpful is the pat-

tern of long sternal vestiture of most species (Figure 38; vestiture highly distinctive in *S. aberrans*, Figure 37). Also characteristic is the central depression of sternum 6, which has a low, longitudinal median elevation (Figures 66, 99).

DESCRIPTION.—The format and character numbering in the following generic description follow those of McGinley (1986). Characters thought to be nonvariant, or primarily so, for *Sphecodogastra* are presented in small capital letters (if minor variation does occur, this is described in individual species descriptions).

FEMALES: (1) Length 6.6–11.2 mm (mean = 8.5, $n = 40$); (2) wing length 1.9–3.3 mm (mean = 2.6, $n = 40$); (3) abdominal width 2.0–3.3 mm.

Structure: (4) Head short (Figure 129) to moderately elongate (Figure 52); length/width ratio 0.80–1.40 (mean = 0.95, $n = 40$). (5) Gena, at midpoint, exceeded by width of compound eye to greatly exceeded by eye; (6) GENA ROUNDED POSTERIORLY, NOT PRODUCED OR ANGULATE. (7) SUPRACLYPEAL AREA EVENLY ROUNDED, (8) WEAKLY PROTUBERANT. (9) Clypeus projecting approximately 0.40–0.92 times its length below lower margin of eyes; (10) CLYPEAL SURFACE BROADLY ROUNDED; (11) clypeal surface usually without median longitudinal sulcation (present only in *S. noctivaga*). (12) FRONTAL CARINA WEAKLY DEVELOPED, INCONSPICUOUS. (13) Distance between lateral ocellus and eye slightly greater than distance between lateral ocellus and hind margin of vertex (ocular–ocellar distance ranging from approximately 0.5 to 2.0 times lateral ocellar diameter); (14) distance between lateral ocelli slightly to greatly exceeding ocular–ocellar distance; (15) LATERAL OCELLI JOINED ABOVE BY AT MOST A WEAK, INCONSPICUOUS IMPRESSED LINE. (16) Inner margins of compound eyes converging below or nearly parallel. (17) HYPOSTOMAL CARINA WELL DEVELOPED AND UNIFORM; (18) ANTERIOR ANGLE OF HYPOSTOMAL CARINA NARROWLY ROUNDED; (20) ANTERIOR CARINA NEARLY PERPENDICULAR TO LONGITUDINAL CARINA. (21) Scape reaching top of vertex or slightly beyond (*S. noctivaga*, *S. texana*); (22) PEDICEL SLIGHTLY LONGER THAN WIDE, slightly shorter than flagellomere 1 (*S. noctivaga*, *S. texana*), or lengths subequal; (23) FLAGELLOMERE 1 SUBEQUAL IN LENGTH TO FLAGELLOMERE 2; flagellum with distinctive sensillar patterns in *S. antiochensis* and *S. lusoria* (Figures 42, 76). (24) LABRUM WITH BASAL AREA AND DISTAL PROCESS; unlike most species, basal area in Texana Group much broader than long (Figures 108, 142); (25) BASAL ELEVATION WELL DEVELOPED; (26) BASAL LATERAL DEPRESSIONS ABSENT; (27) DISTAL KEEL NARROW AS SEEN IN FRONTAL VIEW; (28) DISTAL LATERAL PROJECTIONS ABSENT (present in many *Lasioglossum* (McGinley, 1986, fig. 7)); (29) FIMBRIAL SETAE ACUTELY POINTED. (30) Mandible moderate in length to conspicuously elongate; (31) MANDIBLE USUALLY WITH DEFINED SUBAPICAL TOOTH (broadly rounded, not defined in *S. danforthi*).

(32) PRONOTAL LATERAL ANGLE BROADLY OBTUSE; (33) PRONOTAL LATERAL RIDGE BROADLY INTERRUPTED BY OBLIQUE LATERAL SULCUS; (34) LOWER PORTION OF LATERAL

RIDGE BROADLY ROUNDED. (35) MESOSCUTAL ANTERIOR EDGE ROUNDED, NOT BILOBED, AND (36) MODERATELY ELEVATED FROM PRONOTUM AT CENTER; (37) MEDIAN MESOSCUTAL LINE USUALLY NOT IMPRESSED (impressed only in *S. antiochensis*); (38) PARAPSIDAL LINES ELONGATE, APPROXIMATELY 0.40–0.50 TIMES LENGTH OF MESOSCUTUM, WITH WEAKLY IMPRESSED LINE EXTENDING TO POSTERIOR EDGE OF MESOSCUTUM (e.g., Figures 98, 145). (39) MEDIAN SCUTELLAR IMPRESSION VIRTUALLY ABSENT (best developed in *S. aberrans*). (40) Dorsal surface of propodeum 0.59–0.78 times length of scutellum and approximately 1.13–1.50 times length of metanotum, (41) ONLY FAINTLY DEPRESSED CENTRALLY, (42) POSTERIOR MARGIN ROUNDED; (43) PROPODEAL TRIANGLE INCONSPICUOUS, WITHOUT ELEVATED, MEDIAN V-SHAPED AREA OR DISTINCT LATERAL MARGINS; (44) lateral propodeal carinae on posterior vertical face well developed and complete to weakly developed and extending no more than one-third basal length of posterior surface. (45) Inner hind tibial spur usually with 4 or 5 moderately elongate teeth (e.g., Figures 58, 60); teeth somewhat longer and more numerous (up to 7) in *S. antiochensis* (Figure 59); teeth shorter and less numerous (3 or 4) in Texana Group (Figures 64, 65).

(46) Lateral edge of metasomal T2 rounded to nearly straight.

Sculpture: (47) FACE SHINY, (48) DENSELY AND CONTIGUOUSLY PUNCTATE BELOW OCELLI; AREA BETWEEN OCELLI AND ANTENNAE UNIFORMLY PUNCTATE OR WITH PUNCTURES SEPARATED BY 1–2 TIMES THEIR WIDTHS IMMEDIATELY ABOVE AND LATERAD OF ANTENNAE (*S. noctivaga*, *S. texana*). (49) PUNCTATION OF VERTEX NEAR EYE MUCH MORE SPARSE AND FINE THAN THAT ON LOWER FACE, PUNCTURES SEPARATED BY 1–3 TIMES THEIR WIDTH; (50) VERTEX BEHIND OCELLI OBSCURELY PUNCTATE, WITHOUT TRANSVERSE STRIATIONS. (51) Supraclypeal area polished or granulate, (52) densely to sparsely punctate. (53) Clypeus entirely polished or tessellate basally; (54) punctation sparse, most punctures separated by 1–5 times their widths. (55) Hypostoma striolate, becoming smooth and polished on anterior half in some species, PUNCTATION OBSCURE, VIRTUALLY ABSENT.

(56) Mesoscutum shiny and polished with surface tessellation between punctures confined to anterior one-third or mesoscutum moderately dull with surface entirely tessellate; (57) punctation moderately dense, most punctures separated by 1–2 times their widths. (58) SCUTELLAR PUNCTATION SIMILAR TO THAT OF MESOSCUTUM, BUT USUALLY FINER. (59) METANOTUM GRANULATE TO RUGULOSE, PUNCTATION OBSCURE OR ABSENT. (60) PRE-EPISTERNUM USUALLY RUGULOSE (very fine in *S. noctivaga*); (61) HYPOEPIMERAL AREA AND MESEPISTERNUM USUALLY RUGULOSE (finely so in *S. lusoria*, extremely fine in *S. noctivaga*; mesepisternum weakly strigulate ventrally in *S. texana*), WITHOUT DISTINCT PUNCTURES; (62) UPPER PORTION OF METEPISTERNUM STRIGULATE, BECOMING GRANULATE BELOW. (63) Dorsal surface of propodeum strongly rugo-striate (Figure 15), rugulose (Figure 16) to ruguloso-striolate (Figure 19);

(64) surface smooth or alveolated. (65) T1 usually shiny and polished (somewhat dull tessellate in *S. noctivaga*); (66) punctation fine to extremely fine, moderately dense (punctures separated by their widths) to very sparse (punctures separated by 2–3 times their widths).

Coloration: (67) HEAD AND THORAX DARK BROWN, abdomen mostly orange (*S. noctivaga*, *S. texana*) or dark brown (other species); T1–T4 OR T2–T4 WITH APICAL HYALINE BANDS THAT COVER ABOUT ONE-FOURTH OF TERGAL SURFACE (presence of hyaline band on T1 variable among species; bands relatively inconspicuous in species with orange abdomens). (68) CLYPEUS WITHOUT MACULATION; LABRUM DARK BROWN. (69) Flagellum dark brown to amber. (70) Tegula yellow-translucent to brown. (71) Wing membrane hyaline to pale yellowish brown; veins and stigma pale yellowish amber to brown. (72) Legs usually darkly pigmented (mostly amber in Texana Group).

Vestiture: (73) PUBESCENCE OF HEAD BETWEEN VERTEX AND ANTENNAE PLUMOSE (hairs conspicuously short in Texana Group); (74) white to pale yellowish brown. (75) Pubescence of thorax white to pale yellowish brown; (76) mesoscutal hairs elongate and sparse to short and adpressed; pleuron with or without short, suberect to adpressed hairs. (77) HIND TIBIAL HAIRS WHITE TO YELLOWISH WHITE; HAIRS CONCOLOROUS (HAIRS OF DORSAL SURFACE NOT DARKER THAN THOSE ON OTHER AREAS). (78) ANTERIOR HAIRS ON T1, (79) BASAL HAIR BANDS ON T2–T4 WHITE. (80) ACARINARIUM ON ANTERIOR SURFACE OF T1 ABSENT. (81) Basal hair bands on T2–T4 present (at most, covering basal one-fourth of terga) to absent; apical hair bands sometimes present on T3 and T4.

MALES: As described for females except as follows: (1) length 6.4–9.7 mm (mean = 7.9, $n = 40$); (2) wing length 1.4–2.8 mm (mean = 2.1, $n = 40$); (3) abdominal width 1.4–2.4 mm.

Structure: (4) Head length/width ratio 1.00–1.14 (mean = 1.1, $n = 40$). (10) CLYPEAL SURFACE BROADLY ROUNDED (this differs from the flattened clypeal surface characteristic of the males of most New World *Lasioglossum*, sensu stricto). (16) INNER MARGINS OF COMPOUND EYES CONVERGING BELOW. (21) SCAPE MUCH SHORTER THAN IN FEMALES, AT MOST JUST REACHING LEVEL OF MEDIAN OCELLUS (Texana Group); (22) PEDICEL SLIGHTLY WIDER THAN LONG, CLEARLY SHORTER THAN FLAGELLOMERE 1; (23) flagellomere 2 approximately 1.5–2.0 times length of flagellomere 1. (24) LABRUM WITHOUT DISTAL PROCESS (apical edge of basal process slightly projecting only in *S. aberrans* (Figure 55)); (25) BASAL ELEVATION ABSENT; (26) BASAL LATERAL DEPRESSIONS ABSENT; (30) MANDIBLE SHORT, JUST REACHING OPPOSING CLYPEAL ANGLE, (31) WITHOUT SUBAPICAL TOOTH.

(37) Median mesoscutal line impressed or not impressed. (44) LATERAL PROPODEAL CARINAE PRESENT ON VERTICAL FACE, NOT REACHING DORSAL SURFACE OF PROPODEUM. (45) INNER HIND TIBIAL SPUR SERRATE ON BOTH EDGES.

Sculpture: (51) SUPRACLYPEAL AREA TESSELLATE, (52) DENSELY PUNCTATE (punctures separated by less than the width of their diameter). (53) CLYPEUS SOMEWHAT DULL, NOT HIGHLY POLISHED.

(57) MESOSCUTAL PUNCTATION DENSE, PUNCTURES SEPARATED BY LESS THAN THEIR DIAMETERS. (66) PUNCTATION ON T1 BETTER, STRONGER THAN IN FEMALES (punctures only moderately fine, separated by 1–2 times their diameters).

Coloration: (68) CLYPEUS WITH APICAL YELLOW MACULATION; LABRUM YELLOW (yellow pigmentation relatively limited in *S. potosi*). (70) Tegula yellow-translucent to brown. (72) TARSI YELLOW; TIBIAE YELLOW AT BOTH ENDS, VARYING AMOUNTS OF DARK PIGMENTATION MEDIANLY.

Vestiture: (73) UNLIKE FEMALES, SHORT, ADPRESSED HAIRS PRESENT ON FACE (from base of clypeus to area immediately dorsad of antennae or extending to vertex, as in *S. lusoria*, *S. antiochensis*). (76) Mesoscutal hairs elongate and sparse to short and adpressed; pleuron with or without short, suberect to adpressed hairs. (81) APICAL HAIR BANDS NOT DEVELOPED ON

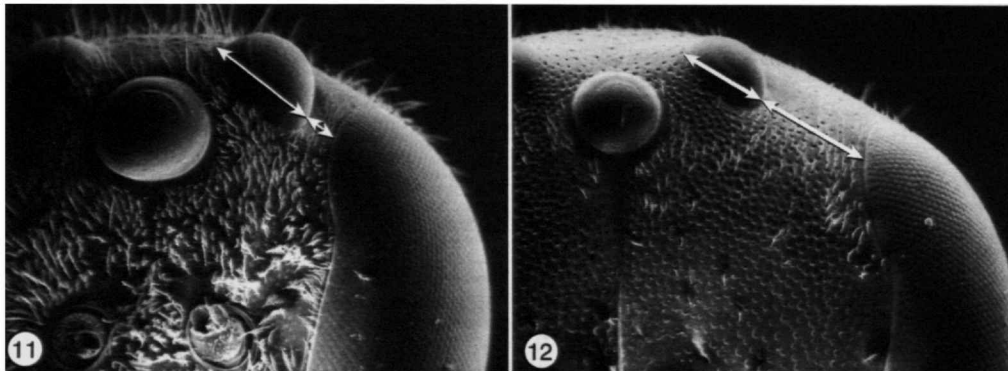
T3 OR T4. (82, 83) VESTITURE ON S4 AND S5 ELONGATE, CONSPICUOUS, hairs confined to apical margin (*S. aberrans*; Figure 37) or distributed over entire sternal surface (Figure 38).

Terminalia: (84) S7 WITH ELONGATE, NARROW, APICALLY ROUNDED MEDIAN PROCESS; lateral arms slender (Figure 91) to moderately developed (Figure 81); (85) S8 usually moderately developed (Figure 81), short and somewhat reduced in *S. danforthi* (Figure 91) and *S. potosi* (Figure 138); apex of median process usually rounded (Figure 81), truncate (Texana Group, Figures 115, 150); (86) GONOBASE WELL DEVELOPED; (87) GONOSTYLUS SIMILARLY SHAPED AMONG SPECIES (somewhat slender in *S. aberrans*, Figure 69); WITHOUT CONSPICUOUS HAIR TUFTS; (88) RETRORSE MEMBRANOUS LOBE PRESENT, WELL DEVELOPED, (89) lobes usually narrow and parallel-sided (e.g., Figure 78, broader basally (*S. aberrans*, *S. lusoria*, Figures 67, 100), to very broad and twisted ventrally (*S. texana*, Figures 146, 149)); (90) VOLSELLA SIMILAR IN SHAPE AMONG SPECIES AS ILLUSTRATED HEREIN.

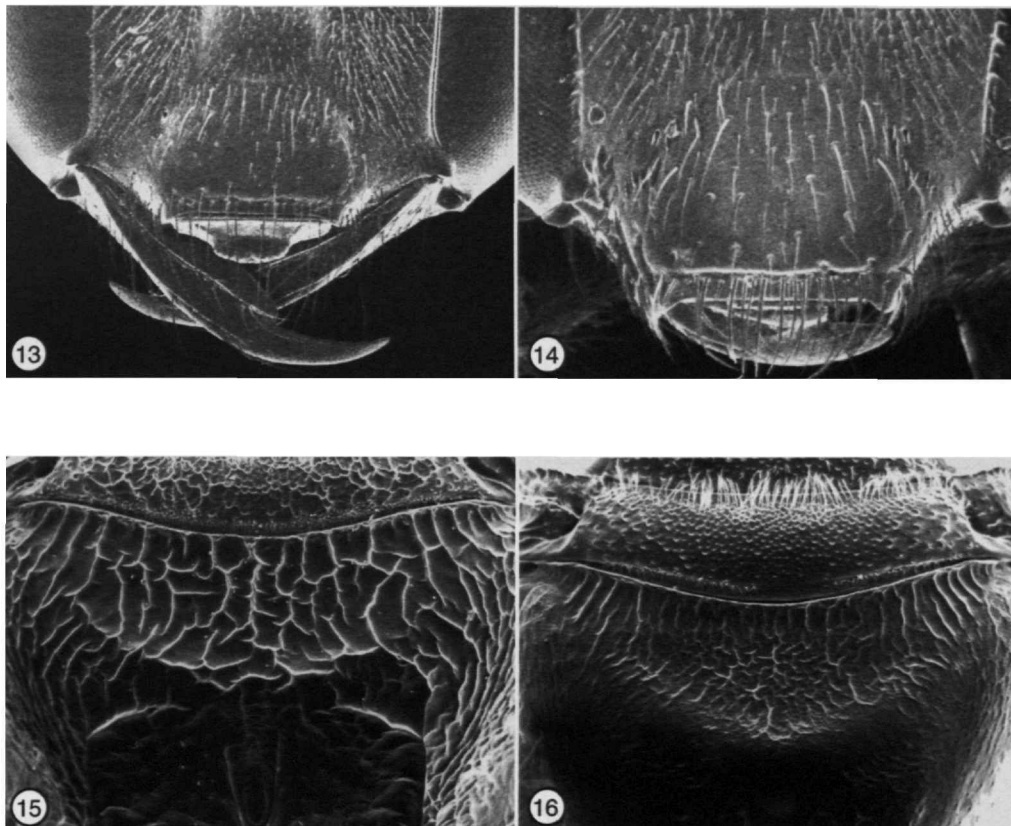
Key to *Sphecodogastra* Females

(See Appendix 1 for figure identifications)

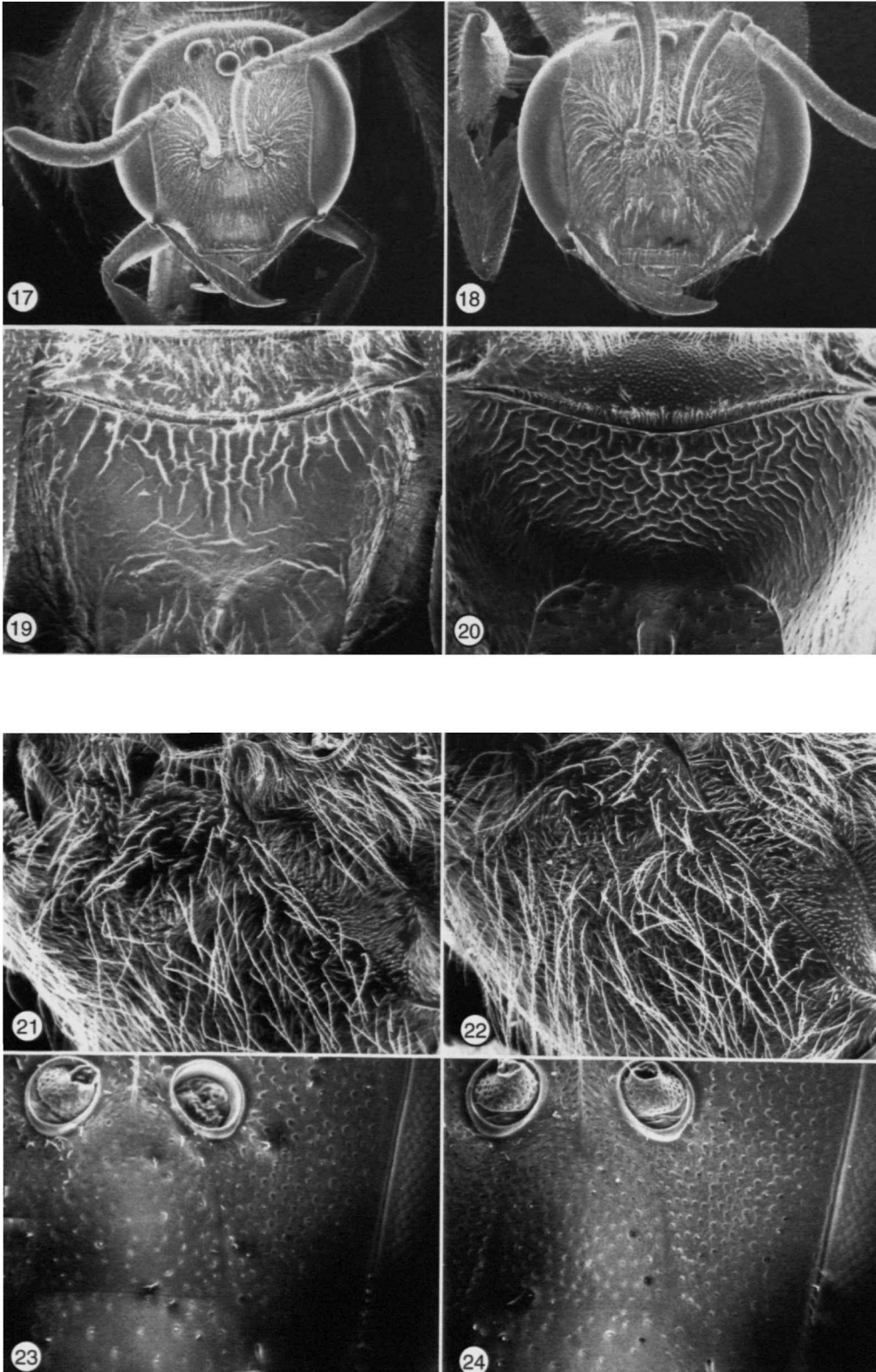
- 1. Abdomen orange; ocelli conspicuously enlarged, distance between compound eye and lateral ocellus less than lateral ocellar diameter [Figure 11] 2
- Abdomen darkly pigmented, brown to dark brown; ocelli moderately large but not conspicuously so, distance between compound eye and lateral ocellus 1.5–2.0 times lateral ocellar diameter [Figure 12]..... 3



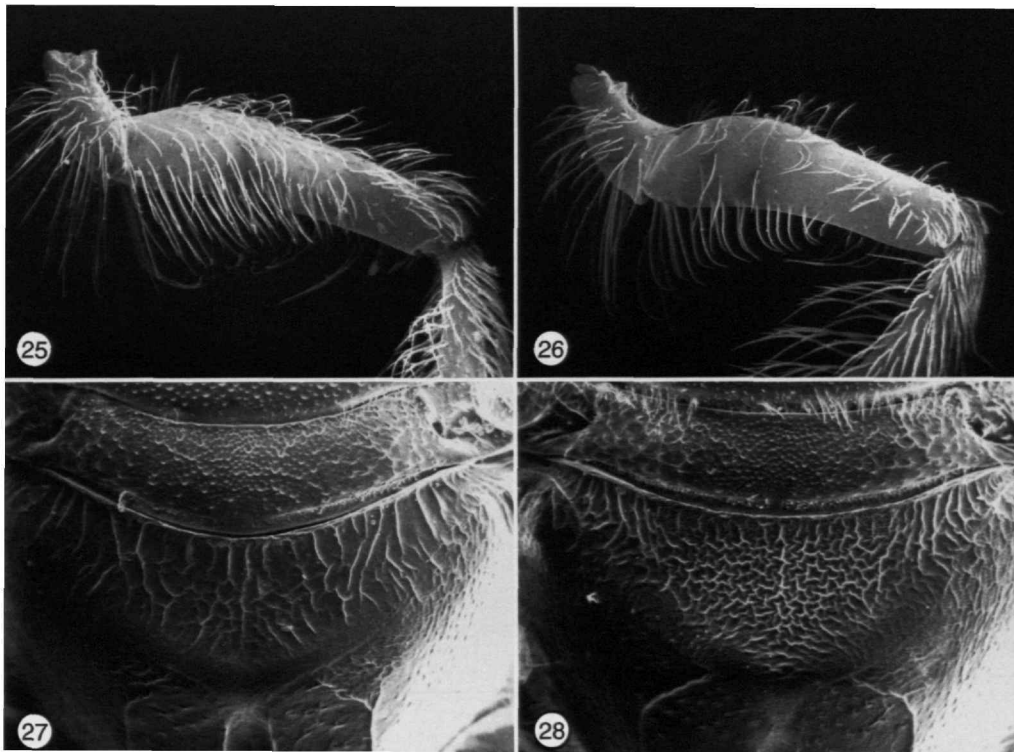
- 2(1). Mandibles conspicuously elongate, clearly extending beyond opposing clypeal angles [Figure 13]; face broad ventrally, inner margins of compound eyes nearly parallel [Figure 106] 5. *S. noctivaga* (Linsley and MacSwain)
- Mandibles not elongate, at most just reaching opposing clypeal angles [Figure 14]; face relatively narrowed ventrally, inner margins of compound eyes converging below [Figure 140] 8. *S. texana* (Cresson)
- 3(1). Dorsal propodeal surface strongly rugo-striate [Figure 15] 6. *S. oenotherae* (Stevens)
- Dorsal propodeal surface rugulose [Figure 16] to ruguloso-striolate [Figure 19] .. 4



- 4(3). Mandibles elongate, extending beyond opposing clypeal angles [Figures 17, 18]; pleuron with short adpressed pubescence beneath elongate pleural hairs. 5
- Mandibles not elongate, at most just reaching opposing clypeal angles [Figure 14]; pleuron with or without short adpressed pubescence beneath elongate pleural hairs 6
- 5(4). Mandibles straight-edged laterally, extending conspicuously beyond clypeus [Figure 17]; mandibular subapical tooth poorly defined, broadly rounded [Figure 86]; propodeal dorsal surface ruguloso-striolate [Figure 19]; currently known only from western Texas [Figure 83]. 3. *S. danforthi*, new species
- Mandibles broadly curved laterally, not extending conspicuously beyond clypeus [Figure 18]; subapical tooth well defined [Figure 18]; propodeal dorsal surface rugulose [Figure 20]; known from Mexico and southern New Mexico [Figure 83] 7. *S. potosi*, new species
- 6(4). Pleuron with short, adpressed pubescence beneath elongate pleural hairs [Figure 21]; supraclypeal area polished, punctation sparse, many punctures separated by 3–4 times their diameters [Figure 23]; wing membranes hyaline 4. *S. lusoria* (Cresson)
- Pleuron without short, adpressed pubescence [Figure 22]; supraclypeal area dull, distinctly to obscurely granulate, punctation dense, most punctures separated by twice their diameters or less [Figure 24]; wing membranes pale yellowish brown 7



