The Bee Family Oxaeidae
with a Revision of the
North American Species
(Hymenoptera: Apoidea)

PAUL D. HURD, JR.
and
E. GORTON LINSLEY

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Paul D. Hurd, Jr.
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ABSTRACT

Hurd, Paul D., Jr., and E. Gorton Linsley. The Bee Family Oxaeidae with a Revision of the North American Species (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology*, number 220, 75 pages, 68 figures, 3 plates, 3 maps, 2 tables, 1976.—This study is a comparative treatment of the natural history of the family Oxaeidae. Information is presented on the biology, behavior, intrafloral ecology, and systematics of these bees together with a historical review of their classification and phylogeny. Included are diagnoses of the family and genera with a revision of the North American species. Characters useful for identification of the species are illustrated and complete distributional, biological, and synonymical data are provided and discussed. New taxa are *Mesoxaea* (type-species: *Oxaea nigerrima* Friese), *Notoxaea* (type-species: *Oxaea ferruginea* Friese) and *Protoxaea australis*, *P. micheneri*, *Mesoxaea clypeata*, and *M. rufescens*.
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The Bee Family Oxaeidae
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North American Species
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Introduction

This study is intended as a contribution to our knowledge of the family Oxaeidae, a group of moderately large, rather robust, fast-flying bees found only in the Western Hemisphere. Although as a group the Oxaeidae are primarily centered in the tropics, a few species occur or are centered in the warm temperate areas of both continents. None of the species is known to inhabit the West Indies or for that matter any other islands.

The group is one for which the taxonomic status and phylogenetic placement has long been in dispute. Twenty species are presently known, including those described below, and these are equally divided between North and South America, only one of which is shared between the continents.

Their known intrafloral relationships suggest a rather narrow dependence