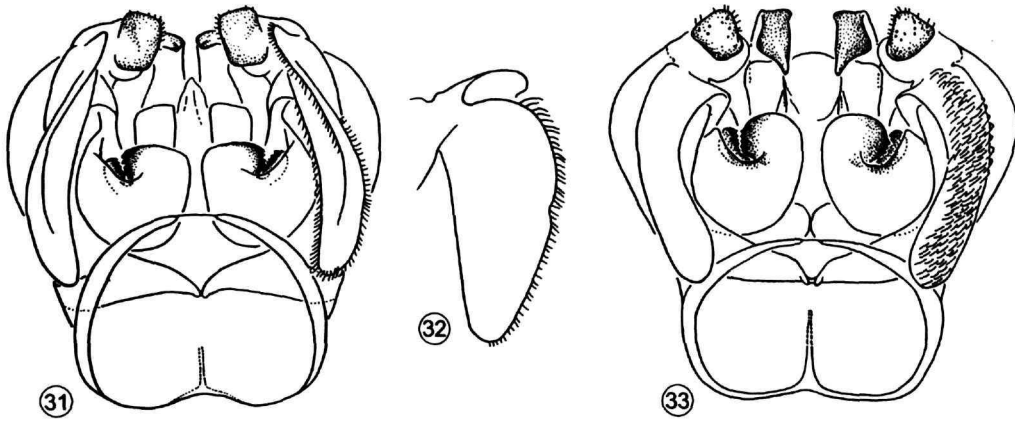
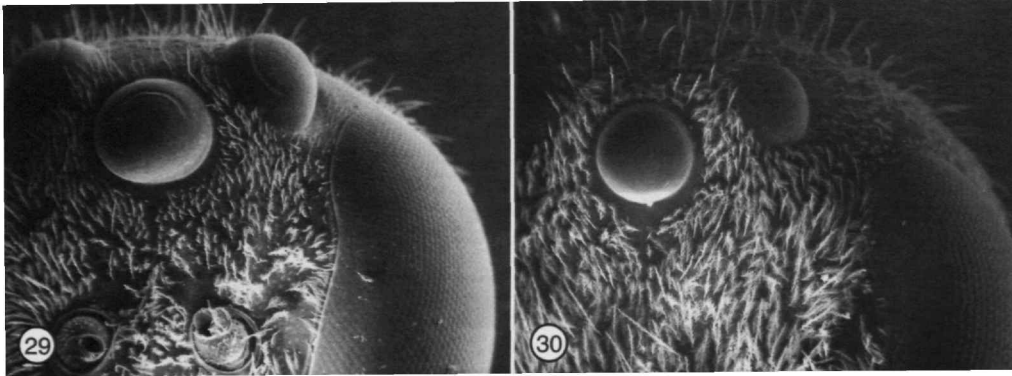
- 7(6). Scopal hair fringe on hind femur not sharply differentiated from surrounding hairs [Figure 25]; clypeus with basal area polished, subapical area with widely separated, small punctures; dorsal propodeal surface coarsely ruguloso-striolate [Figure 27]; known only from Antioch (Contra Costa County), California [Figure 92] 2. *S. antiochensis*, new species
- Scopal hair fringe on hind femur sharply differentiated from surrounding hairs [Figure 26]; clypeus with basal area tessellate, subapical area with contiguous, large punctures; dorsal propodeal surface finely rugulose [Figure 28]; wide-spread in western North America, known in California only from Plumas and Riverside counties [Figure 51] 1. *S. aberrans* (Crawford)



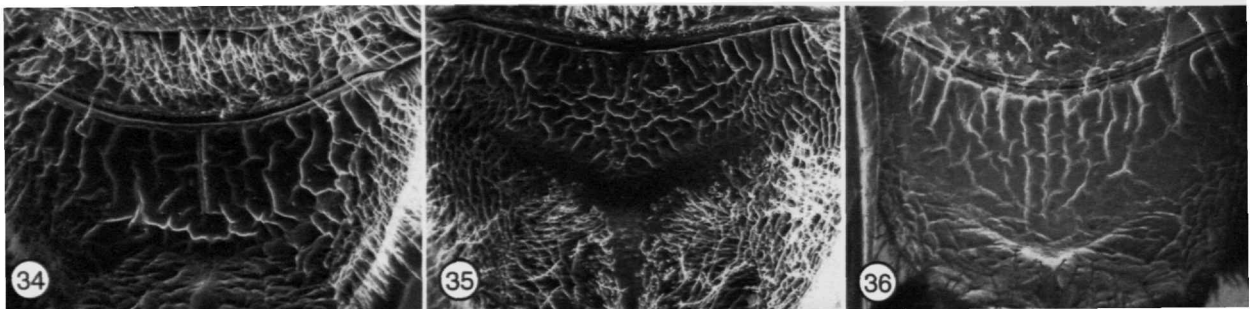
Key to *Sphecodogastra* Males

(See Appendix 1 for figure identifications)

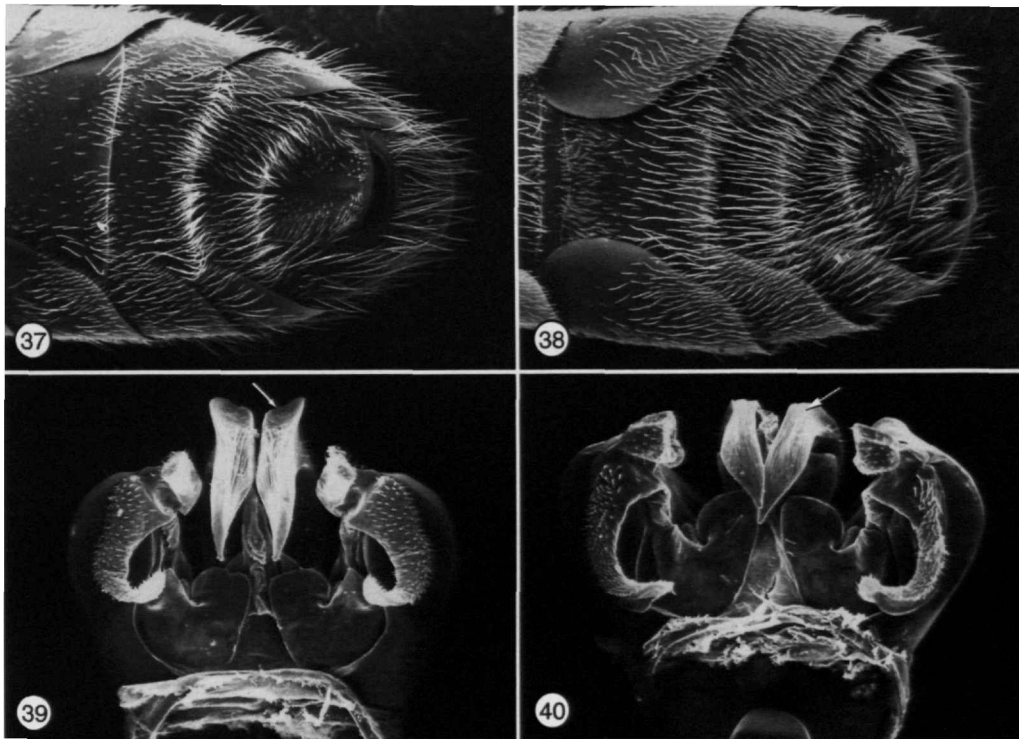
1. Abdomen orange; ocelli conspicuously enlarged, distance between compound eye and lateral ocellus less than lateral ocellar diameter [Figure 29] 2
 - Abdomen darkly pigmented, brown to dark brown; ocelli moderately large, distance between compound eye and lateral ocellus slightly greater than lateral ocellar diameter [Figure 30] 3
 - 2(1). Retrorse lobes of genitalia very broad and twisted ventrally [Figures 31, 32] 8. *S. texana* (Cresson)
 - Retrorse lobes of genitalia narrow, flat, not twisted ventrally [Figure 33] 5. *S. noctivaga* (Linsley and MacSwain)
- [I know of no reliable external characters to differentiate the males of these two species; see "Diagnosis" for *S. noctivaga*.]



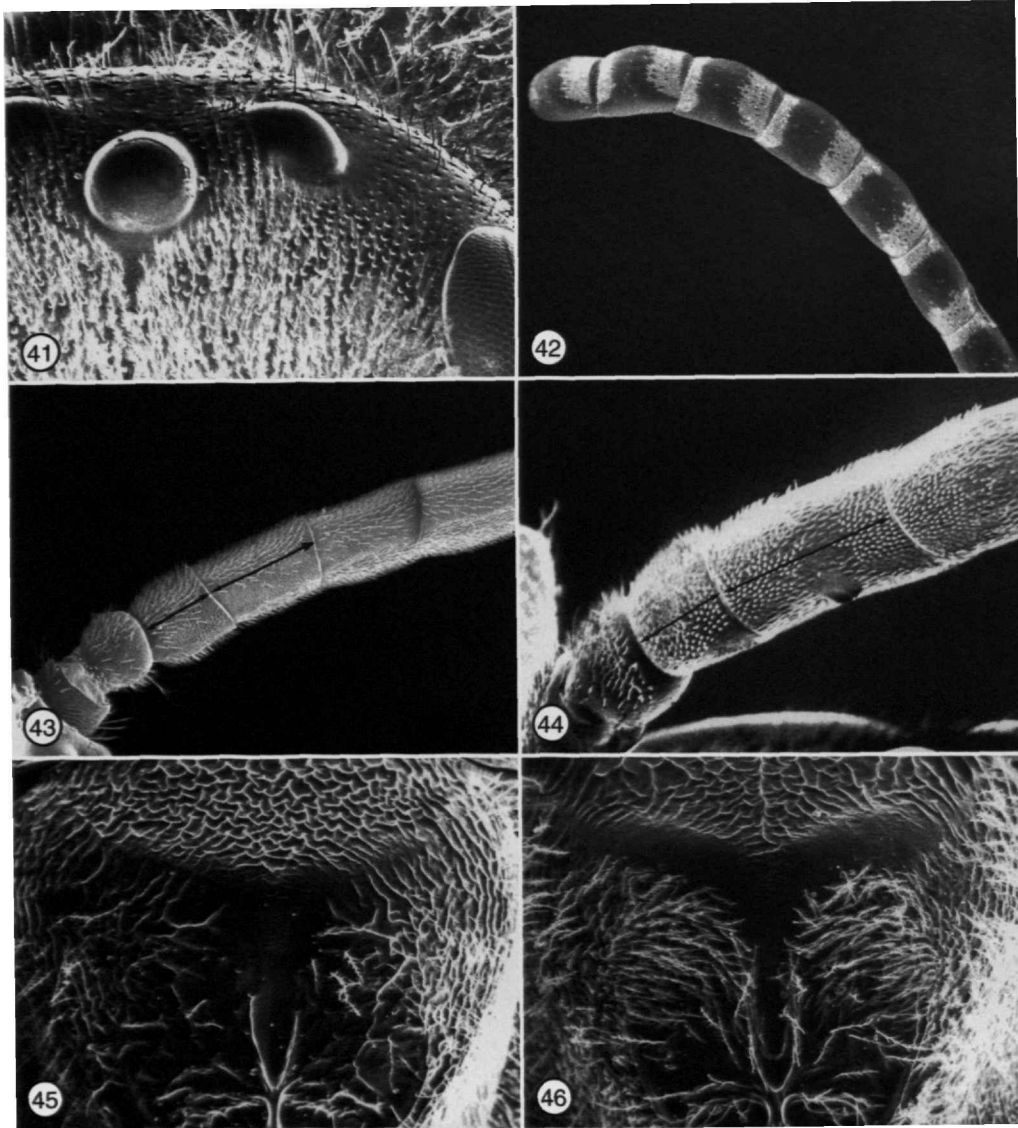
- 3(1). Dorsal propodeal surface strongly rugo-striate [Figure 34]; primarily from eastern North America [Figure 117] 6. *S. oenotherae* (Stevens)
 Dorsal propodeal surface finely rugulose [Figure 35] to at most ruguloso-striolate [Figure 36]; primarily from central and western North America [Figures 51, 83, 92] 4



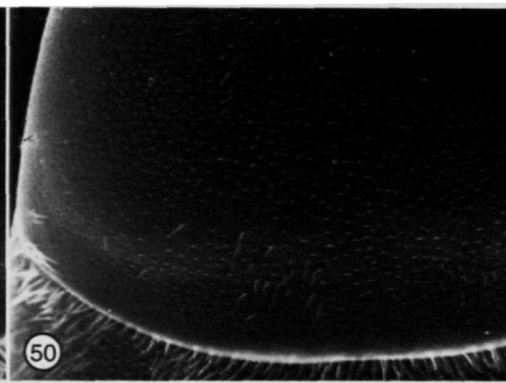
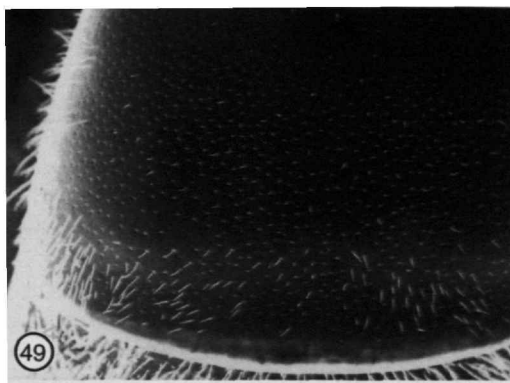
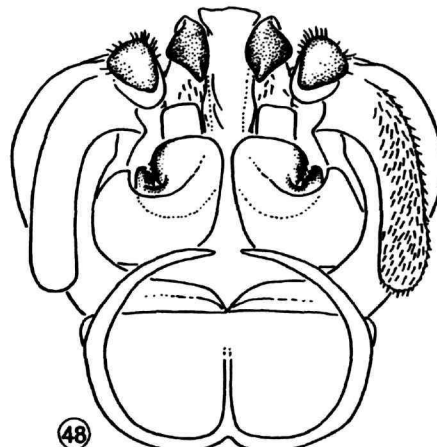
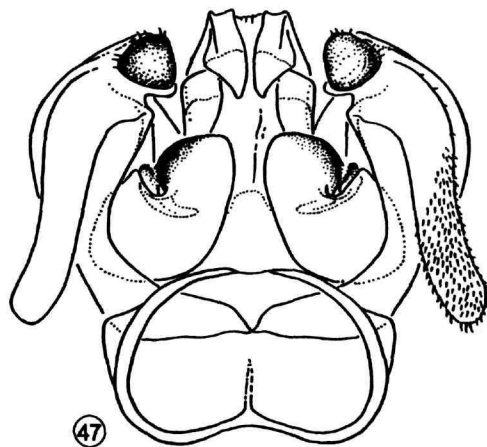
- 4(3). Fringe hairs on posterior margins of S4 and S5 conspicuously developed, clearly differentiated from shorter vestiture on S3 [Figure 37]; antennal flagellum without distinctive sensillar pattern; central depression of S6 extremely well developed [Figures 37, 66]; penis valves sharply angulate [Figure 39], dorsal and apical surfaces concave and sharply carinate laterally [Figure 39] 1. *S. aberrans* (Crawford)
- Fringe hairs on posterior margins of S4 and S5 similar to posterior hair fringe on S3 [Figure 38]; antennal flagellum with [Figure 42] or without distinctive sensillar pattern; central depression of S6 only moderately developed [Figure 38]; penis valves rounded [Figure 40], dorsal and apical surfaces rounded [Figure 40] 5



- 5(4). Antennal flagellum without distinctive sensillar pattern; vertex and ocellar area without short, adpressed pubescence [Figure 41]; antennae only moderately elongate, second flagellomere approximately 1.3–1.5 times the length of flagellomere 1 [Figure 43]; posterior propodeal surface lacking short adpressed hairs [Figure 45] 6
- Antennal flagellum with distinctive sensillar pattern [Figures 42, 76]; vertex and ocellar area with short, adpressed pubescence [Figure 30]; antennae elongate, second flagellomere nearly twice the length of flagellomere 1 [Figure 44]; posterior propodeal surface with short adpressed hairs [Figure 46] 7



- 6(5). Mandible with extensive area of yellow pigmentation; apical half of retrorse lobes of genitalia curved laterad [Figure 47] 3. *S. danforthi*, new species
 Mandible darkly pigmented, without extensive area of yellow; apical half of retrorse lobes straight, not curved laterad [Figure 48] 7. *S. potosi*, new species
- 7(5). T1 punctation dense at center of disc, most punctures separated by 2–3 times their width [Figure 49; difficult to see on SEM image, much more obvious under light microscope]; known only from Antioch (Contra Costa County), California [Figure 92]. 2. *S. antiochensis*, new species
 T1 punctation less dense at center of disc, relatively sparse, most punctures separated by 3–4 times their width [Figure 50; see above comment]; widespread in western North America from Canada to Mexico, known in California only from the south in Inyo, Riverside, and San Bernardino counties [Figure 92] 4. *S. lusoria* (Cresson)



1. *Sphecodogastra aberrans* (Crawford), new combination

FIGURES 51–58, 66–71

Halictus aberrans Crawford, 1903:336 [females].—Cockerell, 1906b:427 [floral records].—1907a:242 [key].—1907b:119 [contrasted with *H. galpinsiae*].—Crawford, 1907:186, 188 [key; compared with *H. galpinsiae*].—Graenicher, 1911:224 [compared with *H. galpinsiae*].—Stevens, 1951:61 [association with *Gaura coccinea* and other plants].

Halictus (Evylaeus) aberrans.—Stevens, 1920:36 [taxonomy; compared with *H. galpinsiae*; locality and floral records].

Lasioglossum (Sphecodogastra) aberrans.—Michener, 1951:1111 [catalog].

Lasioglossum (Evylaeus) abberans.—Linsley and MacSwain, 1962:45 [lapsus calami].

Evylaeus aberrans.—Moldenke and Neff, 1974:60 [floral records].—Bohart and Youssef, 1976:186 [compared with *E. galpinsiae*].—Hurd, 1979:1958 [catalog].—Hurd et al., 1980:66 [association with *Helianthus*].—Moure and Hurd, 1987:68 [catalog].

Lasioglossum aberrans.—Poole, 1996:431 [checklist].

TYPE MATERIAL.—Crawford based his description of *Halictus aberrans* on a syntype series of three females with the following data: “Sioux Co., Nebr., June 3, on *Symphoricarpos*; Crawford, Nebr., July 28, on *Cleome*; Manitou, Colorado.” None of these specimens could be located, and they are pre-

sumed to be lost. Because of the long-standing confusion between this species and *Sphecodogastra lusoria* (see “Species Descriptions and Synonymies” in systematic history section) I am designating a neotype that was also collected in Sioux County, Nebraska. The specimen is deposited in the entomology collection of the University of Nebraska and is labeled “Sioux Co[unty] Neb.[raska] May/L. Bruner Collector/NEOTYPE *Halictus aberrans* Crawford des.[ignated by] R.J. McGinley” [red label]. It is missing the right antenna, nine distal flagellomeres of the left antenna, and two distal tarsomeres of the right middle leg, and its abdomen is glued on the left side to the second specimen label. Despite this damage, the specimen is otherwise in excellent condition and shows all diagnostic features needed to differentiate it from *S. lusoria* and other known *Sphecodogastra* species.

DISTRIBUTION (Figure 51).—*Sphecodogastra aberrans* has the most northern known distribution of the genus, having been collected from southern Alberta, Manitoba, and Saskatchewan. *Sphecodogastra lusoria* is the only other species known from central Canada, at Cardston and Medicine Hat, Alberta (Figure 92). Both species appear to be widely

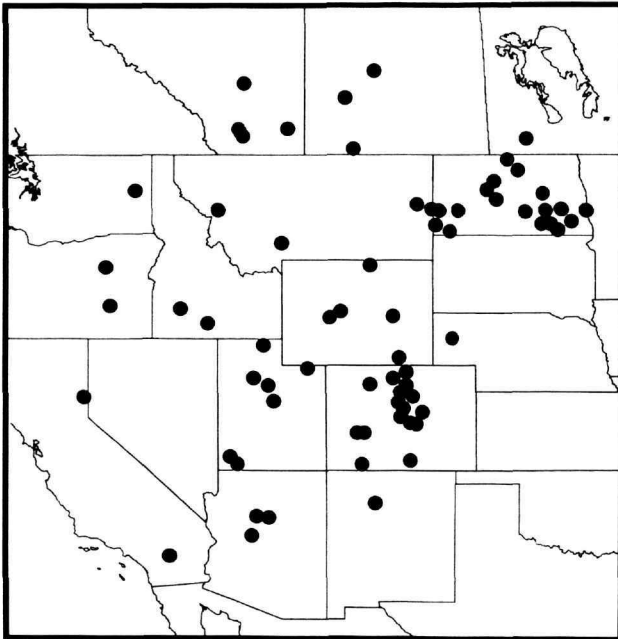


FIGURE 51.—Distribution of *Sphecodogastra aberrans*.

sympatric throughout the Great Basin and the intermountain region of the central and western United States, with *S. aberrans* extending south only to southern California (Riverside County), central Arizona, and northern New Mexico. *Sphecodogastra lusoria* in addition includes a more southeastern distribution, east to Nebraska, Kansas, Oklahoma, and Texas and south through southern Arizona, New Mexico, and central Mexico (Hidalgo state). Bohart and Youssef (1976:186) noted that “in Colorado, collection records indicate that the two species may fly together,” which is known from other collections. They also indicated that *S. lusoria* “nests in open, sandy areas with typically xeric surroundings,” whereas *Evylaeus aberrans* “is generally found in more mesic and highland surroundings, on brush-covered slopes or open woodlands.”

The distribution records for *S. aberrans* listed by Moure and Hurd (1987) are understandably misleading because they include records for *S. lusoria*; however, they listed a record from Coahuila, Mexico, presumably associated with *S. lusoria*. I have not seen specimens of this species from this state, but its occurrence there is not unexpected. They also listed a record for one or the other of these species from Wisconsin, which would seem to be a dubious but possible extension for either species—most likely for *S. aberrans*.

DIAGNOSIS.—The absence of short, adpressed pleural hairs differentiates the females of *S. aberrans*, *S. antiochensis*, and *S. oenotherae* from all other known *Sphecodogastra* females. The coarsely rugo-striate dorsal propodeal surface of *S. oenotherae* easily separates it from the other two species. The punctuation on the supraclypeal area of *S. aberrans* is only moderately

dense, with most punctures separated by twice their diameters (Figure 24); this area is densely punctate in *S. antiochensis*, with punctures separated by less than the width of their diameters. The femoral scopa of *S. aberrans* is sharply delimited as in other species of the genus (e.g., Figure 26), whereas these hairs in *S. antiochensis* are relatively diffused in pattern (i.e., not forming a distinctly sharp row of apically curved hairs; Figure 25). Consideration of distribution is probably the easiest way to separate these two species (Figures 51, 92) because *S. antiochensis* is found only in the area of Antioch, California, where *S. aberrans* is not known to occur.

Males of *S. aberrans* can be distinguished from those of other *Sphecodogastra* by their distinctive sternal vestiture (Figure 37); the fringe hairs on the posterior margins of sterna 4 and 5 are conspicuously developed and differentiated from vestiture on other sternal margins. Other distinctive characters are presented in couplet four of “Key to *Sphecodogastra* Males.”

DESCRIPTION.—FEMALE: (1) Length 7.8–9.4 mm (mean = 8.4, $n = 5$); (2) wing length 2.4–2.7 mm (mean = 2.6, $n = 5$); (3) abdominal width 2.3–2.7 mm (mean = 2.6, $n = 5$).

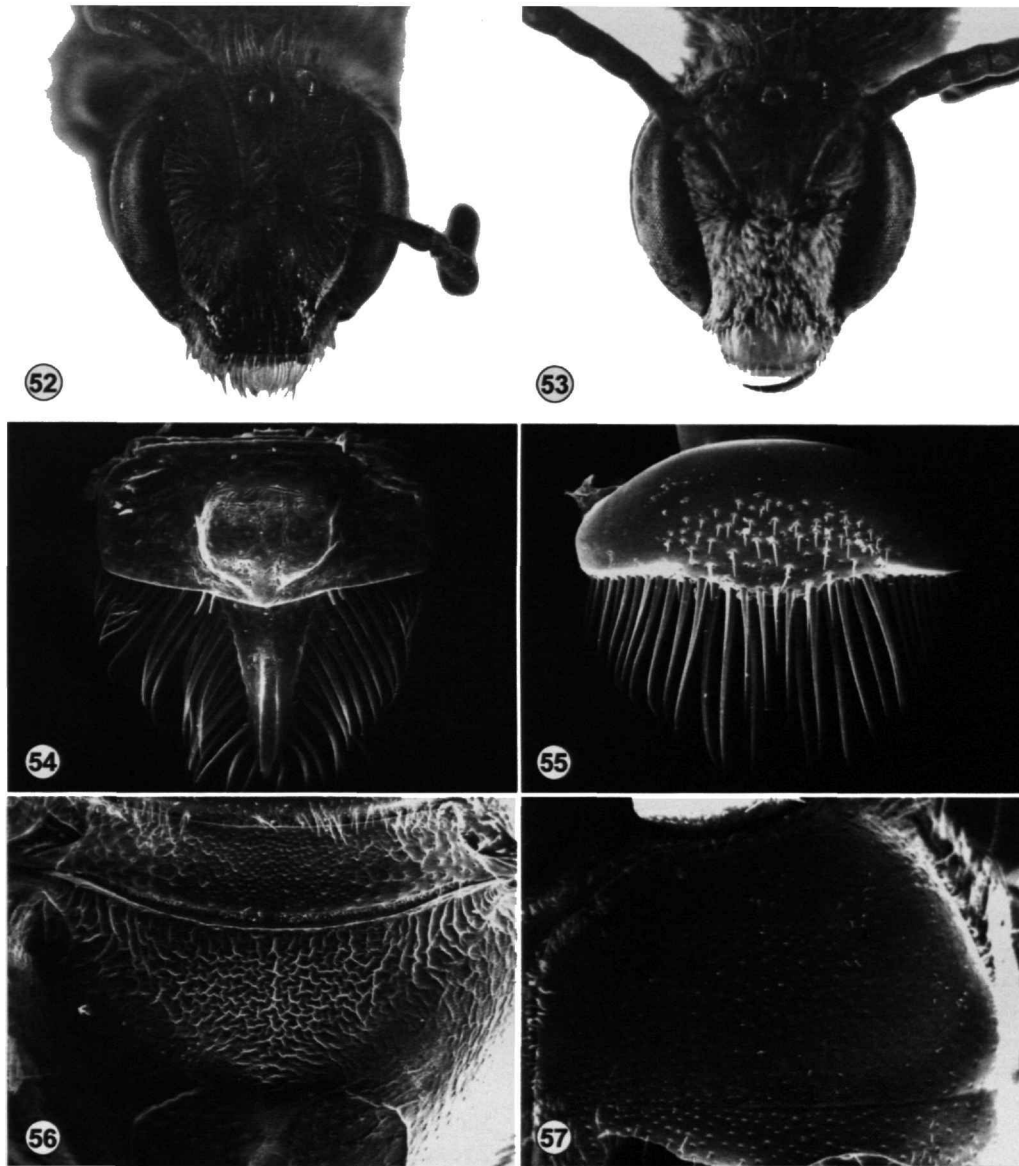
Structure: (4) Head moderately elongate (Figure 52); length/width ratio 1.00–1.03 (mean = 1.01, $n = 5$). (5) Gena, at midpoint, subequal to or slightly exceeding compound eye in width. (9) Clypeus projecting approximately 0.69 times its length below lower margin of eyes; (11) clypeal surface without median longitudinal sulcation. (13) Ocular–ocellar distance greater than distance between lateral ocellus and hind margin of vertex (ocular–ocellar space approximately 2.0 times lateral ocellar diameter); (14) distance between lateral ocelli slightly exceeding ocular–ocellar distance. (16) Inner margins of compound eyes converging below. (21) Scape reaching top of vertex; (22) pedicel subequal in length to flagellomere 1. (30) Mandible moderate in length, extending to opposing clypeal angle.

(40) Dorsal surface of propodeum about 0.60 times the length of scutellum and approximately 1.25 times the length of metanotum; (44) lateral propodeal carinae well developed, extending to dorsal propodeal surface. (45) Inner hind tibial spur with 4 or 5 moderately elongate teeth (Figure 58).

(46) Lateral edge of metasomal T2 broadly rounded anteriorly, becoming straight to faintly sinuate posteriorly.

Sculpture: (51) Supraclypeal area granulate, (52) punctuation moderately dense, most punctures separated by 1–2 times the width of their diameters (Figure 24). (53) Clypeus tessellate basally; (54) subapical area with contiguous, large punctures. (55) Hypostoma striolate.

(56) Mesoscutum somewhat dull, surface tessellate over anterior half or more, (57) punctuation as in Figure 57, punctures separated by 1–3 times their diameters. (63) Dorsal surface of propodeum rugulose over basal three-fourths (Figure 56), (64) surface alveolated. (65) T1 shiny and polished, (66) punctuation fine, moderately dense, most punctures separated by their diameters.

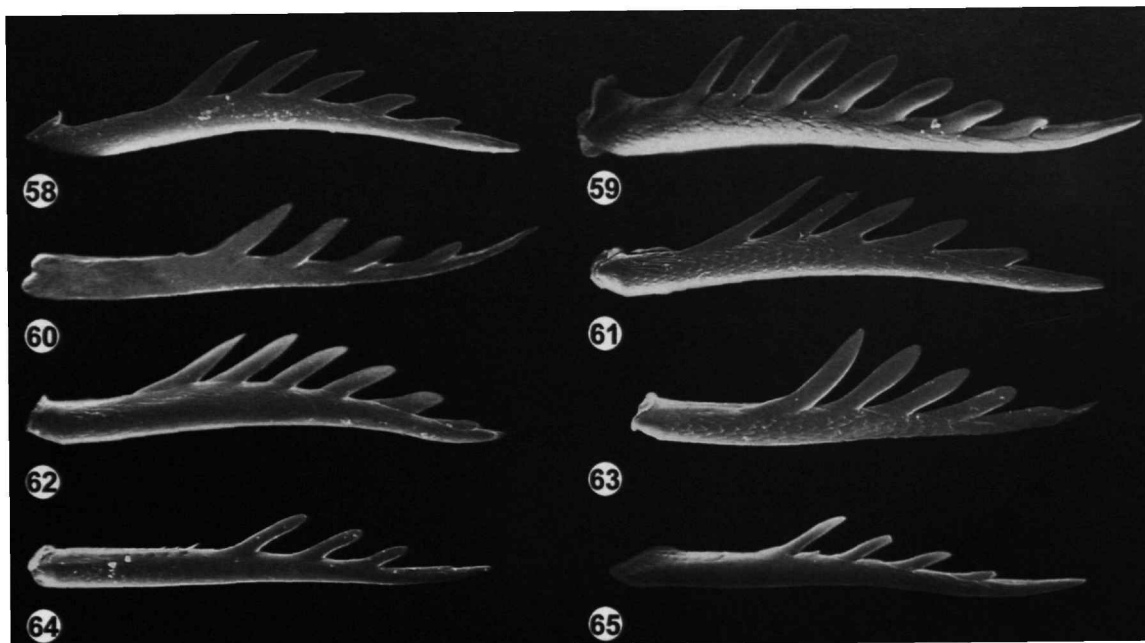


FIGURES 52-57.—*Sphecodogastra aberrans*: 52, female head; 53, male head; 54, female labrum; 55, male labrum; 56, female propodeum; 57, female mesoscutum.

Coloration: (67) Abdomen dark brown. (69) Flagellum brown. (70) Tegula light brown. (71) Wing membrane pale yellowish brown; veins and stigma amber. (72) Legs dark brown.

Vestiture: (74) Head hairs pale yellowish brown. (75) Pubescence on thorax pale yellowish brown; (76) mesoscutal hairs elongate, approximately 1.5 times median ocellar diameter; mesoscutum and pleuron without short suberect or adpressed hairs. (81) Basal hair bands on T2-T4 present, covering basal one-fourth of tergal surface; moderately developed apical hair bands present on T3 and T4.

MALE: As described for female except as follows: (1) Length 7.7-9.3 mm (mean = 8.7, $n = 5$); (2) wing length 2.0-2.2 mm (mean = 2.2, $n = 5$); (3) abdominal width 1.8-2.0 mm (mean = 1.9, $n = 5$). (4) Head (Figure 53) length/width ratio 1.10-1.12 (mean = 1.11, $n = 5$). (23) Flagellomere 2 approximately 1.8 times length of flagellomere 1. (37) Median mesoscutal line impressed. (70) Tegula yellow-translucent. (73) Short, adpressed hairs on face extending dorsad to just below median ocellus. (76) Mesoscutum with moderately elongate hairs (short, adpressed hairs absent); pleuron without short,



FIGURES 58-65.—*Sphecodogastra* female inner tibial spurs: 58, *S. aberrans*; 59, *S. antiochensis*; 60, *S. danforthi*; 61, *S. lusoria*; 62, *S. oenotherae*; 63, *S. potosi*; 64, *S. noctivaga*; 65, *S. texana*.

adpressed hairs. (82, 83) Unlike other *Sphecodogastra*, elongate vestiture on S4 and S5 confined to apical margin (Figure 37; vestiture distributed over entire sternal surface in other species, e.g., Figure 38); (83a) central depression of S6 extremely well developed (Figure 66).

Terminalia (Figures 67-70): (84) S7 lateral arms slender (Figure 70); (85) S8 moderately developed (Figure 70); apex of median process slightly concave; (89) retrorse membranous lobe narrow, becoming slightly broader basally. Unlike other *Sphecodogastra*, penis valve sharply angulate in lateral view,

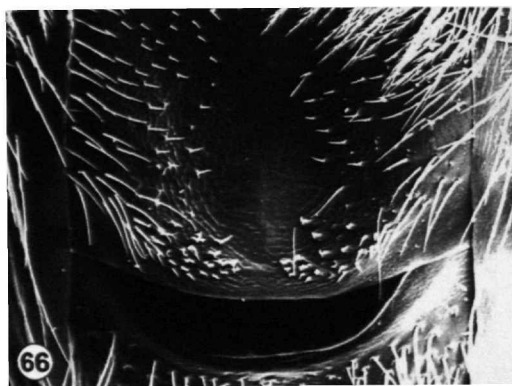


FIGURE 66.—*Sphecodogastra aberrans*, male S6.

dorsal surface concave, and sharply carinate laterally (Figure 67).

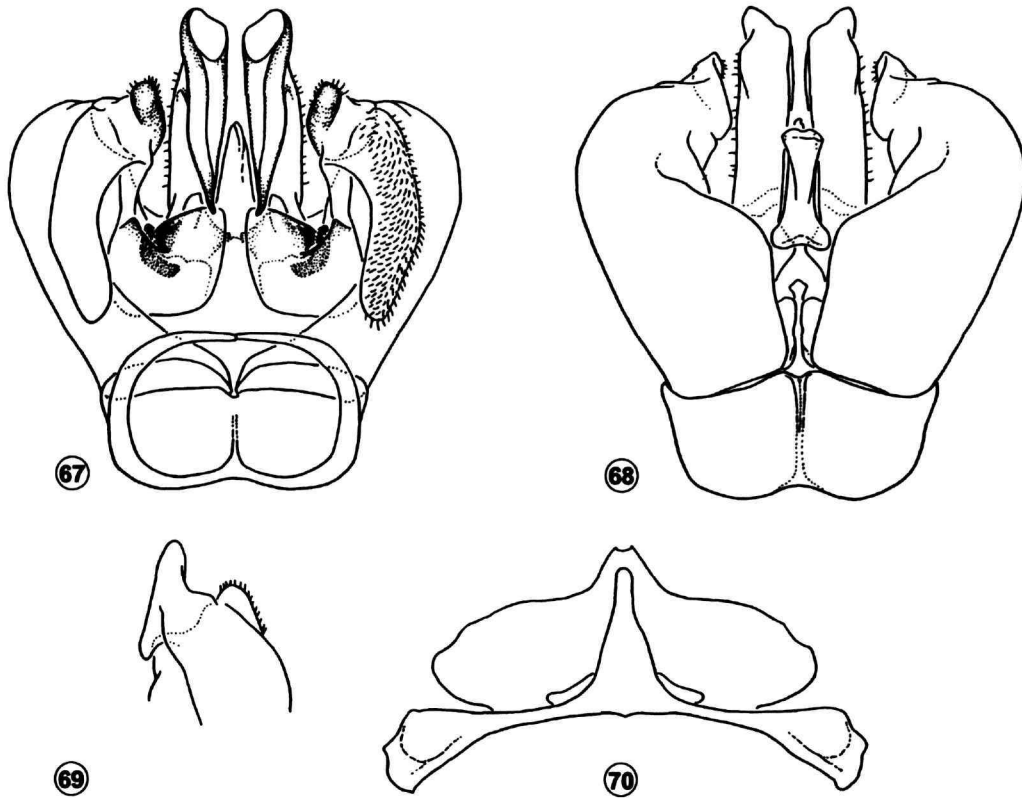
FLIGHT RECORDS (Figure 71).—Females of *S. aberrans* were collected from May through October, with most records (98%) from June through August. Males appear to be active somewhat later, with an apparent peak during July.

REMARKS.—See "Species Descriptions and Synonymies" in systematic history section.

SPECIMENS EXAMINED.—426 (327 females, 99 males).

CANADA. ALBERTA: Kipp; Lethbridge; Medicine Hat; Medicine Hat, 25 mi NW; Morrin; Nobleford. MANITOBA: Treesbank. SASKATCHEWAN: Elrose; Saskatoon; Val Marie.

UNITED STATES. ARIZONA: *Coconino Co.*: Flagstaff; Oak Creek (W fork, 16 mi SW Flagstaff); Williams; *Yavapai Co.*: Prescott; *county/coordinates unknown*: Oayson. CALIFORNIA: *Plumas Co.*: Vinton, 5.5 mi S; *Riverside Co.*: Indio (Pine Flats Camp). COLORADO: *Archuleta Co.*: Piedra; *Boulder Co.*: Altona; Altona, 3 mi SW; Boulder; Copeland Park; Jim Creek (near Boulder); Lyons, 9 mi NW; Ward; *Clark Co.*: Lake George; *Clear Creek Co.*: Echo Lake (Mt. Evans); *Denver Co.*: Denver; *Elbert Co.*: Elbert; *El Paso Co.*: Colorado Springs; Manitou [male specimen; not part of type series]; *Gunnison Co.*: Mt. Princeton Hot Springs; Sapinero, 4 mi E; *Huerfano Co.*: Cuchara; *Jefferson Co.*: Crossons; Golden; *Larimer Co.*: Cameron Pass; Hewlett Gulch (near Poudre Park); *Montrose Co.*: Buckeye Reservation; Cimarron, 1.2 mi W; *Park Co.*: Wilkerson Pass; *Routt Co.*: Oak Creek (20 mi S Steamboat



FIGURES 67-70.—*Sphecodogastra aberrans*, male terminalia: 67, genital capsule, ventral view; 68, genital capsule, dorsal view; 69, right gonostylus, posterior view; 70, S7 and S8, ventral view.

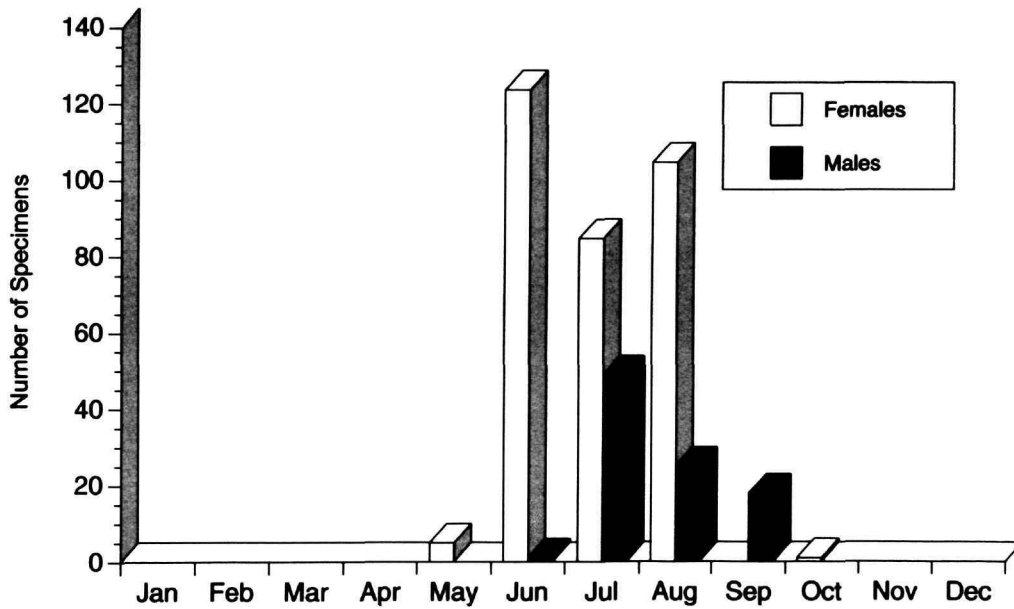


FIGURE 71.—*Sphecodogastra aberrans* flight records, by month of collection.

Springs); *Teller Co.*: Florissant; *county/coordinates* unknown: Mishawauka. IDAHO: *Elmore Co.*: Mountain Home; *Twin Falls Co.*: Twin Falls, 18 mi S. MONTANA: *Dawson Co.*: Glendive; *Gallatin Co.*: Bozeman; *Missoula Co.*: Missoula. NEBRASKA: *Sioux Co.* NEW MEXICO: *Sandoval Co.*: Jemez Springs. NORTH DAKOTA: *Barnes Co.*: Valley City; *Bottineau Co.*: Bottineau; *Bowman Co.*: Gascoyne; *Cass Co.*: Fargo; *Dickey Co.*: Oakes; *Golden Valley Co.*: Beach; Sentinel Butte; *Kidder Co.*: Tappen; *La Moure Co.*: Kulm; LaMoure; *McLean Co.*: Garrison; Washburn; *Pierce Co.*: Rugby; *Ransom Co.*: Lisbon; *Slope Co.*: Marmarth; *Stark Co.*: Dickinson; *Stutsman Co.*: Jamestown; Kensal; *Ward Co.*: Lone Tree. OREGON: *Grant Co.*: Long Creek, 3.6 mi S; *Harney Co.*: Narrows, 20 mi S; *Sherman Co.*: Maryhill Ferry (3 mi E Briggs). UTAH: *Cache Co.*: Logan (Green Canyon); *Daggett Co.*: Pallsade Park Camp; Sheep Creek Canyon; *Sanpete Co.*: Fairview; *Tooele Co.*: Tooele; *Utah Co.*: Provo; *Washington Co.*: Lower Deep Creek; Virgin; Pinto; Upper Deep Creek; Zion National Park. WASHINGTON: *Adams Co.*: Ritzville, 4 mi N. WYOMING: *Albany Co.*: Laramie; Laramie, 2 mi S; Laramie, 8 mi SSE; *Converse Co.*: Glenrock; *Fremont Co.*: Lander, 8.5 mi SW (Sinks Canyon); Riverton; *Sheridan Co.*: Sheridan.

2. *Sphecodogastra antiochensis*, new species

FIGURES 59, 72–82

As *Lasioglossum (Sphecodogastra) aberrans* (Crawford).—Turner, 1966 [foraging activity, host plant biology, mating biology, predation, parasitism, nest site].

TYPE MATERIAL.—The holotype female, from the collection of the Bee Biology and Systematics Laboratory, Utah State University, has been deposited in the National Museum of Natural History, Smithsonian Institution. It is in excellent condition and is labeled "Antioch Calif.[ornia] IV[April]-4-[19]39 [handwritten]/GE Bohart Collector/HOLOTYPE *Sphecodogastra antiochensis* R.J. McGinley" [red label]. Paratypes are listed in "Specimens Examined," below.

ETYMOLOGY.—The specific name was a label manuscript name used by George E. Bohart, who along with P.H. Timberlake was among the first workers to recognize this species as being distinct. As the name implies, this species is known only from the vicinity of Antioch, Contra Costa County, California.

DISTRIBUTION (Figure 92).—*Sphecodogastra antiochensis* is a geographically isolated species of this genus. It is known to occur only in the sand dune habitat of Antioch, Contra Costa County, California. Its host plant is a similarly isolated subspecies of primrose, *Oenothera deltooides howellii* (Klein, 1970). The nearest occurrences of another *Sphecodogastra* species I am aware of are two separate collections of *S. lusoria* from Delhi and Livingston, Merced County, California, approximately 70 miles southeast of Antioch (Figure 92).

DIAGNOSIS.—Females: see "Diagnosis" for *S. aberrans*. Males: see "Diagnosis" for *S. lusoria*.

DESCRIPTION.—FEMALE: (1) Length 8.2–9.5 mm (mean = 8.8, $n = 5$); (2) wing length 2.6–3.0 mm (mean = 2.8, $n = 5$); (3) abdominal width 2.6–2.9 mm (mean = 2.7, $n = 5$).

Structure: (4) Head moderately elongate (Figure 72); length/width ratio 0.95–1.00 (mean = 0.98, $n = 5$). (5) Gena, at midpoint, slightly exceeding width of compound eye. (9) Clypeus projecting approximately 0.63 times its length below lower margin of eyes; (11) clypeal surface without median longitudinal sulcation. (13) Ocular–ocellar distance exceeding distance between lateral ocellus and hind margin of vertex (ocular–ocellar space approximately 1.5 times lateral ocellar diameter); (14) distance between lateral ocelli slightly exceeding ocular–ocellar distance. (16) Inner margins of compound eyes converging below. (21) Scape reaching top of vertex; (22) pedicel subequal in length to flagellomere 1. (30) Mandible moderate in length, reaching opposing clypeal angle.

(40) Dorsal surface of propodeum about 0.59 times the length of scutellum and approximately 1.13 times the length of metanotum; (44) lateral propodeal carinae well developed, extending to dorsal propodeal surface. (45) Inner hind tibial spur with 5–7 teeth, more numerous and somewhat longer than those of other *Sphecodogastra* species (Figure 59).

(46) Lateral edge of metasomal T2 rounded anteriorly, becoming straight to faintly sinuate posteriorly.

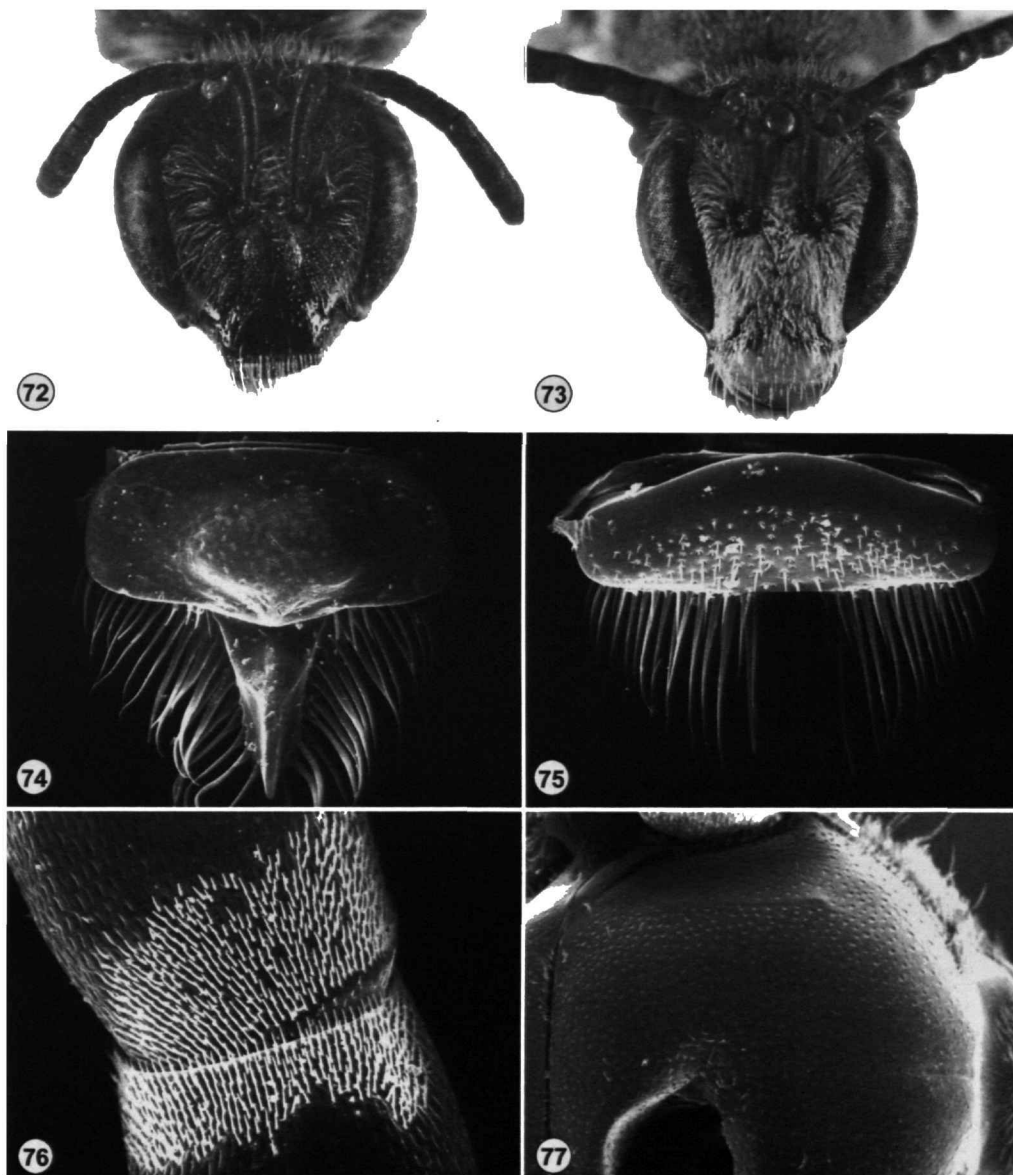
Sculpture: (51) Supraclypeal area mostly polished, tessellate only near lateral margins, (52) very densely punctate, most punctures separated by less than the width of their diameters. (53) Clypeus polished; (54) punctation extremely sparse, apical punctures only slightly larger than basal ones, most separated by at least three times their diameters. (55) Hypostoma striolate throughout.

(56) Mesoscutum somewhat dull, tessellate on anterior half, (57) punctation as in Figure 77, most punctures separated by 1–2 times their diameters. (63) Dorsal surface of propodeum ruguloso–striolate, nearly to posterior edge (Figure 27), (64) surface alveolated. (65) T1 shiny and polished, (66) punctation fine, moderately sparse, punctures separated by 1–2 times their diameters.

Coloration: (67) Abdomen dark brown. (69) Flagellum dark brown. (70) Tegula brown to light brown. (71) Wing membrane pale yellowish brown; veins and stigma amber. (72) Legs dark brown.

Vestiture: (74) Hairs on head pale yellowish brown. (75) Pubescence on thorax pale yellowish white; (76) mesoscutal hairs elongate, length approximately 1.5 times median ocellar diameter; mesoscutum and pleuron without short, suberect or adpressed hairs. (81) Basal hair bands on T2–T4 present, covering basal one-fourth of tergal surface; moderately developed apical hair bands on T3 and T4.

MALE: As described for female except as follows: (1) Length 8.0–9.3 mm (mean = 8.5, $n = 5$); (2) wing length 2.2–2.6 mm (mean = 2.4, $n = 5$); (3) abdominal width 1.7–2.2 mm (mean = 2.0, $n = 5$). (4) Head (Figure 73) length/width ratio 1.08–1.11 (mean = 1.09, $n = 5$). (23) Flagellomere 2 ap-



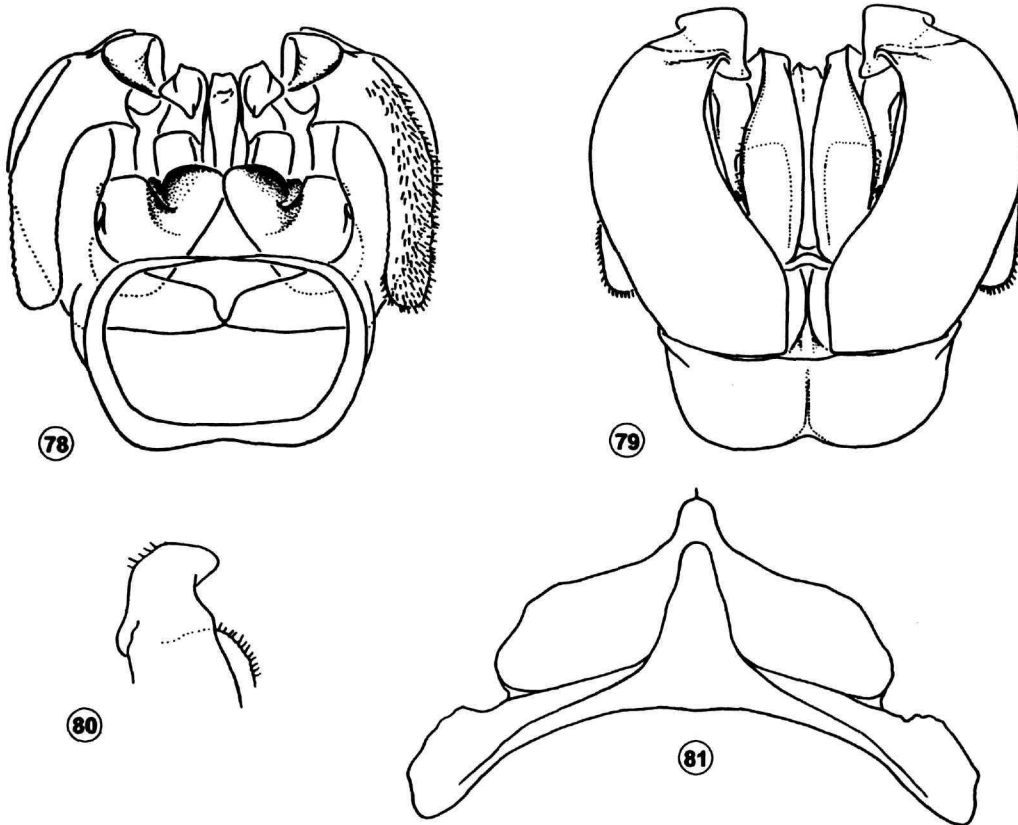
FIGURES 72–77.—*Sphecodogastra antiochensis*: 72, female head; 73, male head; 74, female labrum; 75, male labrum; 76, male flagellum; 77, female mesoscutum.

proximately 2.0 times length of flagellomere 1. (37) Median mesoscutal line impressed. (70) Tegula yellow-translucent to brown. (73) Short, adpressed hairs on face extending dorsad to ocellar area, nearly enclosing median ocellus. (76) Mesoscutum with moderately elongate hairs and extensive layer of short, adpressed hairs; pleuron with short, adpressed hairs.

Terminalia (Figures 78–81): (84) S7 lateral arms moderately well developed; (85) S8 moderately developed; apex of median process rounded; (89) retrorse membranous lobe narrow.

FLIGHT RECORDS (Figure 82).—Females of *S. antiochensis* examined in this study were collected from March through August, with most records (67%) collected during May. Male collections ranged from May through October, with an overwhelming number (96%) taken in June.

Turner (1966) reported the earliest records of female flight activity as 15 March and 5 April. During his 1964–1965 study, females were first active usually in late April. The flight period of this species normally extends through August; however, in



FIGURES 78-81.—*Sphecodogastra antiochensis*, male terminalia: 78, genital capsule, ventral view; 79, genital capsule, dorsal view; 80, right gonostylus, posterior view; 81, S7 and S8, ventral view.

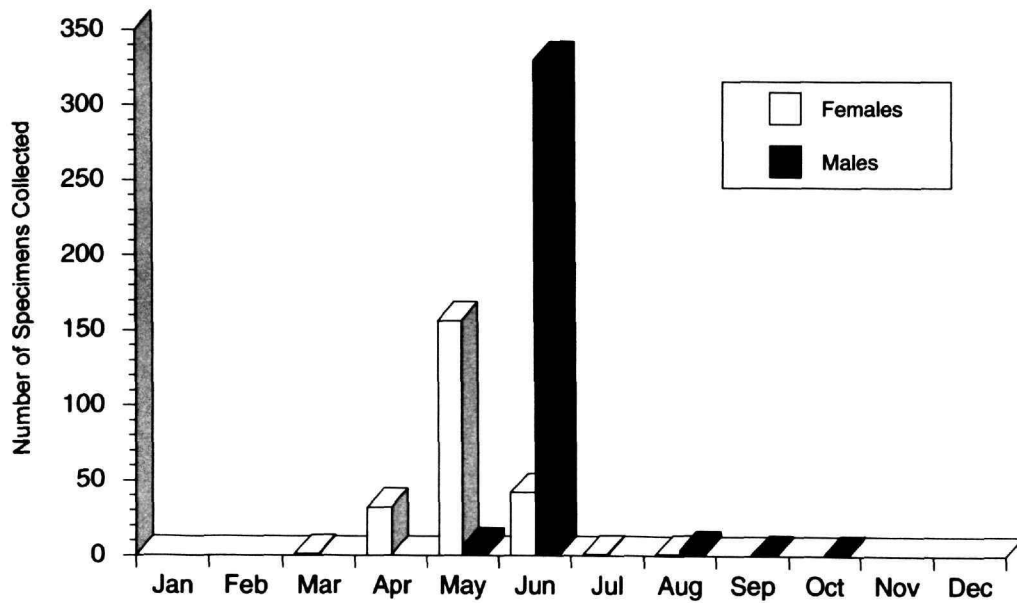


FIGURE 82.—*Sphecodogastra antiochensis* flight records, by month of collection.

1965, unusual rainfall prolonged the season, with females and males being observed as late as 19 and 22 September, respectively. Turner indicated that *Sphecodogastra antiochensis* apparently produced two generations each year.

REMARKS.—*Sphecodogastra antiochensis* is known exclusively from the bluffs of Antioch, Contra Costa County, California, as is its host plant, *Oenothera deltooides howellii* (Klein, 1970). This area was recognized in 1980 as the Antioch Dunes National Wildlife Refuge, largely for the protection of the endangered Lange's metalmark butterfly (*Apodemia mormo langei*) and its host plant, *Eriogonum nudum* (Caterino, 1997). Caterino indicated that under protection and proper dune management the situation for the butterfly and its host plant looked relatively good.

Jerry Powell, who has long been involved with conservation efforts on behalf of the Antioch Dunes (e.g., Powell, 1978), added (Powell, pers. comm., 1996) the following:

The last time I checked on *Sphecodogastra* at Antioch was June 1982, and it was present then (22 individuals, 0630–0830). Although I have visited a few times in early A.M. in recent years to look for *Apodemia* larvae, I didn't look for *Sphecodogastra*. Since that time there has been a concerted effort to plant *Oenothera*, even including trucking in and contouring whole new sandhills, with considerable success. The plant is much more abundant now than in the lowest ebb, when weediness was choking out seedling establishment. The plants set seed, so I assume the bee population has increased. I don't know that it will be of any advantage to propose the population as endangered because the property is already in Federal hands and because they target the *Oenothera* as an endangered species in their recovery plans.

I agree with Powell's opinion that it is probably unnecessary to propose endangered species status for *S. antiochensis*, but I hope this unique *Oenothera*–*Sphecodogastra* relationship will be monitored in the future.

SPECIMENS EXAMINED.—574 (233 females, 341 males); 573 paratypes are designated and so labeled. They are deposited in the following collections: KU, NMNH, UCB, UCR, UIM, UNL, and USU.

3. *Sphecodogastra danforthi*, new species

FIGURES 60, 83–91

TYPE MATERIAL.—The female holotype of *S. danforthi* is deposited in the NMNH collection. It is in excellent condition and is labeled "K07461/TEXAS: Winkler Co. Rd. 404, 8 mi E Hwy 18 10-IX-1989 J.L. Neff/on flowers of *Calylophus Hartwegii*/HOLOTYPE *Sphecodogastra danforthi* des. R.J. McGinley" [red label]. Paratypes (33 females, 5 males) are designated and listed in "Specimens Examined," below.

ETYMOLOGY.—I was originally aware of this undescribed species from one female in very poor condition collected in 1959, 9.5 miles south of Monahans, Texas, but I was reluctant to describe it as new. Subsequently, Bryan N. Danforth, for whom this species is named, sent me a freshly collected sample of 11 females and two males from 10 km northeast of Monahans, which confirmed my initial opinion that the one previously known specimen represented a new species. Later, addi-

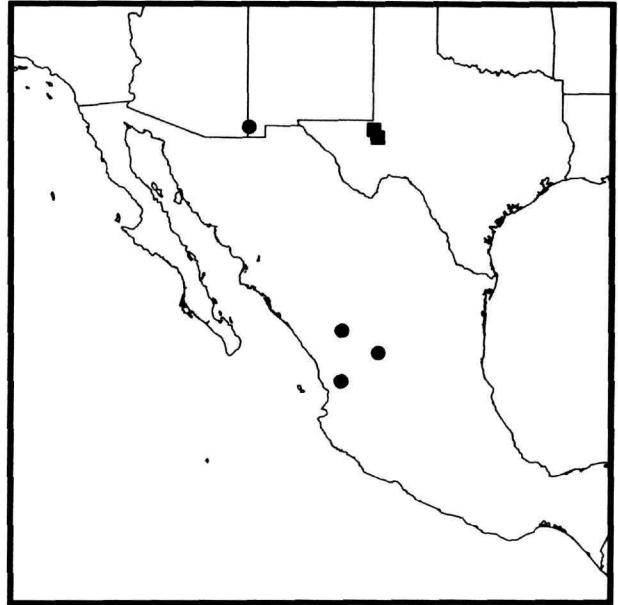
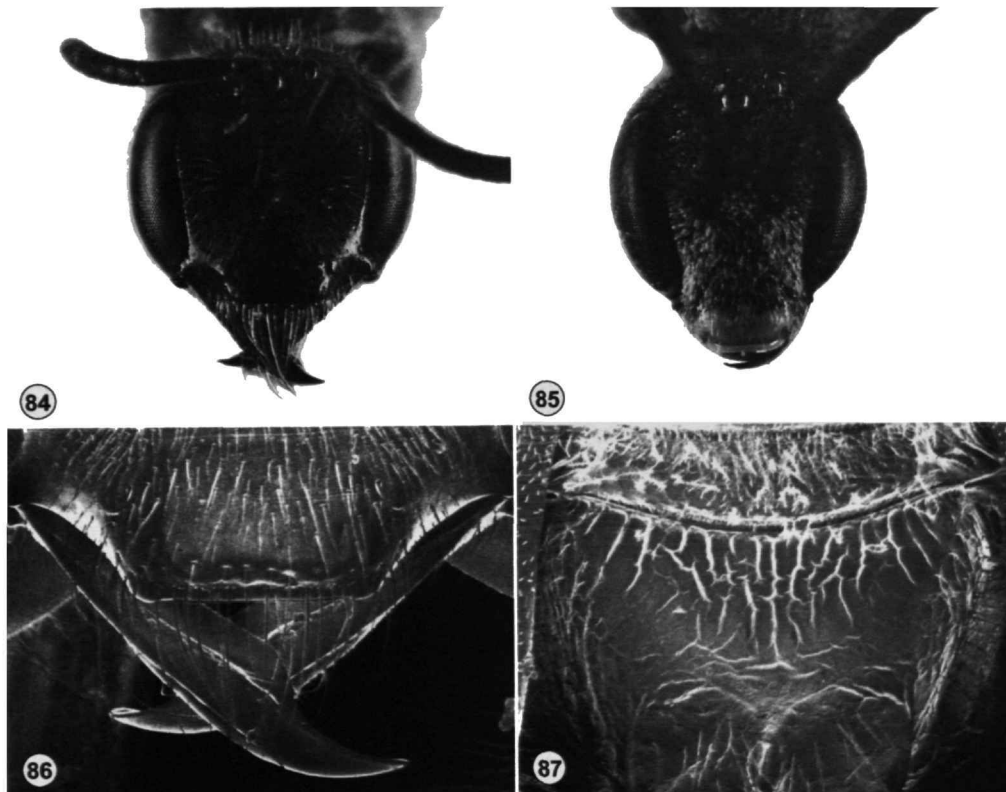


FIGURE 83.—Distribution of *Sphecodogastra danforthi* (squares) and *S. potosi* (bullets).

tional specimens of this rarely collected species were sent to me by J.L. Neff, an important contribution that I would like to acknowledge.

DISTRIBUTION (Figure 83).—*Sphecodogastra danforthi* is presently only known from Ward and Winkler counties, Texas. It is definitely sympatric with *S. lusoria*, *S. noctivaga*, and *S. texana*. From the UCB collection I have examined specimens of all four species collected by D.P. Gregory on 11 May 1959, 9.5 miles south of Monahans, from the flowers of *Calylophus hartwegii* (all specimens had Onagraceae pollen in their scopae).

DIAGNOSIS.—The dark abdomen and conspicuously elongate and projecting mandibles, which lack defined subapical teeth (Figure 86), easily separate *S. danforthi* females from other known congeners. Females of *S. potosi* are similar in having elongate mandibles, but these are broadly rounded laterally, weakly projecting, and have well-defined subapical teeth (Figure 18). The males of *S. danforthi* and *S. potosi* are difficult to differentiate, a situation parallel to *S. noctivaga* and *S. texana* where the females are easily separated on the basis of mandibular morphology but the respective males are nearly identical. The darkly pigmented abdomens of male *S. danforthi* and *S. potosi* in combination with the finely rugulose dorsal propodeal surface and "normal" antennal flagella (lacking distinctive sensillar patterns) will differentiate them from other congeners. The head of male *S. potosi* (Figure 130) appears to be broader than that of *S. danforthi* (Figure 85), but this is not obviously reflected in head length/width ratios (1.04–1.08 for the former and 1.10–1.14 for the latter).



FIGURES 84–87.—*Sphecodogastra danforthi*: 84, female head; 85, male head; 86, female mandibles; 87, female propodeum.

DESCRIPTION.—FEMALE: (1) Length 6.7–7.7 mm (mean = 7.2, $n = 5$); (2) wing length 2.0–2.2 mm (mean = 2.1, $n = 5$); (3) abdominal width 2.0–2.3 mm (mean = 2.2, $n = 5$).

Structure: (4) Head short, rounded (Figure 84); length/width ratio 0.91–0.95 (mean = 0.95, $n = 5$). (5) Gena, at midpoint, exceeding compound eye in width. (9) Clypeus projecting approximately 0.77 times its length below lower margin of eyes; (11) clypeal surface without median longitudinal sulcation. (13) Ocular–ocellar distance slightly shorter than distance between lateral ocellus and hind margin of vertex (ocular–ocellar space approximately 1.5 times lateral ocellar diameter); (14) distance between lateral ocelli exceeding ocular–ocellar distance. (16) Inner margins of compound eyes only slightly converging below, nearly parallel. (21) Scape reaching top of vertex; (22) pedicel nearly subequal in length to flagellomere 1. (30) Mandible conspicuously elongate, strongly projecting beyond clypeus (Figure 86); (31) unlike other *Sphecodogastra*, subapical tooth broadly rounded, not defined.

(40) Dorsal surface of propodeum about 0.71 times the length of scutellum and approximately 1.36 times the length of metanotum; (44) lateral propodeal carinae well developed, ex-

tending to dorsal propodeal surface. (45) Inner hind tibial spur usually with four moderately elongate teeth (Figure 60).

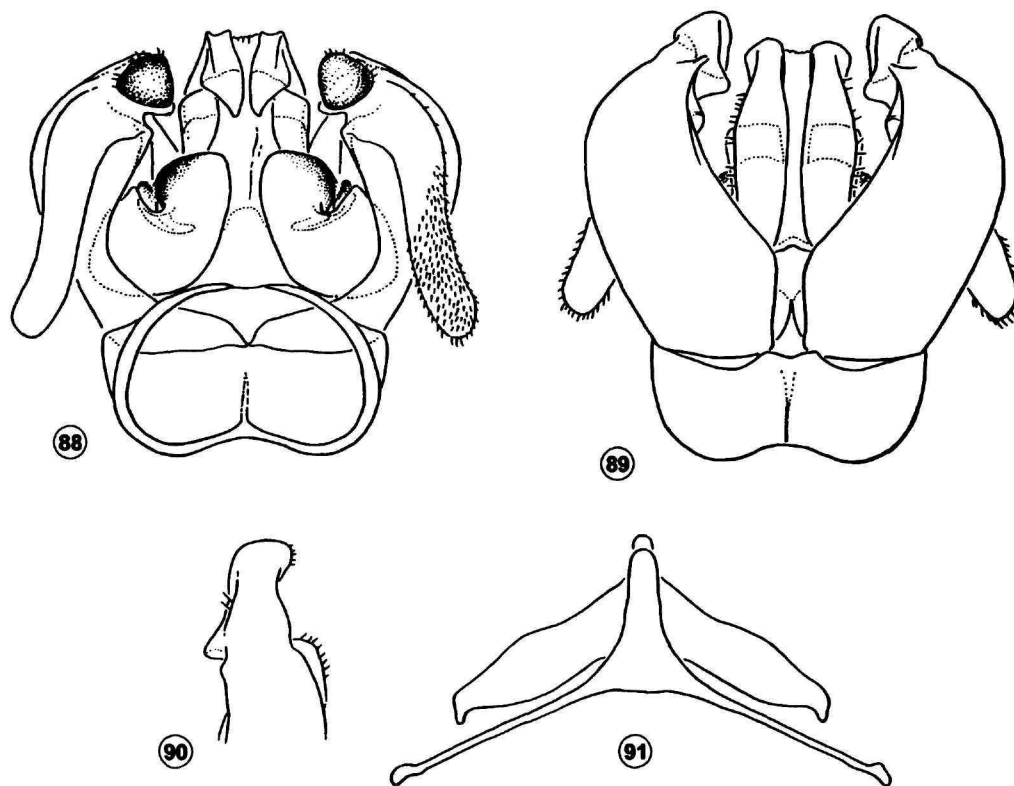
(46) Lateral edge of metasomal T2 straight.

Sculpture: (51) Supraclypeal area finely granulate, (52) punctation moderately dense, most punctures separated by two times the width of their diameters. (53) Clypeus weakly tessellate basally, mostly polished and shiny; (54) subapical area with a few large, poorly defined punctures. (55) Hypostoma smooth, nonstriolate.

(56) Mesoscutum somewhat dull, surface tessellate over anterior half or more; (57) mesoscutal punctures separated by their diameters or slightly less. (63) Dorsal surface of propodeum ruguloso–striolate throughout (Figure 87), (64) surface shiny, nonalveolate. (65) T1 shiny and polished, (66) punctation extremely fine and sparse, most punctures separated by 2–5 times their diameters.

Coloration: (67) Abdomen dark brown. (69) Flagellum brown. (70) Tegula light brown. (71) Wing membrane pale yellowish brown; veins and stigma amber. (72) Legs dark brown.

Vestiture: (74) Head hairs yellowish white-brown. (75) Pubescence on thorax pale yellowish brown; (76) mesoscutal hairs moderately short, only slightly exceeding diameter of me-



FIGURES 88–91.—*Sphecodogastra danforthi*, male terminalia: 88, genital capsule, ventral view; 89, genital capsule, dorsal view; 90, right gonostylus, posterior view; 91, S7 and S8, ventral view.

dian ocellus; mesoscutum and pleuron without short suberect or adpressed hairs. (81) Basal hair bands on T2–T4 absent; apical hair bands on T3 and T4 absent.

MALE: As described for female except as follows: (1) length 6.4–7.7 mm (mean = 7.0, $n = 5$); (2) wing length 1.4–1.8 mm (mean = 1.8, $n = 5$); (3) abdominal width 1.4–1.8 mm (mean = 1.7, $n = 5$). (4) Head (Figure 85) length/width ratio 1.10–1.14 (mean = 1.12, $n = 5$). (23) Flagellomere 2 approximately 1.3 times length of flagellomere 1. (37) Median mesoscutal line not impressed. (70) Tegula yellow-translucent. (73) Short, adpressed hairs on face extending dorsad to ocellar area, not on vertex. (76) Mesoscutal hairs mostly very short, adpressed (longer hairs relatively inconspicuous); pleuron with very short, adpressed to suberect hairs.

Terminalia (Figures 88–91): (84) S7 lateral arms very slender; (85) S8 short, somewhat reduced; apex of median process rounded; (89) retrorse membranous lobe narrow, parallel sided, curved laterad.

FLIGHT RECORDS.—Only three collections of *S. danforthi* have been made. Females were taken in May, August, and September; males were taken in August and September.

REMARKS.—The elongate, blade-like mandibles of *S. danforthi* females (Figure 86) are similar to those of *S. noctivaga*

(Figure 13). The mandibles of the latter species differ by having small but defined subapical teeth. Elongate mandibles are also found in *S. potosi* (Figure 18) and *S. oenotherae*, but in these species they are broadly rounded, not straight and blade-like on their outer edges.

It is possible these elongate mandibles are important in harvesting onagraceous pollen. Knerer and MacKay (1969) reported that *S. oenotherae* females worked pollen free from the anthers by using their mandibles. *Sphecodogastra antiochensis*, which have “normal” mandibles, apparently use them to clamp themselves to *Oenothera* anthers. Once so anchored the bees use both their front and middle legs to remove pollen and transfer it to the scopae on the hind legs (Turner, 1966). Additional observations of pollen harvesting among *Sphecodogastra* species would be interesting, especially a comparison between the closely related *S. noctivaga* with elongate mandibles (Figure 13) and *S. texana* with “normal” mandibles (Figure 14).

SPECIMENS EXAMINED.—39 (34 females, 5 males).

UNITED STATES. TEXAS: *Ward Co.*: Monahans, 9.5 mi S., 11 May 1959, *Oenothera hartwegii*, D.P. Gregory (1 female; UCB); Monahans, 10 km (6.2 mi) NE, 29 Aug 1986, B.N. Danforth, A.M. Simons (11 females; 2 males; KU); *Winkler Co.*:

Road 404 (8 mi E Highway 18), 10 Sep 1989, *Calylophus hartwegii*, J.L. Neff (22 females; 3 males; gift to NMNH; one male and four female paratypes from this series have been deposited in the CTMI collection).

4. *Sphecodogastra lusoria* (Cresson), new combination

FIGURES 61, 92–104

Halictus lusorius Cresson, 1872:252 [two females].—Dalla Torre, 1896:69 [catalog].—Cockerell, 1897:166 [one female, west fork of Gila River, New Mexico, July 16].—Crawford, 1907:186 [noted that *lusorius* was excluded from key].

Halictus amicus, var. a, Cockerell, 1901:126 [female].

Halictus galpinsiae Cockerell, 1903:342 [female].—1906a:294 [recorded from Pecos, Las Vegas, New Mexico].—1907b:119 [locality, floral records; contrasted with *H. aberrans*].—1919:288 [recorded from Rocky Mountain National Park, just above timberline].—Crawford, 1907:186–188 [key].—Graenicher, 1911:224 [compared with *H. aberrans*]. [New synonymy.]

Halictus gelidus Vachal, 1904:481 [male].—Crawford, 1907:188 [synonymy].

Lasioglossum (Sphecodogastra) lusorium.—Michener, 1951:1111 [catalog].

Lasioglossum (Evyllaenus) galpinsiae.—Linsley and MacSwain, 1962:45 [taxonomy].—Linsley et al., 1963:19, 42, 43 [pollen records from *Gaura* and *Oenothera*].—Gregory, 1964:394 [floral records].—Linsley et al., 1973:38, 39 [pollen records from *Oenothera*].

Lasioglossum (Evyllaenus) lusorium.—Linsley and MacSwain, 1962:45 [taxonomy].

Evyllaenus galpinsiae.—Bohart and Youssef, 1976:185–234 [nesting biology, life history, taxonomy].

Evyllaenus lusorius.—Hurd, 1979:1960 [catalog].—Moure and Hurd, 1987:75 [catalog].

Lasioglossum lusorius.—Poole, 1996:578 [checklist].

TYPE MATERIAL.—The female lectotype of *Halictus lusorius*, herein designated, is deposited in the Academy of Natural Sciences of Philadelphia. The specimen is in good condition but is missing the three distal tarsomeres of the left hind leg, and the hairs over most of the body are slightly soiled and matted. Label data are as follows: “Tex.[Texas]/TYPE No. 2115 [red label]/*Halictus lusorius* 667 Cr [handwritten on folded label]/ANSP [yellow label]/LECTOTYPE *Halictus lusorius* Cresson des. [designated by] McGinley [red label].”

The female holotype of *Halictus galpinsiae*, in the collection of the University of Colorado, Boulder, is in excellent condition and is labeled “Pecos. N.M.[New Mexico], June 22. (Ckll.)/Collecting pollen from *Galpinsia fendleri* [= *Calylophus hartwegii fendleri*], 7.30 P.M./*Halictus galpinsiae* Ckll. TYPE” [handwritten with red-inked borders].

Vachal's male holotype of *Halictus gelidus* is in the collection of the Naturhistorisches Museum, Wien (Vienna, Austria). The specimen is in good condition but is missing the five distal flagellomeres of the right antenna; the terminalia have been extruded, which apparently resulted in soiling of the pleurae, portion of the left scutum, and left gena. Label data are as follows: “Morrison Colorado 1879. I./gelidus Vachal det.[determined] J. Vachal/H. gelidus Vach.[Vachal]/LASIOGLOSSUM o Evyllaenus gelidum (Vach. 1906) Holotypus, Unikum det. A.W. Ebmer 1980” [red-inked right border].

DISTRIBUTION (Figure 92).—See “Distribution” for *S. aberrans*.

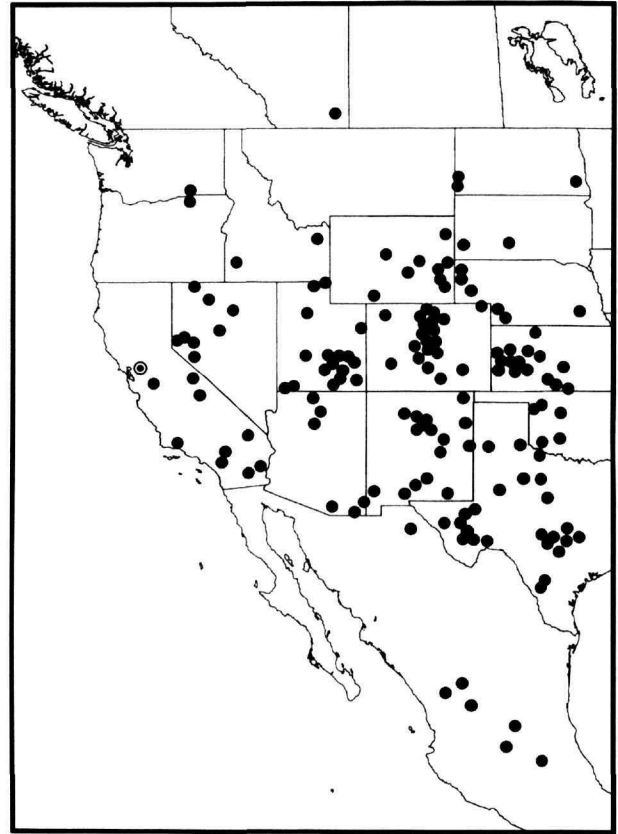
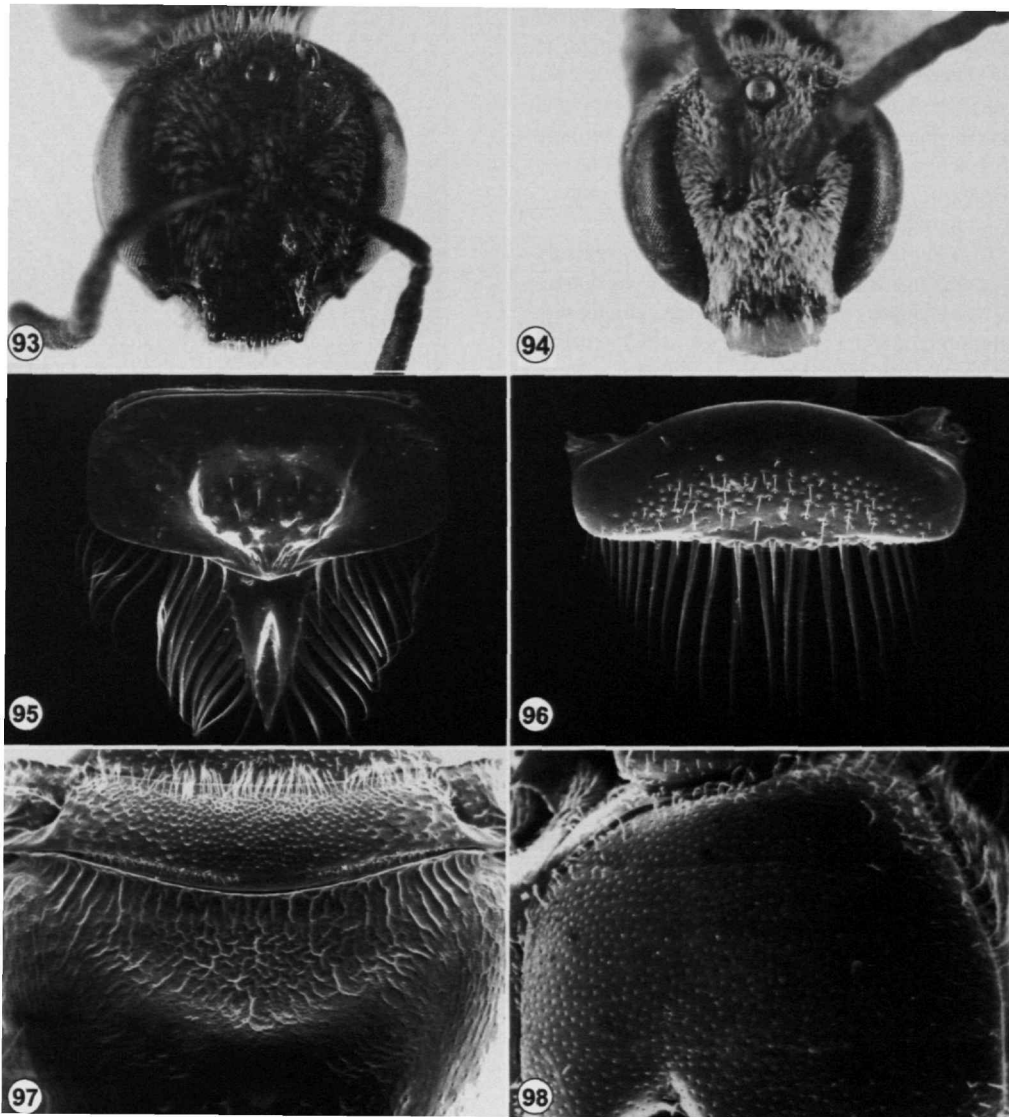


FIGURE 92.—Distribution of *Sphecodogastra lusoria* (bullets) and *S. antiochensis* (circled dot).

DIAGNOSIS.—The short, adpressed pubescence on the pleura, beneath longer hairs will distinguish the females of *Sphecodogastra lusoria* and *S. potosi* from other *Sphecodogastra* having dark abdomens. The head of female *S. lusoria* is only moderately broad (Figure 93) and has short mandibles that at most extend as far as the opposing clypeal angle (e.g., Figure 14). *Sphecodogastra potosi* has a conspicuously broad head (Figure 18) and moderately elongate mandibles that slightly exceed the opposing clypeal angles.

Males of both *S. lusoria* and *S. antiochensis* have distinctive antennal sensillar patterns: flagellomeres are primarily covered by plate sensillae, with peg sensillae found only on the anterior surface and further limited to areas immediately adjacent to flagellomere margins (Figures 42, 76). This pattern can be seen through the light microscope, where the areas with peg sensillae appear lighter or darker than the surrounding surfaces. In addition, these are the only males having short, adpressed hairs extending from the clypeal base to the vertex (in other species, the short, adpressed hairs do not reach the vertex, extending only slightly above the antennae). The only detected morphological differences between the males of these two species are



FIGURES 93–98.—*Sphecodogastra lusoria*: 93, female head; 94, male head; 95, female labrum; 96, male labrum; 97, female propodeum; 98, female mesoscutum.

that *S. antiochensis* are larger (body length mean = 8.5 mm versus 7.2 mm for *S. lusoria*) and have slightly denser punctation on tergum 1 than do the males of *S. lusoria* (Figures 49, 50). The easiest way to differentiate these species is to consider distribution data; the two are not known to be sympatric—*S. antiochensis* is found only in the Antioch area of California (Figure 92) where *S. lusoria* is not known to occur.

DESCRIPTION.—FEMALE: (1) Length 7.5–9.1 mm (mean = 8.4, $n = 5$); (2) wing length 2.4–2.7 mm (mean = 2.6, $n = 5$); (3) abdominal width 2.4–2.7 mm (mean = 2.5, $n = 5$).

Structure: (4) Head moderately rounded (Figure 93); length/width ratio 0.99–1.40 (mean = 1.07, $n = 5$). (5) Gena, at

midpoint, slightly exceeded by width of compound eye. (9) Clypeus projecting approximately 0.70 times its length below lower margin of eyes; (11) clypeal surface without median longitudinal sulcation. (13) Ocular–ocellar distance slightly greater than distance between lateral ocellus and hind margin of vertex (ocular–ocellar space approximately 1.5 times lateral ocellar diameter); (14) distance between lateral ocelli slightly exceeding ocular–ocellar distance. (16) Inner margins of compound eyes converging below. (21) Scape reaching top of vertex; (22) pedicel subequal in length to flagellomere 1. (30) Mandible moderate in length, extending to opposing clypeal angle.

(40) Dorsal surface of propodeum about 0.78 times the length of scutellum and approximately 1.5 times the length of metanotum; (44) lateral propodeal carinae well developed over three-fourths of propodeum, often reaching dorsal propodeal surface (weakly developed in some specimens). (45) Inner hind tibial spur with 4 or 5 moderately elongate teeth (Figure 61).

(46) Lateral edge of metasomal T2 broadly rounded anteriorly, becoming straight to faintly sinuate posteriorly.

Sculpture: (51) Supraclypeal area polished, (52) sparsely punctate, many punctures separated by 3–4 times their diameters (Figure 23). (53) Clypeus mostly polished (sometimes with obscure tessellation basally), (54) with large, widely spaced punctures over apical half. (55) Hypostoma striolate posteriorly, becoming smooth and shiny on anterior half.

(56) Mesoscutum mostly shiny and polished; tessellation, if present, confined to anterior one-fourth; (57) punctation as in Figure 98, most punctures separated by 1–2 times their diameters. (63) Dorsal surface of propodeum rugulose (Figure 97), (64) surface alveolated. (65) T1 shiny and polished; (66) punctation extremely fine, very sparse; punctures separated by 2–3 times their diameters.

Coloration: (67) Abdomen dark brown. (69) Flagellum brown to amber ventrally. (70) Tegula light brown to yellow-translucent. (71) Wing membrane hyaline; veins and stigma pale yellowish amber. (72) Legs dark brown.

Vestiture: (74) Hairs on head white. (75) Pubescence on thorax white; (76) mesoscutal hairs moderately short, subequal in length to median ocellar diameter; mesoscutum and especially pleuron with short, adpressed hairs. (81) Basal hair bands on T2–T4 present, covering basal one-fourth of tergal surface; moderately developed apical hair bands on T3 and T4.

MALE: As described for female except as follows: (1) length 6.7–8.0 mm (mean = 7.2, $n = 5$); (2) wing length 1.6–2.0 mm (mean = 1.8, $n = 5$); (3) abdominal width 1.3–1.7 mm (mean = 1.5, $n = 5$). (4) Head (Figure 94) length/width ratio 1.07–1.10 (mean = 1.09, $n = 5$). (23) Flagellomere 2 approximately 2.0 times length of flagellomere 1. (37) Median mesoscutal line not impressed. (70) Tegula yellow-translucent. (73) Short, adpressed hairs on face extending dorsad to vertex, enclosing median ocellus. (76) Mesoscutal hairs primarily short, adpressed (longer hairs relatively inconspicuous); pleuron with conspicuous short, suberect to adpressed hairs. (76a) Central depression of S6 only moderately developed (Figure 99).

Terminalia (Figures 100–103): (84) S7 lateral arms moderately well developed; (85) S8 moderately developed; apex of median process rounded; (89) retrorse membranous lobe narrow, becoming broader basally.

FLIGHT RECORDS (Figure 104).—Females of *S. lusoria* have been collected from March through October, with most records (87%) from May through July. Males appear to be active somewhat later than the females, with an apparent peak in June.

At Cornish, Utah, Bohart and Youssef (1976) reported flight activity for this species to range from late May until Septem-

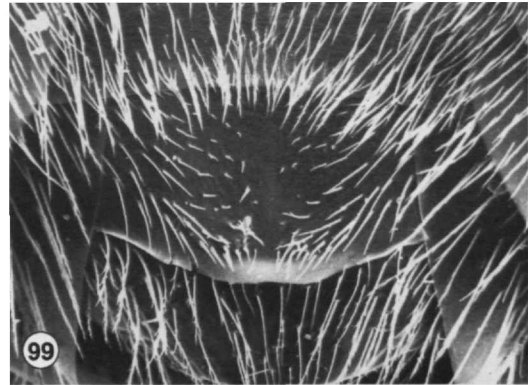


FIGURE 99.—*Sphecodogastra lusoria*, male S6.

ber. In most years two full generations and a partial third were produced. Bohart and Youssef indicated that the number of generations produced was primarily dependent on the availability of *Oenothera* pollen.

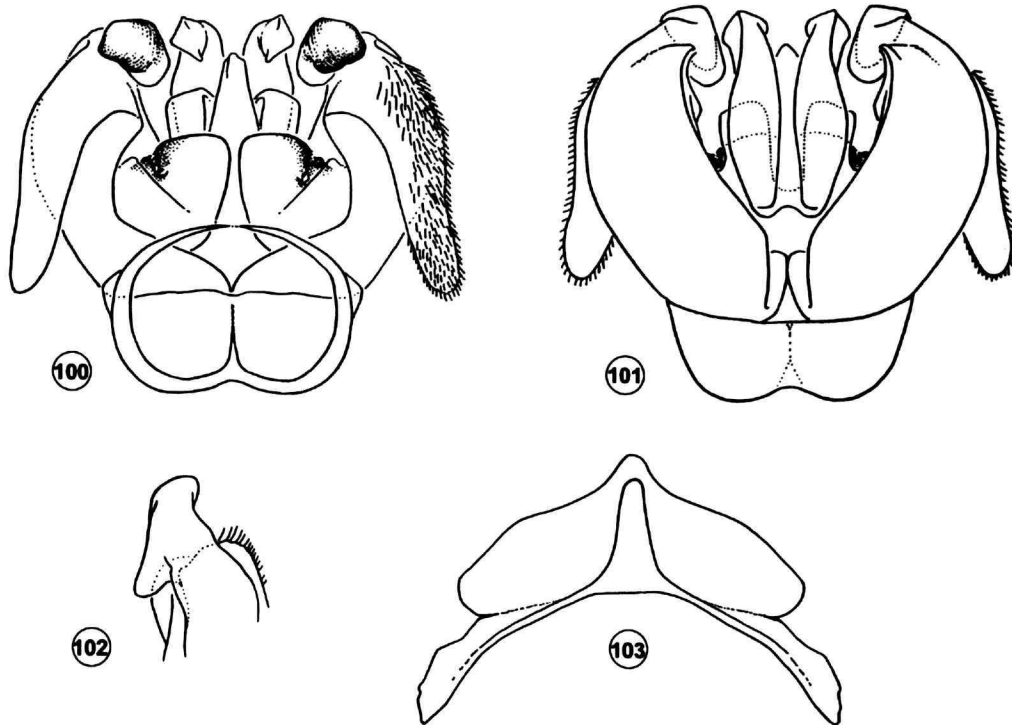
REMARKS.—See “Species Descriptions and Synonymies” in “*Sphecodogastra* Systematic History.”

SPECIMENS EXAMINED.—918 (633 females, 285 males).

CANADA. ALBERTA: Cardston, 3 mi N; Medicine Hat.

MEXICO. CHIHUAHUA: Ahumada. DURANGO: Durango. GUANAJUATO: Silao. HIDALGO: Tlaxcoapan, 5.6 mi E. SAN LUIS POTOSÍ: San Luis Potosí, 16 mi E. ZACATECAS: Fresnillo, 5 mi S; Fresnillo, 5–11 mi N; Juan Aldama.

UNITED STATES: ARIZONA: *Cochise Co.*: Douglas, 1 mi E; Portal, 2 mi NE; Portal, 5 mi W (Southwestern Research Station); *Coconino Co.*: Cameron; Flagstaff, 10 mi N (San Francisco Mountains); Flagstaff, 20 mi N; Vermillion Cliffs; *Mari-copa Co.*: Mesa, 1 mi N; *Pima Co.*: Continental; *Yavapai Co.*: Granite Dells, 4 mi N. CALIFORNIA: *Inyo Co.*: Bartlett; Big Pine, 3 mi N; Wyman Canyon (White Mountains); *Merced Co.*: Delhi, 2.5 mi S; Livingston, 2 mi SW; *Riverside Co.*: Hopkins Well, 2 mi W; Riverside; *San Bernardino Co.*: Apple Valley; Kelso Dunes. COLORADO: *Adams Co.*: Berkeley; Utah Junction; *Boulder Co.*: Beaver Reservoir; Boulder; Longs Peak; Nederland; Niwot Ridge (near Ward); Pinecliffe; Ward, 2 mi E; *Clark Co.*: Lake George; *Clear Creek Co.*: Bear Creek Canyon; Clear Creek; Echo Lake (Mt. Evans); Guanella Pass; *Custer Co.*: Westcliff, 7.5 mi W; *Denver Co.*: Denver; Franktown, 5 mi SSE; Larkspur; *El Paso Co.*: Colorado Springs; Foster Ranch; *Gunnison Co.*: Mt. Princeton Hot Springs, 1 mi E; Salida, 1.5 mi N (Highway 291); *Gilpin Co.*: Lump Gulch, near Gilpin; *Huerfano Co.*: Walsenburg, 3 mi W; *Jefferson Co.*: Coal Creek Canyon (7 mi S Crescent Village); Conifer; *Lar-imer Co.*: Buckhorn Creek; Estes Park; Ft. Collins; Glen Haven; Hewlett Gulch (near Poudre Park); White Rock; *Moffat Co.*: Maybell; *Montrose Co.*: Cimarron, 1.2 mi W; *Otero Co.*: La Junta; *Park Co.*: Pennsylvania Mountain; Wilkerson Pass;



FIGURES 100–103.—*Sphecodogastra lusoria*, male terminalia: 100, genital capsule, ventral view; 101, genital capsule, dorsal view; 102, right gonostylus, posterior view; 103, S7 and S8, ventral view.

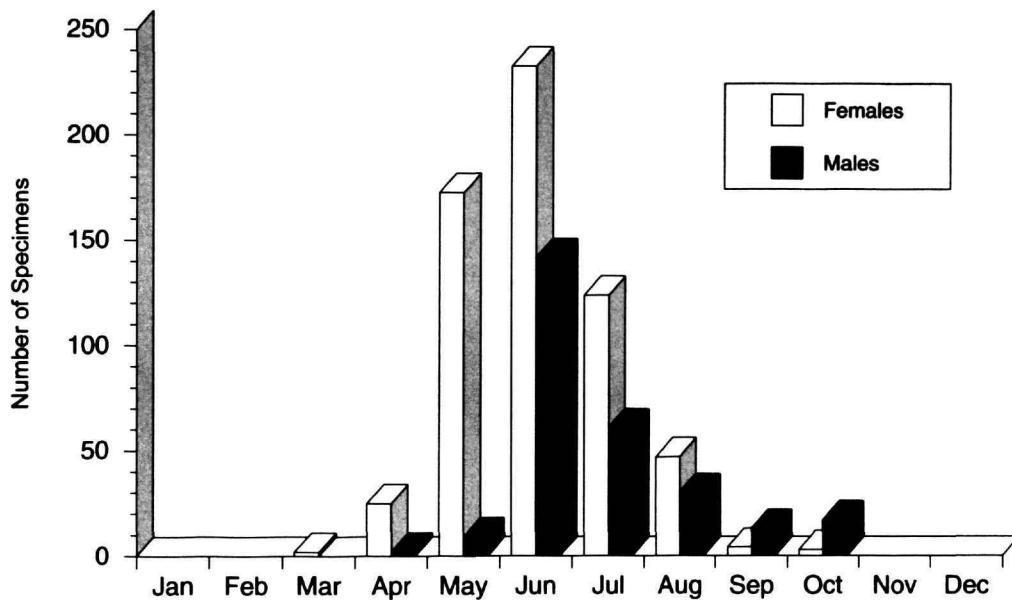


FIGURE 104.—*Sphecodogastra lusoria* flight records, by month of collection.

Sedgwick Co.: Julesburg; *Teller Co.*: Florissant; *Weld Co.*: Nunn (Pawnee Grassland Pasture); Roggen; county/coordinates unknown: Pingee Park; Platts Gunon. IDAHO: *Franklin Co.*: Preston, 5 mi W; St. Anthony; St. Anthony, 5.5 mi WNW; *Owyhee Co.*: Oreana. KANSAS: *Barber Co.*: Medicine Lodge; Medicine Lodge, 4 mi WNW; *Ellis Co.*: Hays; *Finnery Co.*: Garden City; Kalvesta, 15 mi W; *Greeley Co.*: Tribune; *Hamilton Co.*: Syracuse; *Logan Co.*: Monument; *Marshall Co.*: Blue Rapids; *Pratt Co.*: Sawyer, 7 mi N, 3 mi E; *Reno Co.*: Medora (sand dunes); *Scott Co.*: Scott City; *Sheridan Co.*: Quinter, 9 mi N; *Sumner Co.*: Caldwell, 9 mi N; *Wallace Co.*: Wallace; *Wichita Co.*: Leoti. NEBRASKA: *Chase Co.*: Wauneta, 2 mi E; *Morrill Co.*: Bridgeport; *Perkins Co.*: Grant, 3 mi N; *Saline Co.*: Crete; *Scotts Bluff Co.*: Mitchell; Scottsbluff, 12 mi N; *Sioux Co.*: Agate. NEVADA: *Churchill Co.*: Fallon, 14 mi S and 10 mi W; Fallon, 25 mi SE (Sand Mountain); *Eureka Co.*: Eureka, 70.8 mi N; *Humboldt Co.*: Winnemucca; Winnemucca, 11 mi N; *Lander Co.*: Austin; Austin, 9.5 mi W; *Mineral Co.*: Hawthorne; *Washoe Co.*: Reno, 10 mi S on Highway 395; Wadsworth, 10–17 mi W. NEW MEXICO: *Chaves Co.*: Mesa, 2 mi NW; *DeBaca Co.*: Ft. Sumner, 10 mi S; Ft. Sumner, 15 mi E; *Dona Ana Co.*: Las Cruces; *Eddy Co.*: Carlsbad, 19 mi E; *Guadalupe Co.*: Dilia, 1 mi S; Santa Rosa; *McKinley Co.*: Gallup, 19 mi N; *Otero Co.*: Silver Spring Canyon (Mescalero Apache Indian Reservation); White Sands National Monument; *Quay Co.*: Logan; Logan, 6.3 mi NE; *Roosevelt Co.*: Clovis, 10 mi SW; *San Miguel Co.*: Las Vegas; Pecos; *Sandoval Co.*: Jemez Springs; *Santa Fe Co.*: Santa Fe; *Torrance Co.*: Clines Corners; *Union Co.*: Grenville; *Valencia Co.*: Pueblo Laguna. NORTH DAKOTA: *Golden Valley Co.*: Beach; *Richland Co.*: Walcott, 11 mi W; *Slope Co.*: Marmarth. OKLAHOMA: *Ellis Co.*: Gage; *Grady Co.*: Rush Springs, 11 mi N; *Jackson Co.*: Altus; *Kingfisher Co.*: Dover, 4 mi N; *Woodward Co.*: Woodward; Woodward, 6.4 km (4 mi) NE. OREGON: *Harney Co.*: Denio, 2.5 mi NE; *Umatilla Co.*: Hermiston; Umatilla. SOUTH DAKOTA: *Custer Co.*: Custer; *Jones Co.*: Murdo, 10 mi S. TEXAS: *Blanco Co.*: Davis Ranch (NW part of county); *Brewster Co.*: Alpine; Big Bend National Park; Marathon, 39 mi S; *Brown Co.*: Bangs; *Comal Co.*: New Braunfels; *Culberson Co.*: Van Horn, 14.5 mi S; *Fisher Co.*: Roby, 9 mi E; *Gillespie Co.*: Cherry Spring; Harper; *Hall Co.*: Estelline, 3 mi W; *Howard Co.*: Big Spring; *Jeff Davis Co.*: Ft. Davis, 10 mi W; *Kerr Co.*: Kerrville; *Lamb Co.*: Olton; *La Salle Co.*: Cotulla; Encinal; *Lee Co.*: Fedor; *Reeves Co.*: Toyahvale, 19 mi S; *Shackelford Co.*: Albany, 16 mi N; *Terrell Co.*: Sanderson; Sanderson, 30 mi W; *Ward Co.*: Barstow, 3 mi SW; Monahans, 6.7 mi W; Monahans, 9.5 mi S; *Wilbarger Co.*: Vernon, 19 mi N. UTAH: *Cache Co.*: Cornish, 1.2 mi N; *Carbon Co.*: Greenriver, 15 mi S; *Emery Co.*: Calf Canyon (San Rafael Swell); Gilson Butte (3.2–4.0 mi N); Goblin Valley State Preserve (2 mi N); Little Gilson Butte (2 mi E); San Rafael Desert (Temple Mountain, 3 mi SSE); South Temple Wash (San Rafael Reef); Wild Horse Creek (N of Goblin Valley); *Garfield Co.*: Blind Trail Wash (SSE Notom); Lake Powell (4 mi NNW Bullfrog); Ticaboo, 6 mi S; *Grand Co.*: Crescent Junction;

Moab; *Kane Co.*: Bullfrog; *Millard Co.*: Hatton; *San Juan Co.*: Kane Springs (E of Natural Bridges National Monument); *Tooele Co.*: Tooele, 3.6 mi S; *Uintah Co.*: Bonanza; *Washington Co.*: Leeds Canyon; Shivwits. WASHINGTON: *Benton Co.*: Richland; *Kittitas Co.*: Yakima River (Morgan's Ferry). WYOMING: *Albany Co.*: Laramie, 8 mi SE (Dirt Farm); *Carbon Co.*: Kortess Dam; *Converse Co.*: Glenrock; *Fremont Co.*: Shoshoni, 5 mi N; Shoshoni, 5 mi S; *Niobrara Co.*: Lusk; *Platte Co.*: Chugwater; Glendo; Wheatland; *Sweetwater Co.*: Bitter Creek, 25 mi S; *Weston Co.*: Upton, 4 mi N.

5. *Sphecodogastra noctivaga* (Linsley and MacSwain)

FIGURES 64, 105–116

Lasioglossum (*Sphecodogastra*) *noctivaga* Linsley and MacSwain, 1962:46 [female].—Linsley et al., 1963:43 [locality records; floral association with *Oenothera hartwegii*].—Gregory, 1964:394 [floral records].

Sphecodogastra noctivaga.—Hurd, 1979:1962 [catalog].—Moure and Hurd, 1987:85 [catalog].

Lasioglossum noctivaga.—Poole, 1996:611 [checklist].

TYPE MATERIAL.—The female holotype is the property of the University of California, Berkeley, and is on loan deposit to the California Academy of Sciences, San Francisco. The specimen is missing the four distal tarsomeres of the hind left leg but otherwise is in excellent condition. It is labeled "Roosevelt [Uintah County], Ut.[Utah], VI[June]-15-1956/J.L. Eastin Collector/HOLOTYPE *Lasioglossum* (*Sphecodogastra*) *noctivagum* Linsley & MacSwain" [red label].

DISTRIBUTION (Figure 105).—*Sphecodogastra noctivaga* is sympatric with the closely related and more widely distributed *S. texana* (Figure 139) through portions of New Mexico, Nebraska, Oklahoma, and northwestern Texas. Unlike *S. texana*,

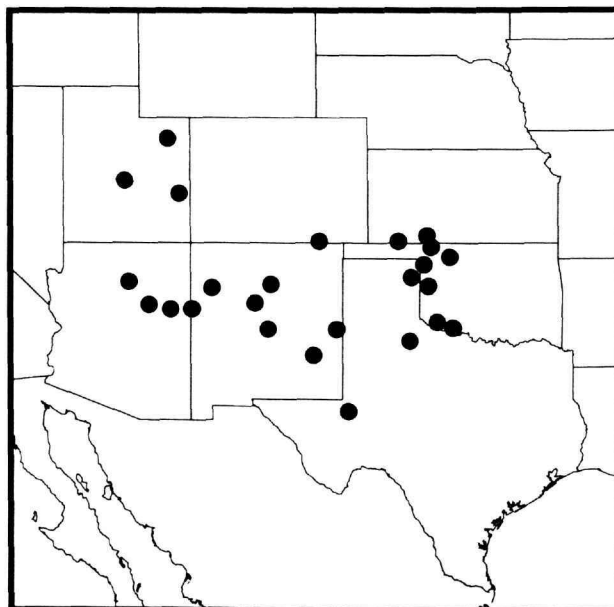
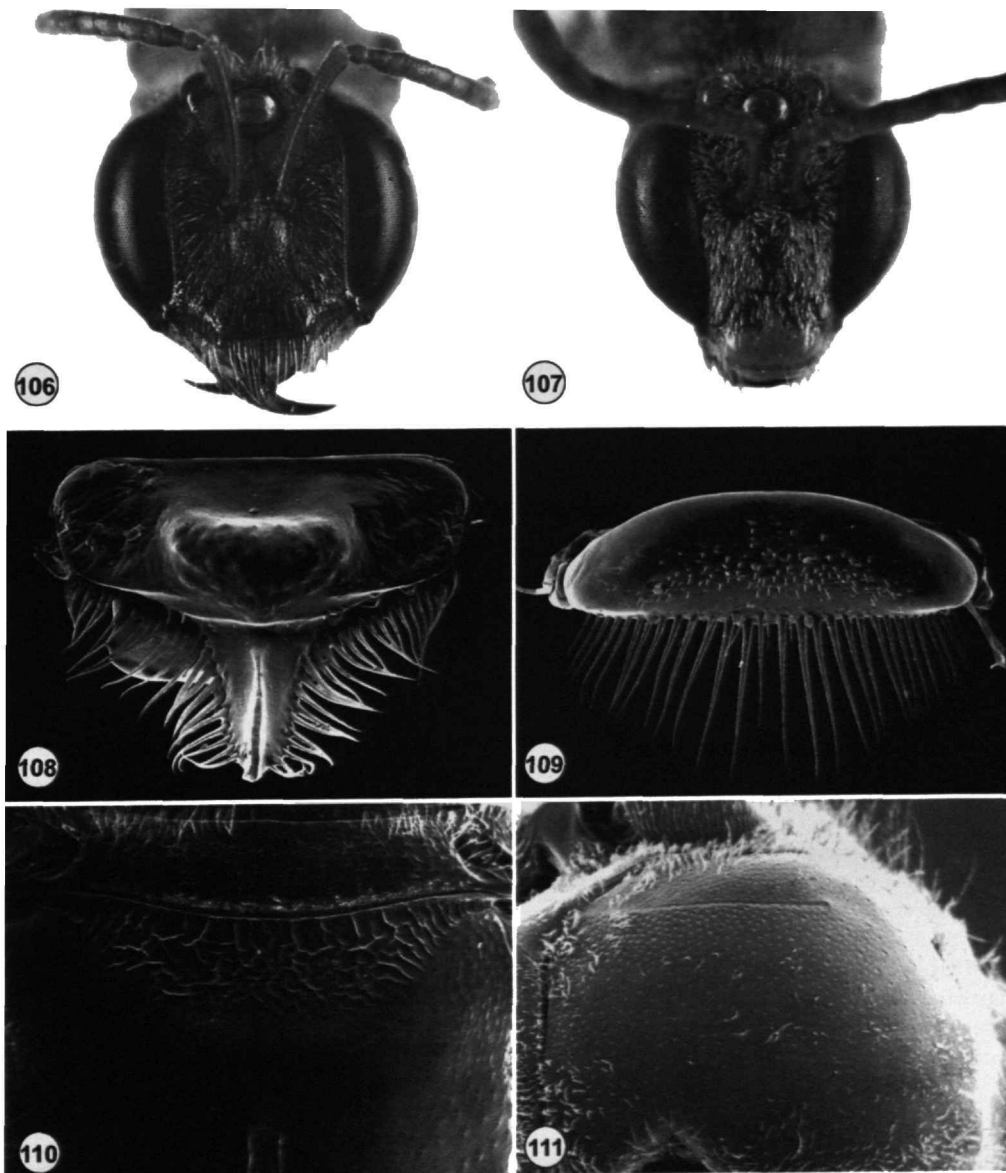


FIGURE 105.—Distribution of *Sphecodogastra noctivaga*.

S. noctivaga has been recorded from Utah. *Sphecodogastra texana* is known from southeastern Montana, North Dakota, east to Michigan, and south to Michoacán and Veracruz, Mexico, which are the most southern records known for the genus. Moure and Hurd (1987) listed *S. texana* from Indiana. I have not seen specimens from this state, but its occurrence there would not be unexpected. Specimens of *S. noctivaga* from Arizona, Kansas, and Oklahoma examined in this study apparently represent new state records.

DIAGNOSIS.—The orange abdomen and conspicuously enlarged ocelli (Figures 11, 106) will distinguish both sexes of *S.*

noctivaga and *S. texana* from other known species of *Sphecodogastra*. The elongate mandibles of female *S. noctivaga* (Figure 13) easily distinguish them from female *S. texana*, which have short ("normal") mandibles (Figure 14). The males can be differentiated on the basis of the morphology of the genitalic retrorse lobes. These lobes are very broad and twisted ventrally in *S. texana* (Figures 31, 32) but are narrow and flat in *S. noctivaga* (Figure 33). Unfortunately, I currently know of no external characters that will reliably distinguish the males of these two species. The head of male *S. noctivaga* appears to be slightly broader than that of *S. texana*. The head length/width



FIGURES 106–111.—*Sphecodogastra noctivaga*: 106, female head; 107, male head; 108, female labrum; 109, male labrum; 110, female propodeum; 111, female mesoscutum.

ratio for *S. noctivaga* is 1.03–1.07 (mean = 1.05, $n = 5$) and for *S. texana* is 1.00–1.03 (mean = 1.02, $n = 5$). The sternal vestiture, especially on sternum 5, appears to be more flocculent in *S. noctivaga* than in *S. texana*. The only other detected difference appears to be in the coloration of the middle tibiae—the central, pigmented portion being brown to dark brown in *S. texana* and very pale, yellowish brown in *S. noctivaga*. These characters appear to be somewhat variable and are difficult to define and use.

DESCRIPTION.—FEMALE: (1) Length 8.5–11.1 mm (mean = 10.2, $n = 5$); (2) wing length 2.8–3.3 mm (mean = 3.1, $n = 5$); (3) abdominal width 2.6–3.3 mm (mean = 3.0, $n = 5$).

Structure: (4) Head broad (Figure 106); length/width ratio 0.80–0.88 (mean = 0.82, $n = 5$). (5) Gena, at midpoint, greatly exceeded by width of compound eye. (9) Clypeus projecting approximately 0.49 times its length below lower margin of eyes; (11) clypeal surface with weakly impressed, median longitudinal depression. (13) Ocular–ocellar distance less than distance between lateral ocellus and hind margin of vertex (ocelli enormous, ocular–ocellar space approximately 0.5 times lateral ocellar diameter); (14) distance between lateral ocelli approximately 4.0 times ocular–ocellar distance. (16) Inner margins of compound eyes nearly parallel. (21) Scape reaching beyond top of vertex; (22) pedicel slightly shorter than flagellomere 1. (30) Mandible conspicuously elongate, reaching beyond opposing clypeal angle (Figures 13, 106).

(40) Dorsal surface of propodeum about 0.70 times the length of scutellum and approximately 1.35 times the length of metanotum; (44) lateral propodeal carinae absent or weakly developed, extending no more than one-third the distance of posterior surface. (45) Inner hind tibial spur with 3 or 4 moderately short teeth (Figure 64), similar to those of *S. texana* (Figure 65).

(46) Lateral edge of metasomal T2 nearly straight.

Sculpture: (51) Supraclypeal area tessellate near lateral margins, (52) punctation moderately dense, most punctures separated by their diameters. (53) Clypeus mostly polished, tessellate only along basal and lateral margins; (54) apical punctures only slightly larger than basal ones, very sparse, separated by 2–5 times their diameters. (55) Hypostoma striolate throughout.

(56) Mesoscutum somewhat dull, surface tessellate throughout, (57) punctation as in Figure 111, most punctures separated by 1–2 times their diameters. (63) Dorsal surface of propodeum rugulose over basal half (Figure 110), (64) surface conspicuously alveolated. (65) T1 somewhat dull, surface obscurely tessellate, (66) punctation extremely fine, sparse, most punctures separated by twice their diameters.

Coloration: (67) Abdomen mostly orange (tergum 5 usually orange-brown). (69) Flagellum and (70) tegula light orange-brown. (71) Wing membrane pale yellowish brown; veins and stigma pale amber. (72) Legs light orange-brown.

Vestiture: (74) Hairs on head white. (75) Pubescence on thorax white; (76) mesoscutal hairs short, many suberect or ad-

pressed; pleuron with conspicuous amount of adpressed hairs. (81) Basal hair bands on T2–T4 virtually absent, inconspicuous; moderately developed apical hair band present on T4.

MALE: As described for female except as follows: (1) length 8.0–9.7 mm (mean = 8.8, $n = 5$); (2) wing length 2.4–2.8 mm (mean = 2.6, $n = 5$); (3) abdominal width 2.0–2.4 mm (mean = 2.2, $n = 5$). (4) Head (Figure 107) length/width ratio 1.03–1.07 (mean = 1.05, $n = 5$). (23) Flagellomere 2 approximately 1.5 times length of flagellomere 1. (37) Median mesoscutal line not impressed. (70) Tegula yellow-translucent. (73) Short, adpressed hairs on face extending dorsad to ocellar area, weakly enclosing median ocellus. (76) Mesoscutum with conspicuously short, adpressed hairs and more elongate, less conspicuous hairs; pleuron with short, suberect to adpressed hairs.

Terminalia (Figures 112–115): (84) S7 lateral arms slender; (85) S8 moderately developed; apex of median process truncate; (89) retrorse membranous lobe narrow, parallel sided.

FLIGHT RECORDS (Figure 116).—Females of *S. noctivaga* were collected from May through October, with most records from July. Most males were taken in July, but a few records were collected in September and October.

SPECIMENS EXAMINED.—225 (201 females, 24 males).

UNITED STATES. ARIZONA: *Coconino Co.*: Cameron; *Navajo Co.*: Holbrook, 17 mi NE; Winslow. COLORADO: *Baca Co.*: Springfield, 31 mi SSW. KANSAS: *Clark Co.*; *Seward Co.*: Liberal. NEW MEXICO: *Bernalillo Co.*: Albuquerque; *Chaves Co.*; *McKinley Co.*: Pinedale; *Roosevelt Co.*: Portales; Portales, 3.5 mi N (Oasis State Park); *Santa Fe Co.*: Santa Fe; *Tao Co.*: Ojo Caliente; *Torrance Co.*: Gran Quivira. OKLAHOMA: *Ellis Co.*: Shattuck; *Harper Co.*; *Jackson Co.*: Elmer; *Kiowa Co.*: Lugert; *Meade Co.*: Cimarron River (NW Oklahoma); *Roger Mills Co.*: Cheyenne; *Tillman Co.*: Grandfield; *Woods Co.*: Little Sahara State Park. TEXAS: *Dickens Co.*: Dumont, 9 mi SW; *Hemphill Co.*: Canadian; Canadian, 4–8 mi NE; *Ward Co.*: Monahans, 9.5 mi S; Monahans State Park. UTAH: *Emery Co.*: Big Flat Top, 2.5 mi NE (Dugout Springs); Gilson Butte; Little Gilson Butte, 2 mi W; San Rafael Desert (3 mi SSE Temple Mountain); Wild Horse Creek (N of Goblin Valley); *Grand Co.*: Moab; *Uintah Co.*: Roosevelt.

6. *Sphecodogastra oenotherae* (Stevens), new combination

FIGURES 62, 117–128

Halictus (Evyllaes) oenotherae Stevens, 1920:37 [female; compared with *H. aberrans*, *H. pectoralis*].

Halictus ralenci Crawford, 1932:70 [female].—Mitchell, 1960:365 [synonymy].

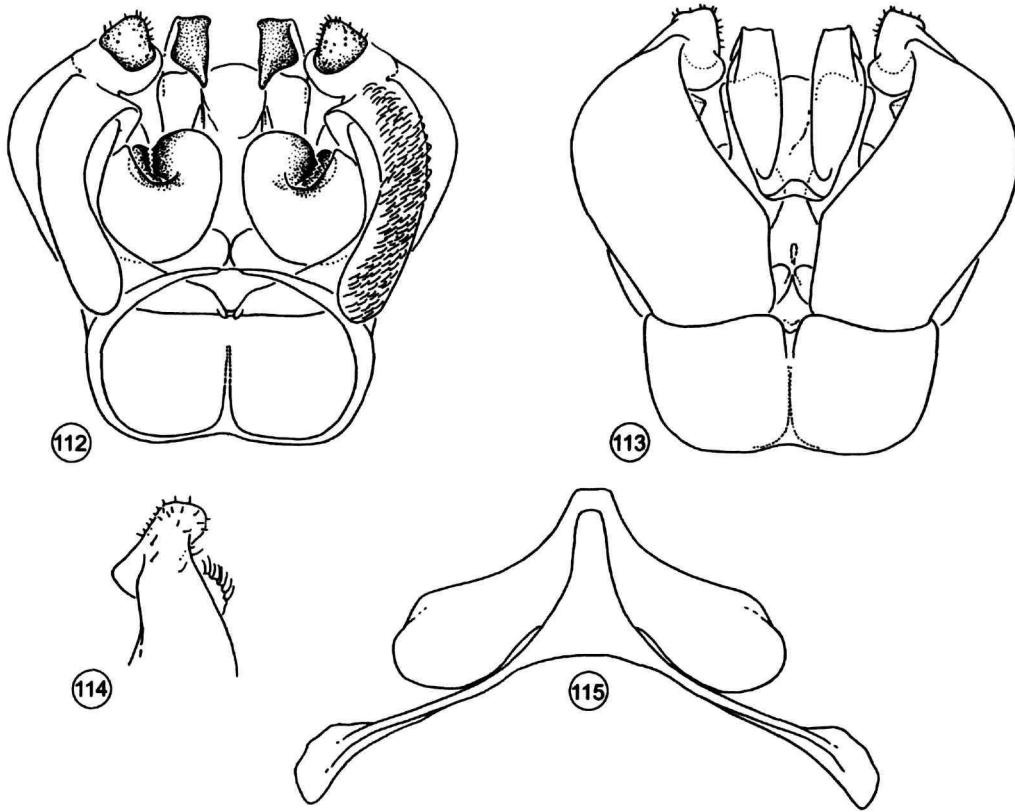
Lasioglossum (Evyllaes) ralenci.—Michener, 1951:1110 [catalog].

Lasioglossum (Sphecodogastra) oenotherae.—Michener, 1951:1111 [catalog].

Lasioglossum (Evyllaes) oenotherae.—Linsley and MacSwain, 1962:45 [taxonomy].

Evyllaes oenotherae.—Knerer and Atwood, 1964:958 [taxonomy; noted misidentification of male of this species as *E. truncatus* by Mitchell (1960)].—Knerer, 1969:142 [nesting biology].—Knerer and MacKay, 1969 [biology].—Hurd, 1979:1960 [catalog].—Moure and Hurd, 1987:78 [catalog].

Lasioglossum oenotherae.—Poole, 1996:617 [checklist].



FIGURES 112–115.—*Sphecodogastra noctivaga*, male terminalia: 112, genital capsule, ventral view; 113, genital capsule, dorsal view; 114, right gonostylus, posterior view; 115, S7 and S8, ventral view.

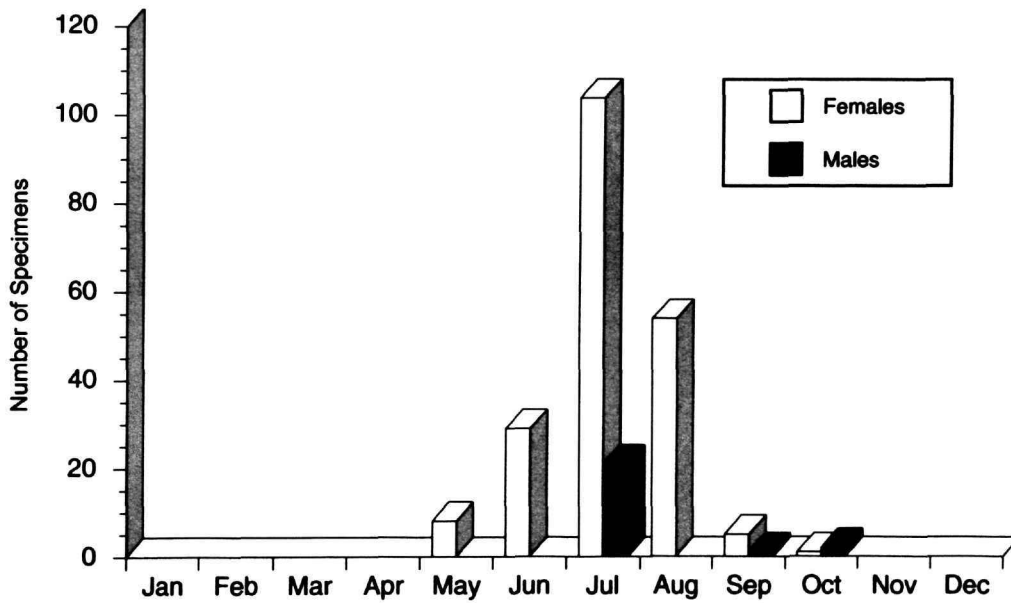


FIGURE 116.—*Sphecodogastra noctivaga* flight records, by month of collection.

TYPE MATERIAL.—The female holotype of *Halictus oenotherae* is in the collection of the National Museum of Natural History, Smithsonian Institution. The specimen is labeled "Blue Rapids, Ks.[Kansas] 8/30 P.M. Jun[e] 20 1919 O.A. Stevens/Megapterium missouriense [handwritten]/12033 [Stevens' type number]/Type No. 23848 U.S.N.M. [red label]/Halictus oenotherae Stevens ♀ type" [handwritten]. The type is in excellent condition except for missing the last tarsomere of the left front leg and the last three tarsomeres of the right front leg. The female holotype of *Halictus ralenci* is deposited in the American Museum of Natural History. It is labeled "Raleigh NC [North Carolina] C S Brimley 29-V[May]-[19]24/Acc. 33827/Halictus ralenci Type Cwfd" [handwritten]. The specimen is missing the last tarsomere of the right middle leg and the entire tarsus of the right hind leg.

DISTRIBUTION (Figure 117).—*Sphecodogastra oenotherae* is the one member of this genus occurring in far eastern North America. Only *S. texana* is also known to occur east of the Mississippi River, being recorded in Wisconsin, Illinois, and Michigan—states in which *S. oenotherae* apparently does not occur. I have seen specimens of *S. oenotherae* from New Brunswick and Ontario, the northern parts of its range. Moure and Hurd (1987) also listed it from Nova Scotia. Its range extends south to Georgia. Interestingly, there are four disjunct locality records of this species west of the Mississippi: Marshall County, Kansas (the type locality); Calcasieu County, Louisiana; and Lee and Upshur counties, Texas. Moure and Hurd (1987) also listed it from North Dakota. Whether this disjunct pattern is real or was a result of inadequate collecting

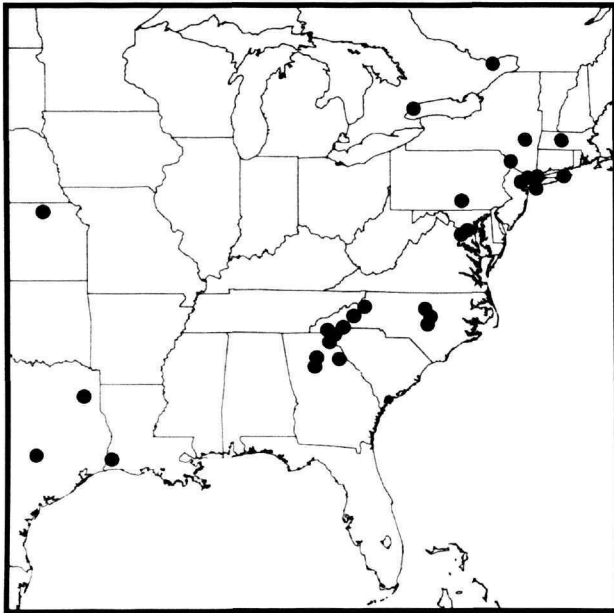


FIGURE 117.—Distribution of *Sphecodogastra oenotherae*.

is unknown. The western records make *S. oenotherae* potentially sympatric, albeit narrowly, with *S. texana* and *S. lusoria* and also with *S. aberrans* if the North Dakota record is correct.

Knerer and MacKay (1969:289) correctly noted that the wide distribution of this species in eastern North America "is seldom reflected in representative local collections." In this current review of *Sphecodogastra* based on approximately 3200 specimens, I have examined only 170 *S. oenotherae*. An effort to collect specimens from *Oenothera* in the early morning hours and twilight period would undoubtedly extend our knowledge of the distribution of this species. *Oenothera laciniata*, an evening primrose from which *S. oenotherae* has been collected, has an eastern distribution (Dietrich and Wagner, 1988) similar to that of *S. oenotherae* and should be considered a primary target for potential sampling.

DIAGNOSIS.—The coarsely rugo-striate dorsal propodeal surface (Figure 122) easily differentiates both males and females of *Sphecodogastra oenotherae* from all other known *Sphecodogastra*.

DESCRIPTION.—FEMALE: (1) Length 6.6–8.2 mm (mean = 7.6, $n = 5$); (2) wing length 1.9–2.3 mm (mean = 2.1, $n = 5$); (3) abdominal width 2.1–2.5 mm (mean = 2.4, $n = 5$).

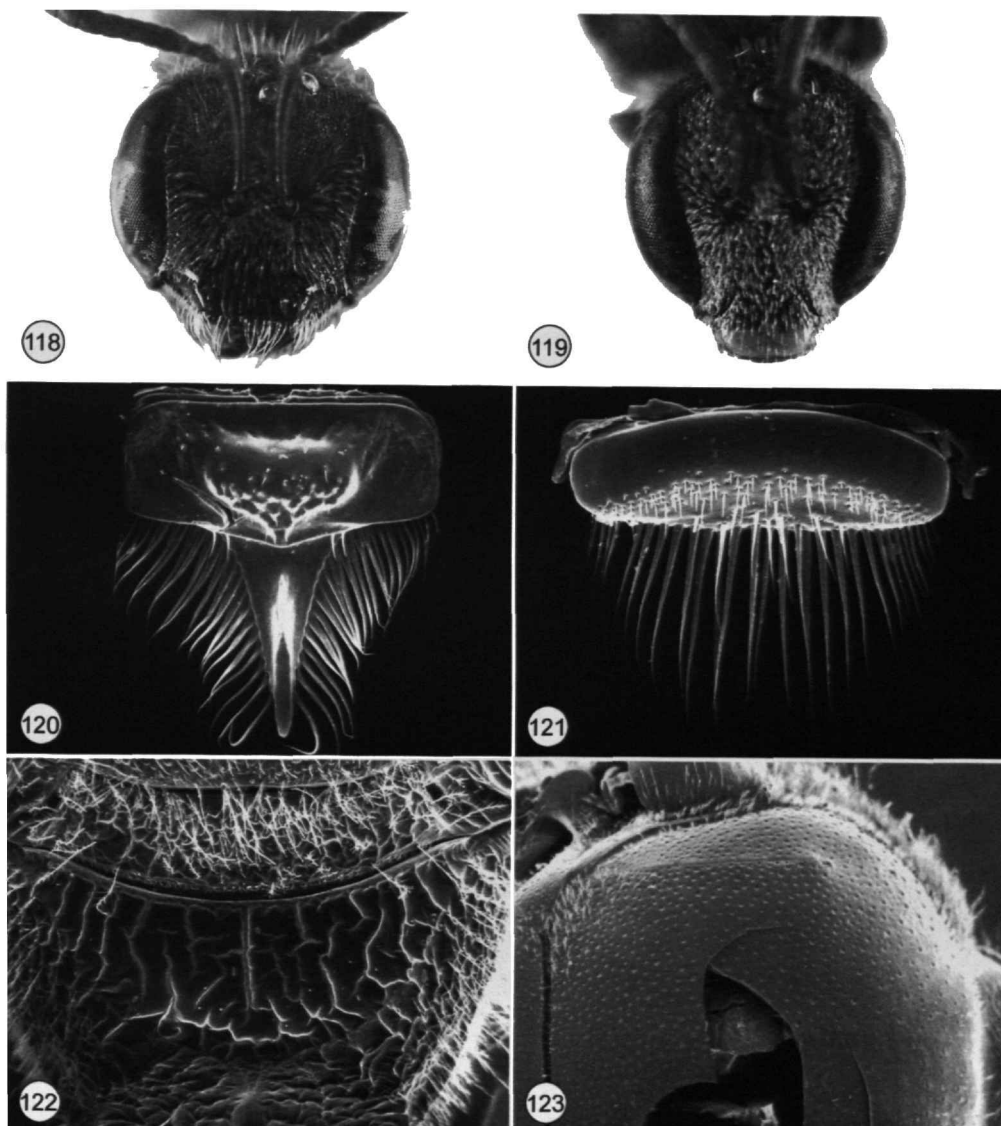
Structure: (4) Head broad (Figure 118); length/width ratio 0.89–0.94 (mean = 0.92, $n = 5$). (5) Gena, at midpoint, slightly exceeding compound eye in width. (9) Clypeus projecting approximately 0.67 times its length below lower margin of eyes; (11) clypeal surface without median longitudinal sulcation. (13) Ocular-ocellar distance subequal to distance between lateral ocellus and hind margin of vertex (ocular-ocellar space approximately 2.0 times lateral ocellar diameter); (14) distance between lateral ocelli slightly exceeding ocular-ocellar distance. (16) Inner margins of compound eyes nearly parallel. (21) Scape reaching top of vertex; (22) pedicel subequal in length to flagellomere 1. (30) Mandible elongate, but because of broad head only reaching opposing clypeal angle; subapical tooth somewhat reduced.

(40) Dorsal surface of propodeum about 0.71 times the length of scutellum and approximately 1.25 times the length of metanotum; (44) lateral propodeal carinae very well developed, encircling propodeal surface. (45) Inner hind tibial spur with 4 or 5 moderately elongate teeth (Figure 62).

(46) Lateral edge of metasomal T2 broadly rounded.

Sculpture: (51) Supraclypeal area polished, (52) punctation sparse, most punctures separated by two times their diameters. (53) Clypeus polished; (54) punctation sparse, punctures small, only slightly larger apically, separated by 2–3 times their diameters. (55) Hypostoma obscurely striolate throughout.

(56) Mesoscutum mostly shiny, tessellation confined to anterior one-fourth, (57) punctation as in Figure 123, most punctures separated by 1–2 times their diameters. (63) Dorsal surface of propodeum strongly and entirely striate (Figure 122), (64) surface smooth, not alveolated. (65) T1 shiny and



FIGURES 118–123.—*Sphecodogastra oenotherae*: 118, female head; 119, male head; 120, female labrum; 121, male labrum; 122, female propodeum; 123, female mesoscutum.

polished, (66) punctation fine, moderately sparse, punctures separated by 1–3 times their diameters.

Coloration: (67) Abdomen dark brown. (69) Flagellum brown. (70) Tegula light brown. (71) Wing membrane pale yellowish brown; veins and stigma light brown. (72) Legs dark brown.

Vestiture: (74) Hairs on head white. (75) Pubescence on thorax white; (76) mesoscutal hairs moderately elongate, approximately 1.5 times median ocellar diameter; mesoscutum and pleuron without short suberect or adpressed hairs. (81) Basal hair bands on T2–T4 weakly developed, inconspicuous; terga lacking apical hair bands.

MALE: As described for female except as follows: (1) Length 7.3–8.1 mm (mean = 7.7, $n = 5$); (2) wing length 1.9–2.0 mm (mean = 2.0, $n = 5$); (3) abdominal width 1.7–1.9 mm (mean = 1.8, $n = 5$). (4) Head (Figure 119) length/width ratio 1.05–1.09 (mean = 1.07, $n = 5$). (23) Flagellomere 2 approximately 1.5 times length of flagellomere 1. (37) Median mesoscutal line impressed. (70) Tegula yellowish brown. (73) Short, adpressed hairs on face extending dorsad just below median ocellus. (76) Mesoscutal hairs moderately elongate; short, adpressed hairs inconspicuous to absent; pleuron without short, suberect to adpressed hairs.

Terminalia (Figures 124–127): (84) S7 lateral arms slender; (85) S8 usually developed; apex of median process rounded; (89) retrorse membranous lobe narrow, parallel sided.

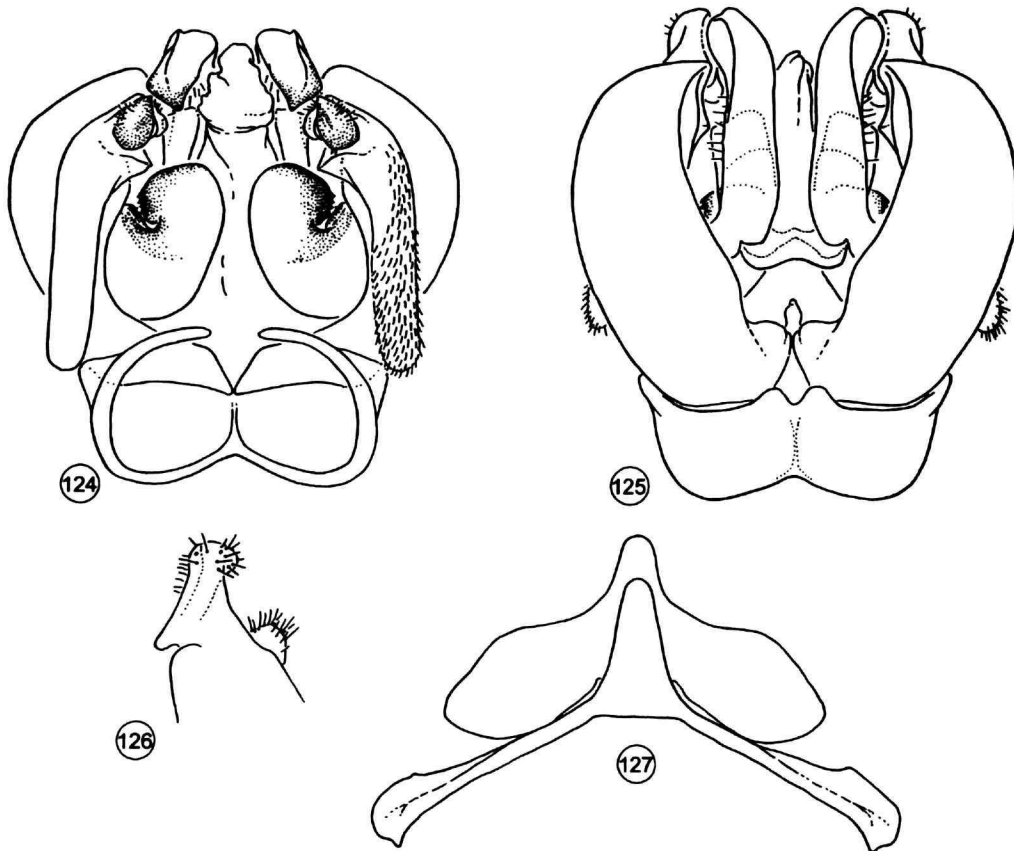
FLIGHT RECORDS (Figure 128).—Females of *Sphecodogastra oenotherae*, like *S. antiochensis*, were most often collected in late spring (unlike the other *Sphecodogastra* species examined in this study), with 64% of specimens taken during May. Males were more often collected in later months, with 87% from July and August.

At Toronto, Canada, Knerer and MacKay (1969) reported activity of this species to be much delayed, apparently to coincide with the *Oenothera* bloom in that area. Females first appeared in mid-June and some nests were not established before July. Males were not observed at flowers until the end of July. Nest activity continued until late August, but all nests remained closed after September. The authors thought *S. oenotherae* to be univoltine at this latitude.

SPECIMENS EXAMINED.—170 (104 females, 66 males).

CANADA. NEW BRUNSWICK: Nerepis. ONTARIO: Ottawa; Toronto.

UNITED STATES. CONNECTICUT: *Fairfield Co.*: Stamford. DISTRICT OF COLUMBIA: Washington, D.C. GEORGIA: *Dade Co.*: Head River; *DeKalb Co.*: Stone Mountain; *Rabun Co.*: Rabun Bald; *White Co.*: Yonah Mountain. KANSAS: *Marshall Co.*: Blue Rapids. LOUISIANA: *Calcasieu Co.*: Vinton. MARYLAND: *Prince Georges Co.*: Greenbelt. MASSACHUSETTS: *Worcester Co.*: Petersham. NEW HAMPSHIRE: *Straford Co.*: Durham. NEW JERSEY: *Bergen Co.*: Alpine; Closter; Ramsey; *Essex Co.*: Great Piece Meadows; *Morris Co.*: Boonton. NEW YORK: *Albany Co.*: Rensselaerville (Huyck Preserve); *Nassau Co.*: Floral Park; *Rockland Co.*: Nyack; *Suffolk Co.*: Orient Point (Cold Spring Harbor), Setauket, Sound Beach; *Sullivan Co.*: White Lake; *Tompkins Co.*: Ithaca (B. Danforth, pers. comm., 1996). NORTH CAROLINA: *Harnett Co.*: Lillington, 10 mi S; *Haywood Co.*; *Macon Co.*: Highlands; Wayah Bald; Wayah Gap; *Transylvania Co.*: Rich Mountain; *Wake Co.*: Raleigh; *Watanga Co.*: Grandfather Mountain; *Yancey Co.*: Mt. Mitchell. PENNSYLVANIA: *Cumberland Co.*: Craigheads. TEXAS: *Lee Co.*: Lexington; *Upshur Co.*: Lake McClellan. VIRGINIA: *Arlington Co.*: Falls Church; Glencarlyn.



FIGURES 124–127.—*Sphecodogastra oenotherae*, male terminalia: 124, genital capsule, ventral view; 125, genital capsule, dorsal view; 126, right gonostylus, posterior view; 127, S7 and S8, ventral view.

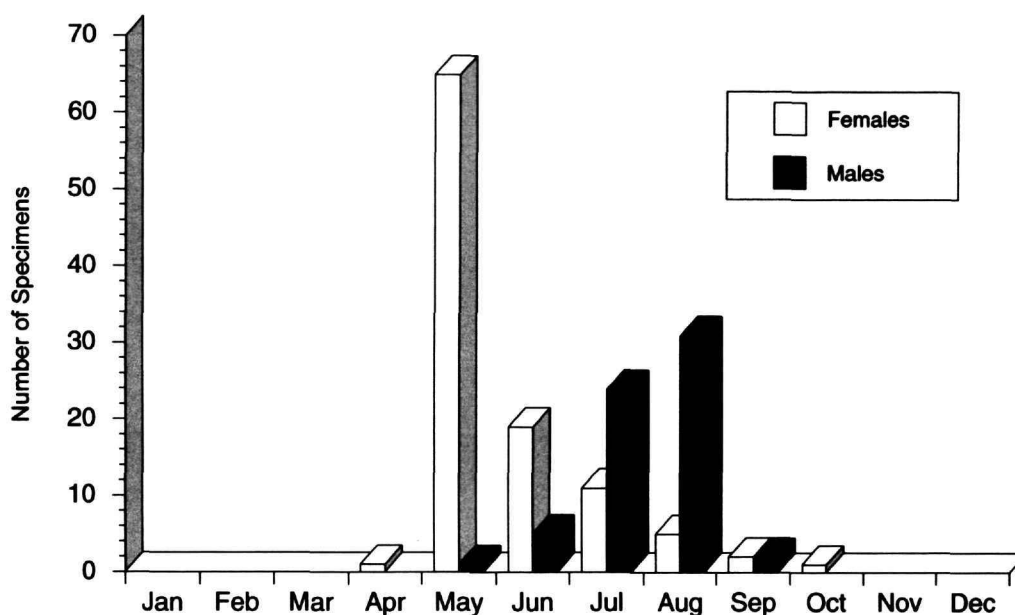


FIGURE 128.—*Sphecodogastra oenotherae* flight records, by month of collection.

7. *Sphecodogastra potosi*, new species

FIGURES 63, 129–138

TYPE MATERIAL.—The female holotype is in excellent condition and is deposited in the National Museum of Natural History, Smithsonian Institution. It is labeled “Durango Dgo. [Durango], MEX. [ico] VIII [August]-13-1962 / Domestic squash/A.E. & M.M. Michelbacher Collectors/200.2 [green label]/0635–0735 [flight activity]/HOLOTYPE *Sphecodogastra potosi* R.J. McGinley” [red label]. Thirty-one paratypes are designated and listed in the “Specimens Examined” section that follows.

ETYMOLOGY.—The specific name is a reference to the Mexican state of San Luis Potosi where the largest series of this species has been collected. This was a label manuscript name used by George E. Bohart who apparently was the first to recognize that these specimens represented a new species.

DISTRIBUTION (Figure 83).—*Sphecodogastra potosi* is known only from Hidalgo County, New Mexico, USA, and the Mexican states of Durango, San Luis Potosí, and Zacatecas. It is currently known to be sympatric only with *S. lusoria*, both having been collected at Fresnillo (Zacatecas state) and adjacent areas in New Mexico.

DIAGNOSIS.—The presence of short, adpressed hairs on the pleuron (e.g., Figure 21) combined with the broad head and elongate mandibles (Figure 18) will distinguish the females of *S. potosi* from other *Sphecodogastra* species having dark abdomens. For further details, see “Diagnosis” for *S. lusoria*.

Males of *S. potosi* can be identified by their darkly pigmented mandibles; mandibles of other congeneric males have

conspicuous areas of yellow pigmentation. Other helpful characteristics for recognizing the males of this species are the lack of antennal sensillar patterns (found in the very common *S. lusoria* as well as *S. antiochensis*, Figures 42, 76) and the relatively broad head (Figure 130).

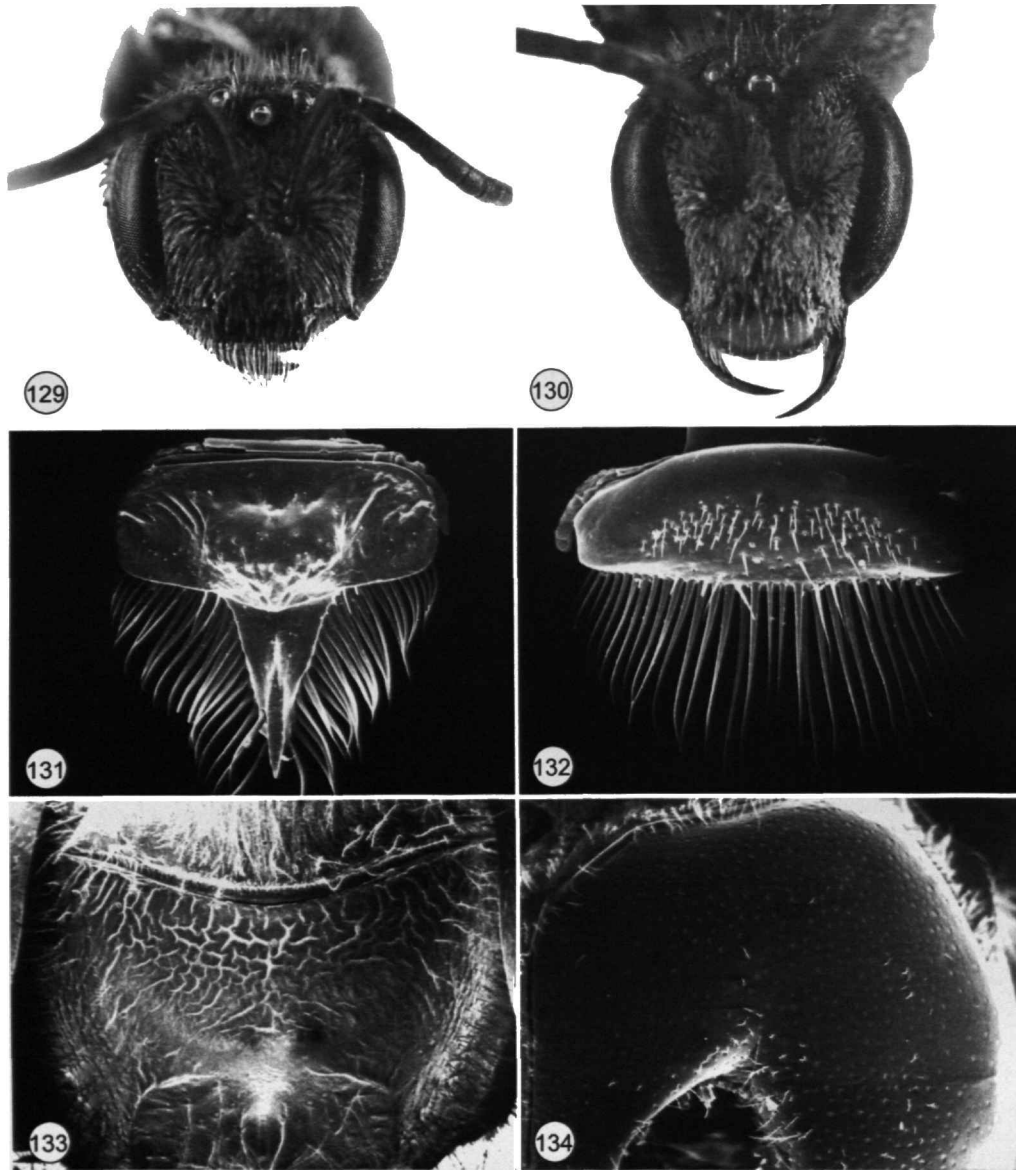
DESCRIPTION.—**FEMALE:** (1) Length 7.2–8.5 mm (mean = 8.0, $n = 5$); (2) wing length 2.3–2.5 mm (mean = 2.4, $n = 5$); (3) abdominal width 2.2–2.6 mm (mean = 2.4, $n = 5$).

Structure: (4) Head broad (Figure 129); length/width ratio 0.90–0.92 (mean = 0.91, $n = 5$). (5) Gena, at midpoint, exceeding width of compound eye. (9) Clypeus projecting approximately 0.63 times its length below lower margin of eyes; (11) clypeal surface without median longitudinal sulcation. (13) Ocular–ocellar distance subequal to distance between lateral ocellus and hind margin of vertex (ocular–ocellar space approximately 2.0 times lateral ocellar diameter); (14) distance between lateral ocelli slightly exceeding ocular–ocellar distance. (16) Inner margins of compound eyes nearly parallel. (21) Scape reaching top of vertex; (22) pedicel subequal in length to flagellomere 1. (30) Mandible elongate, reaching slightly beyond opposing clypeal angle (Figure 18).

(40) Dorsal surface of propodeum about 0.78 times the length of scutellum and approximately 1.38 times the length of metanotum; (44) lateral propodeal carinae well developed, extending to dorsal propodeal surface. (45) Inner hind tibial spur with 4 or 5 moderately elongate teeth (Figure 63).

(46) Lateral edge of metasomal T2 broadly rounded.

Sculpture: (51) Supraclypeal area polished, (52) punctation only moderately dense, most punctures separated by 1–2 times their diameters. (53) Clypeus polished; (54) apical punctures



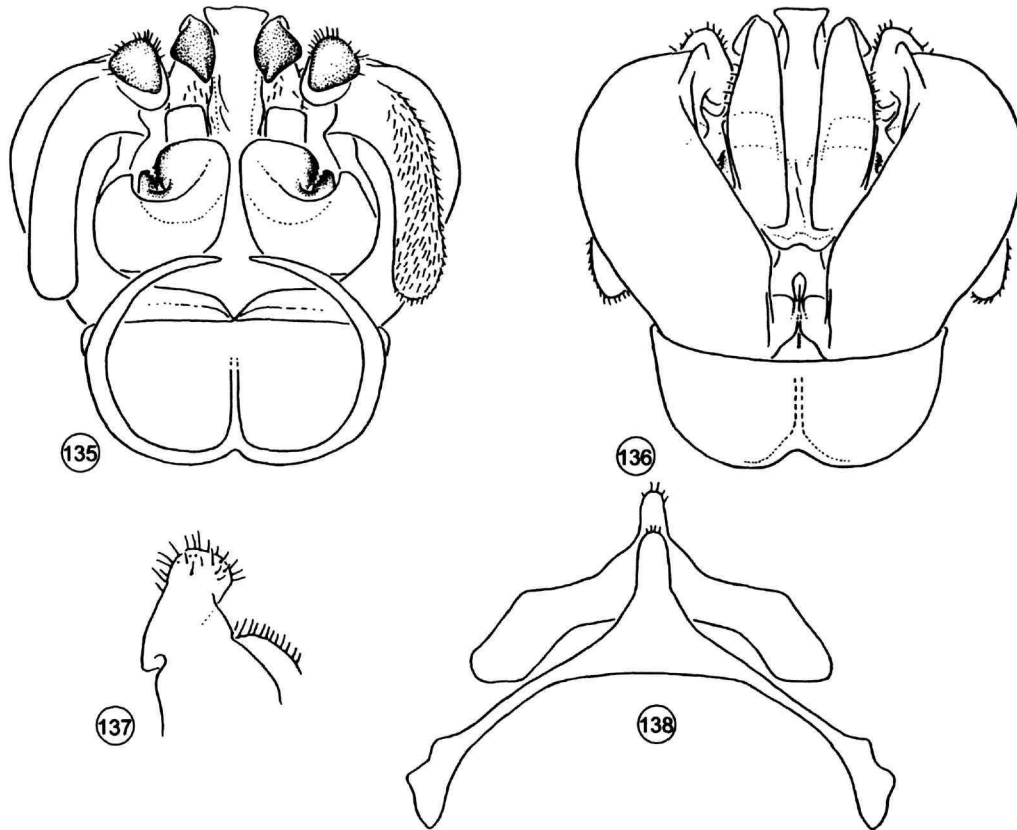
FIGURES 129–134.—*Sphecodogastra potosi*: 129, female head; 130, male head; 131, female labrum; 132, male labrum; 133, female propodeum; 134, female mesoscutum.

slightly larger than basal ones, separated by 2–4 times their diameters. (55) Hypostoma weakly striolate throughout.

(56) Mesoscutum mostly shiny and polished, tessellation confined to the anterior half, (57) punctuation as in Figure 134, most punctures separated by 2–3 times their diameters (somewhat more sparse than other species). (63) Dorsal surface of propodeum entirely rugulose (Figure 133), (64) surface alveolated. (65) T1 shiny and polished, (66) punctuation extremely fine, moderately sparse, punctures separated by 1–3 times their diameters.

Coloration: (67) Abdomen dark brown. (69) Flagellum dark brown. (70) Tegula brown. (71) Wing membrane hyaline; veins and stigma light brown. (72) Legs brown.

Vestiture: (74) Hairs on head white. (75) Pubescence on thorax white; (76) mesoscutal hairs moderately short, length subequal to diameter of median ocellus; mesoscutum and especially pleuron, with short, adpressed hairs. (81) Basal hair bands on T2–T4 present, covering basal one-fourth of tergal surface; moderately developed apical hair bands present on T3 and T4.



FIGURES 135–138.—*Sphecodogastra potosi*, male terminalia: 135, genital capsule, ventral view; 136, genital capsule, dorsal view; 137, right gonostylus, posterior view; 138, S7 and S8, ventral view.

MALE: As described for female except as follows: (1) length 6.6–7.8 mm (mean = 7.2, $n = 5$); (2) wing length 1.8–2.1 mm (mean = 2.0, $n = 5$); (3) abdominal width 1.5–1.8 mm (mean = 1.7, $n = 5$). (4) Head (Figure 130) length/width ratio 1.04–1.08 (mean = 1.05, $n = 5$). (23) Flagellomere 2 approximately 1.5 times length of flagellomere 1. (37) Median mesoscutal line only faintly impressed. (70) Tegula yellowish brown. (73) Short, adpressed hairs on face extending dorsad just below median ocellus. (76) Mesoscutum with both moderately elongate and short, adpressed hairs; pleuron with some short, suberect to adpressed hairs.

Terminalia (Figures 135–138): (84) S7 lateral arms slender; (85) S8 short, somewhat reduced; apex of median process rounded; (89) retrorse membranous lobe narrow, parallel sided.

FLIGHT RECORDS.—Only six collections of *S. potosi* were examined. Females were collected from May through August; males were collected in June and August. Most specimens of both sexes (83%) were collected in June.

SPECIMENS EXAMINED.—32 (18 females, 14 males).

MEXICO. DURANGO: Durango, 13 Aug 1962, *Cucurbita*, A.E. and M.M. Michelbacher (1 ♀, NMNH; holotype). SAN LUIS POTOSÍ: San Luis Potosí, 16 mi E, 18–19 Jun 1966,

Gaura coccinea, D.E. Breedlove (12 ♀, 11 ♂, CU). ZACATECAS: Fresnillo, 9 mi S, 24 Jun 1956, J.W. MacSwain, D.D. Linsdale (2 ♂, UCB); Fresnillo, 17 mi N, 16 Jul 1954, J.W. MacSwain, E.I. Schlinger (3 ♀, UCB).

UNITED STATES. NEW MEXICO: *Hidalgo Co.*: Rodeo, 1 mi W, 3 Aug 1961, J.G. Rozen (1 ♂, AMNH); Rodeo, 3 mi SW, 5 May 1965, J.G. Rozen (2 ♀, AMNH).

8. *Sphecodogastra texana* (Cresson)

FIGURES 65, 139–151

Sphecodes texana Cresson, 1872:249 [female, male, four specimens].—1916:109 [lectotype].

Halictus (Parasphecodes) texanus.—Cockerell, 1898b:45 [key].

Halictus texanus.—Cockerell, 1898a:185 [taxonomy; floral association with pear, *Senecio*].—Pearson, 1933:386, 392 [recorded from Chicago, Illinois area].—Graenicher, 1935:302 [localities; association with *Oenothera rhombipetala*].—Stevens, 1951:61 [floral associations with *Oenothera nuttallii*, *O. strigosa*].

Sphecodogastra texana.—Ashmead, 1899:93 [new genus].—Graenicher, 1911:222, 223, 233 [locality records; association with *Oenothera rhombipetala*].—Mitchell, 1960:365 [redescription, locality, and floral records].—Kerfoot, 1967a [nesting biology; behavior].—1967c [lunar periodicity].—Hurd, 1979:1962 [catalog].—Moure and Hurd, 1987:85 [catalog].

Halictus (Megalopta?) texanus.—Stevens, 1920:35 [taxonomy; floral associations; localities; flight activity].

Sphecodogastra texana.—Hicks, 1936:51 [lapsus calami; nest architecture].

Lasioglossum (Sphecodogastra) texanum.—Linsley and MacSwain, 1962:47 [key separating females of *L. texanum* and *L. noctivaga*].—Linsley et al., 1963:43 [locality records; floral associations with *Oenothera caespitosa*, *O. runcinata*].—Gregory, 1964:400, 417 [floral records].—Kerfoot, 1967b [ocellar size and nocturnal behavior].

Lasioglossum texanus.—Poole, 1996 [checklist].

TYPE MATERIAL.—The female lectotype of *Sphecodes texana* is deposited in the Academy of Natural Sciences of Philadelphia. The specimen is structurally in good condition, but the hairs are soiled and matted. It is labeled "Tex.[Texas]/Lectotype 2134 [red label]/*Sphecodes* Cress., 2 specimens [handwritten and folded]/ANSP" [yellow label].

DISTRIBUTION (Figure 139).—See "Distribution" for *S. noctivaga*.

DIAGNOSIS.—See "Diagnosis" for *S. noctivaga*.

DESCRIPTION.—FEMALE: (1) Length 8.0–11.2 mm (mean = 9.5, $n = 5$); (2) wing length 2.7–3.1 mm (mean = 2.9, $n = 5$); (3) abdominal width 2.5–3.3 mm (mean = 3.0, $n = 5$).

Structure: (4) Head broad (Figure 140); length/width ratio 0.90–0.96 (mean = 0.93, $n = 5$). (5) Gena, at midpoint, greatly

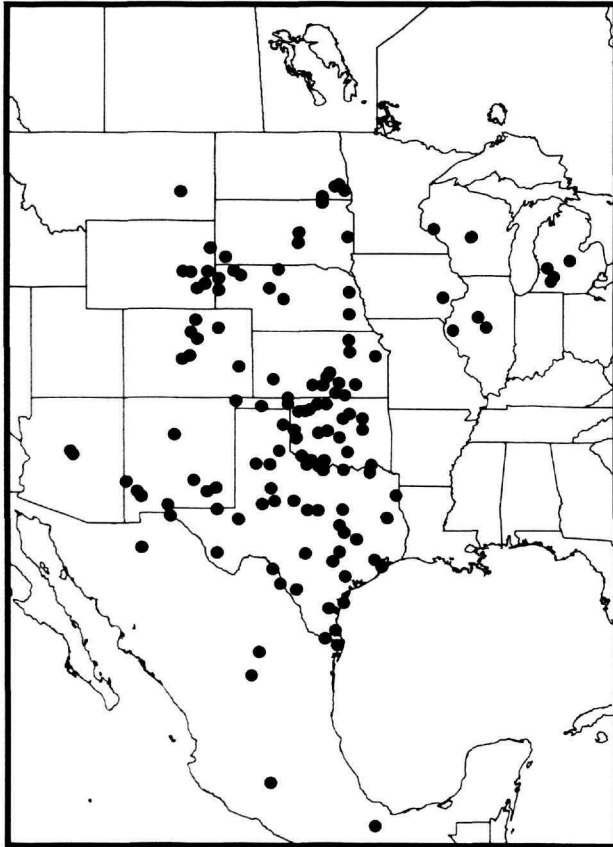


FIGURE 139.—Distribution of *Sphecodogastra texana*.

exceeded by width of compound eye. (9) Clypeus projecting approximately 0.60 times its length below lower margin of eyes; (11) clypeal surface without median longitudinal sulcation. (13) Ocular–ocellar distance less than distance between lateral ocellus and hind margin of vertex (ocelli very large, ocular–ocellar space approximately 0.5 times lateral ocellar diameter); (14) distance between lateral ocelli approximately 4.0 times ocular–ocellar distance. (16) Inner margins of compound eyes converging below. (21) Scape reaching beyond top of vertex; (22) pedicel slightly shorter than flagellomere 1. (30) Mandible moderate in length, reaching opposing clypeal angle (Figure 14).

(40) Dorsal surface of propodeum about 0.66 times the length of scutellum and approximately 1.46 times the length of metanotum; (44) lateral propodeal carinae absent or at most extending one-fourth the distance to dorsal propodeal surface. (45) Inner hind tibial spur with 3 or 4 moderately short teeth (Figure 65), similar to that of *S. noctivaga* (Figure 64).

(46) Lateral edge of metasomal T2 broadly rounded.

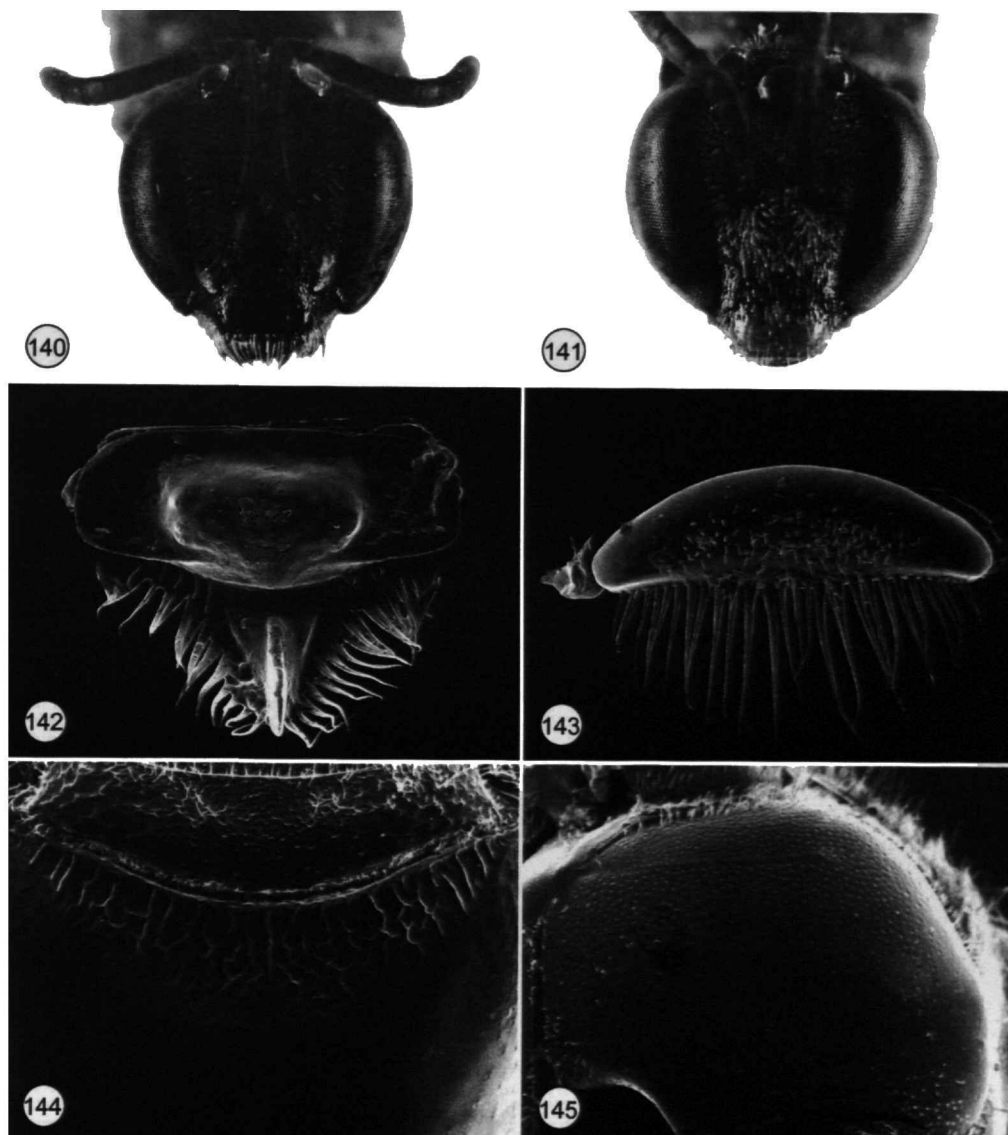
Sculpture: (51) Supraclypeal area tessellate only along extreme lateral margins, (52) punctation somewhat sparse, most punctures separated by 1–2 times their diameters. (53) Clypeus mostly polished, tessellate along basal and lateral margins; (54) apical punctures only slightly larger than basal ones, very sparse, separated by 2–5 times their diameters. (55) Hypostoma striolate, weakly so on anterior half.

(56) Mesoscutum somewhat dull, surface tessellate throughout, (57) punctation as in Figure 145, punctures separated by 1–2 times their diameters. (63) Dorsal surface of propodeum rugulose over basal two-thirds (Figure 144), (64) surface alveolated. (65) T1 shiny and polished, (66) punctation extremely fine, sparse, most punctures separated by twice their diameters.

Coloration: (67) Abdomen mostly orange (T4 and T5 usually dark orange-brown; T3 often darkly pigmented, and rarely, entire abdomen darkly pigmented). (69) Flagellum orange-brown. (70) Tegula light brown. (71) Wing membrane hyaline; veins and stigma amber to light brown. (72) Legs orange-brown.

Vestiture: (74) Hairs on head white. (75) Pubescence on thorax white; (76) mesoscutal hairs short, many suberect or adpressed; pleuron with conspicuous amount of adpressed hairs. (81) Basal hair bands on T2–T4 virtually absent, inconspicuous; moderately developed apical hair band present on T4.

MALE: As described for female except as follows: (1) length 7.1–9.2 mm (mean = 8.3, $n = 5$); (2) wing length 2.0–2.6 mm (mean = 2.3, $n = 5$); (3) abdominal width 1.8–2.4 mm (mean = 2.1, $n = 5$). (4) Head (Figure 141) length/width ratio 1.00–1.03 (mean = 1.02, $n = 5$). (23) Flagellomere 2 approximately 1.5 times length of flagellomere 1. (37) Median mesoscutal line not impressed. (70) Tegula yellow-translucent. (73) Short, adpressed hairs on face extending dorsad to ocellar area, weakly enclosing median ocellus. (76) Mesoscutum with conspicuous short, adpressed hairs and more elongate, less conspicuous hairs; pleuron with short, suberect to adpressed hairs.



FIGURES 140–145.—*Sphecodogastra texana*: 140, female head; 141, male head; 142, female labrum; 143, male labrum; 144, female propodeum; 145, female mesoscutum.

Terminalia (Figures 146–150): (84) S7 lateral arms moderately well developed; (85) S8 moderately developed; apex of median process truncate; (89) unlike other *Sphecodogastra*, retrorse membranous lobe very broad and twisted ventrally.

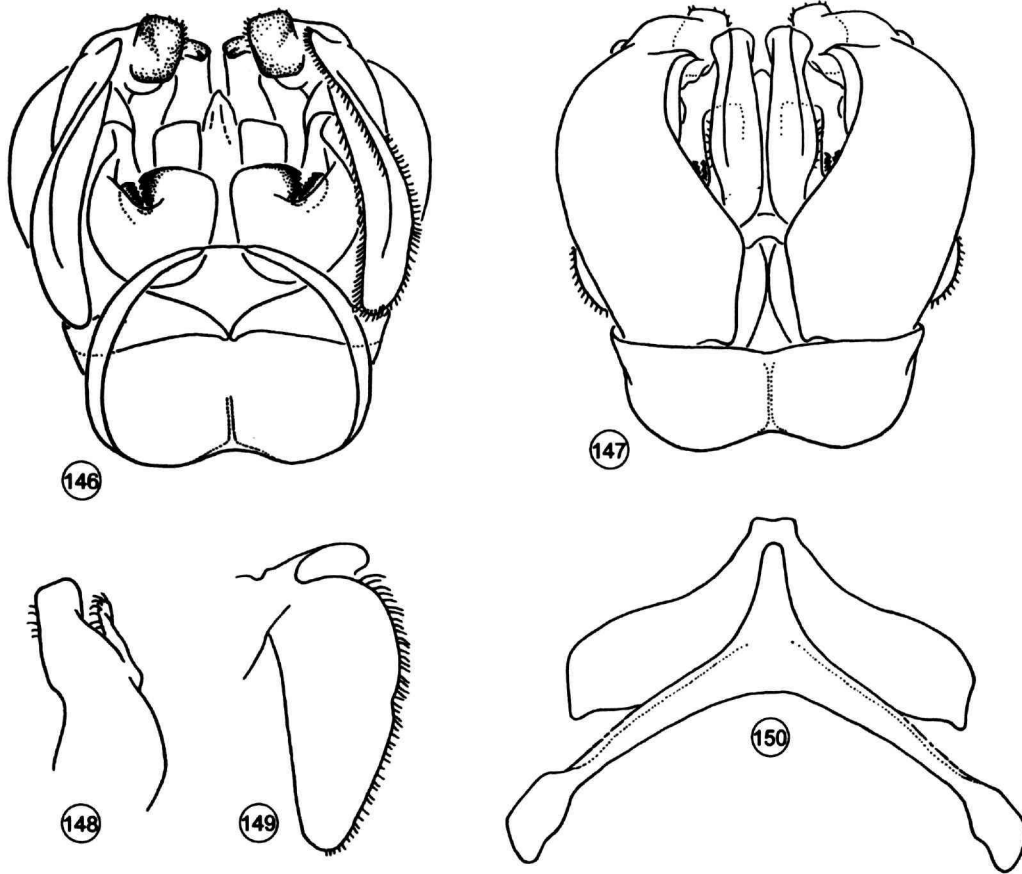
FLIGHT RECORDS (Figure 151).—Females of *S. texana* were collected from April to December, but like most species of *Sphecodogastra*, they were collected primarily from May through July (88%). Males were collected from June through October. Graenicher (1911) reported this species to be active from May to September in northwestern Wisconsin, and Kerfoot (1967a) observed nesting activity during this same

period in Kingman County, Kansas. No information is available concerning the number of generations produced each year.

SPECIMENS EXAMINED.—903 (847 females, 56 males).

MEXICO. CHIHUAHUA: Juarez. COAHUILA: Cabos; Parras, 7 mi N. MICHOACÁN: Morelia, 13 mi W. VERACRUZ: El Naranjo, 10 mi W.

UNITED STATES. ARIZONA: *Yavapai Co.*: Camp Verde; Cornville, 3 mi S. COLORADO: *Boulder Co.*: Boulder; White Rocks; *Clark Co.*: Lake George; *Denver Co.*: Denver; *El Paso Co.*: Colorado Springs; Foster Ranch; *Kiowa Co.*: Eads;



FIGURES 146–150.—*Sphecodogastra texana*, male terminalia: 146, genital capsule, ventral view; 147, genital capsule, dorsal view; 148, right gonostylus, posterior view; 149, right retrorse lobe, lateral view; 150, S7 and S8, ventral view.

Larimer Co.: Fort Collins; *Morgan Co.*: Fort Morgan; county/coordinates unknown: Fuente; Walsenberg, 2 mi W. ILLINOIS: *Henderson Co.*: Gladstone, 1.5 mi SW; *Mason Co.*: Forest City, 4 mi SW; *Morgan Co.*: Meredosia; *Peoria Co.*: Peoria. IOWA: *Johnson Co.*: Iowa City. KANSAS: *Butler Co.*; *Clark Co.*: Kingstown, 1 mi W (State Park); *Cowley Co.*: Winfield; *Douglas Co.*: Lawrence; University of Kansas Natural History Reservation; *Finney Co.*: Garden City; *Kingman Co.*: Kingman; Kingman, 8 mi W; *Marshall Co.*: Blue Rapids; *Pottawatomie Co.*: Little Gobi Desert; *Pratt Co.*: Pratt; *Reno Co.*: Hutchinson; Medora (sand dunes); *Riley Co.*: Manhattan; *Sedgwick Co.*: Wichita; *Seward Co.*; *Summer Co.*: Wellington. MICHIGAN: *Clinton Co.*: Bath; *Ingham Co.*: Dansville; *Kalamazoo Co.*: Gull Lake Biological Station; *Kent Co.*: Grand Rapids; *Livingston Co.*: E. S. George Reserve. MISSOURI: *Buchanan Co.*: Mo-Kan Bridge. NEBRASKA: *Antelope Co.*: Grove Lake; *Cherry Co.*: Valentine, 25 mi S (F. Crowe Ranch); *Cuming Co.*: West Point; *Dawes Co.*: Chadron; *Hooker Co.*: Mullen; Mullen, 1.5 mi N; *Lancaster Co.*: Lincoln; *Scotts Bluff*

Co.: Mitchell; *Sheridan Co.*: Hay Springs; *Sioux Co.*: Agate; *Thomas Co.*: Halsey; Halsey, 2.5 mi W (National Forest). NEW MEXICO: *Catron Co.*: Glenwood, 5 mi N; *Chaves Co.*; *Dona Ana Co.*: Las Cruces; *Eddy Co.*: Artesia; Malaga, 7 mi W; *Grant Co.*: Bayard; Silver City; *Lincoln Co.*: Hondo; *Union Co.*: Clayton Lake (12 mi NW Clayton). NORTH DAKOTA: *Cass Co.*: Leonard; *Dickey Co.*: Oakes; *Ransom Co.*: Sheldon; *Richland Co.*: Walcott Dunes. OKLAHOMA: *Alfalfa Co.*: Cherokee; Great Salt Plains; *Beaver Co.*: Gate; *Beckham Co.*: Sayre; *Caddo Co.*: Hinton; *Canadian Co.*: El Reno; *Choctaw Co.*: Grant; Hugo; *Cimarron Co.*: Kenton, 7 mi E (North Crease Creek); *Jackson Co.*: Elmer; *Jefferson Co.*: Waurika; *Kiowa Co.*: Lugert; *Love Co.*: Oswalt. *Marietta Co.*: Thacker-ville, 1 mi S; *Marshall Co.*: University of Oklahoma Biological Station; *Okfuskee Co.*: Okemah; *Oklahoma Co.*: 11 mi N Oklahoma City; *Okmulgee Co.*: Okmulgee; *Pawnee Co.*: Pawnee; *Payne Co.*: Stillwater; *Pontotoc Co.*: Roff; *Roger Mills Co.*: Cheyenne; *Texas Co.*: Guymon; *Tillman Co.*: Grandfield; *Tulsa Co.*: Tulsa; *Woods Co.*: Little Sahara State Park; Waynoka, 3

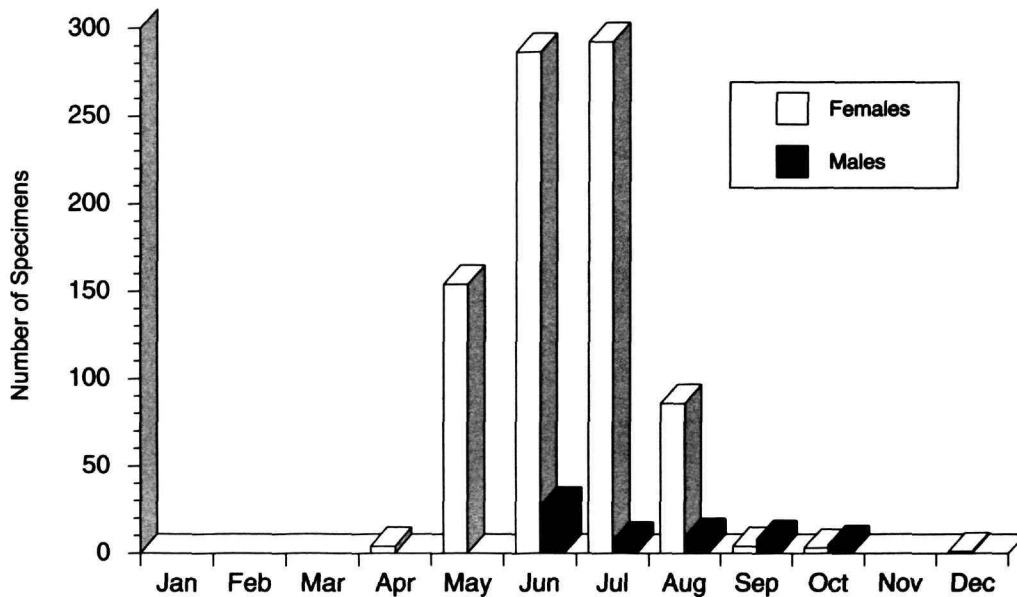


FIGURE 151.—*Sphecodogastra texana* flight records, by month of collection.

mi W; *Woodward Co.*: Mooreland; Woodward. SOUTH DAKOTA: *Brookings Co.*: Brookings; *Brown Co.*: Hecla; *Buffalo Co.*: Ft. Thompson; *Fall River Co.*: Angostura Dam; *Hyde Co.*: Highmore. TEXAS: *Bastrop Co.*: Bastrop; *Brazos Co.*: Bryan; *Brewster Co.*: Alpine; *Cameron Co.*: Brownsville; *Clay Co.*: Henrietta; *Coryell Co.*: Eddy, 12 mi W; Ft. Hood; *Eastland Co.*: Romney; *El Paso Co.*: El Paso; *Gonzales Co.*: Luling; Palmetto State Park; *Hale Co.*: Hale Center; Memphis, 5 mi W; *Harris Co.*: Houston; *Harrison Co.*: Karnack; *Hemphill Co.*: Canadian; *Hildago Co.*: Alamo, 7 mi SE (Santa Ana Wildlife Refuge); *Howard Co.*: Big Spring, 1 mi NW; *Jeff*

Davis Co.: Phantom Lake (Davis Mountains); *Kenedy Co.*: Padre Island National Seashore; *Kerr Co.*: Kerrville; *Kleberg Co.*: Kingsville; *Lamar Co.*: Paris; *Mitchell Co.*: Colorado City; *Nacogdoches Co.*: Nacogdoches; *Randall Co.*: Buffalo Lake State Park; Palo Duro Canyon; *San Patricio Co.*: Port Aransas; *Taylor Co.*: Abilene; Buffalo Gap; *Val Verde Co.*: Del Rio; *Ward Co.*: Monahans, 9.5 mi S; *Wichita Co.*: Burkburnett (Red River); Burkburnett, 4 mi E. WISCONSIN: *Pierce Co.*: Prescott; *Wood Co.*: Port Edwards. WYOMING: *Converse Co.*: Douglas; *Niobrara Co.*: Lusk; *Platte Co.*: Ft. Laramie, 11.5 mi SW; *Wheatland*; *Weston Co.*: Newcastle, 6 mi NW.

Appendix 1

Identification of Figures in Keys

The entries below identify the figures without legends used in the illustrated keys to *Sphecodogastra* species.

Key to *Sphecodogastra* Females

11, *S. texana*, head. 12, *S. aberrans*, head. 13, *S. noctivaga*, mandibles. 14, *S. texana*, mandibles. 15, *S. oenotherae*, propodeum. 16, *S. lusoria*, propodeum. 17, *S. danforthi*, head. 18, *S. potosi*, head. 19, *S. danforthi*, propodeum. 20, *S. potosi*, propodeum. 21, *S. lusoria*, pleuron. 22, *S. aberrans*, pleuron. 23, *S. lusoria*, supraclypeal area. 24, *S. aberrans*, supraclypeal area. 25, *S. antiochensis*, right hind femur, anterior view. 26, *S. aberrans*, right hind femur, anterior view. 27, *S. antiochensis*, propodeum. 28, *S. aberrans*, propodeum.

Key to *Sphecodogastra* Males

29, *S. texana*, head. 30, *S. lusoria*, head. 31, *S. texana*, genital capsule, ventral view. 32, *S. texana*, right retrorse lobe, outer lateral view. 33, *S. noctivaga*, genital capsule, ventral view. 34, *S. oenotherae*, propodeum. 35, *S. antiochensis*, propodeum. 36, *S. danforthi*, propodeum. 37, *S. aberrans*, S3–S6. 38, *S. lusoria*, S3–S6. 39, *S. aberrans*, genital capsule, ventral view. 40, *S. lusoria*, genital capsule, ventral view. 41, *S. potosi*, ocellar area. 42, *S. antiochensis*, flagellum. 43, *S. potosi*, flagellum. 44, *S. lusoria*, flagellum. 45, *S. potosi*, propodeum. 46, *S. lusoria*, propodeum. 47, *S. danforthi*, genital capsule, ventral view. 48, *S. potosi*, genital capsule, ventral view. 49, *S. antiochensis*, T1. 50, *S. lusoria*, T1.

Appendix 2

Onagraceae Taxonomy and Synonymy

Floral records associated with museum specimens and reports in the literature often represent names of Onagraceae that have been synonymized. The following list presents these older names or combinations followed by (=) the currently recognized nomenclature. This information was kindly provided by Warren Wagner, Department of Botany, National Museum of Natural History, Smithsonian Institution.

- Gaura nealleyi* = *G. suffulta nealleyi*
- Oenothera cespitosa* var. *marginata* = *O. caespitosa* ssp. *marginata*
- O. cespitosa* var. *montana* = *O. caespitosa* ssp. *cespitosa*
- O. clavaeformis* var. *aurantiaca* = *Camissonia claviformis* ssp. *aurantica*
- O. clavaeformis* var. *clavaeformis* = *Camissonia claviformis* ssp. *claviformis*
- O. clavaeformis* var. *cruciformis* = *Camissonia claviformis* ssp. *cruciformis*
- O. clavaeformis* var. *integrior* = *Camissonia claviformis* ssp. *integrior*
- O. drummondii* = *O. drummondii* ssp. *drummondii*
- O. greggii* = *Calylophus hartwegii pubescens*
- O. hartwegii* = *Calylophus hartwegii*
- O. hookeri* = *O. elata*
- O. missouriensis*, *Megapterium missouriense* = *O. macrocarpa* ssp. *macrocarpa*
- O. runcinata* = *O. pallida* ssp. *runcinata*
- O. strigosa* = *O. villosa strigosa*
- O. tanacetifolia* = *Camissonia tanacetifolia*
- O. tetragona* = *O. fruticosa glauca*
- O. trichocalyx* = *O. pallida* ssp. *trichocalyx*

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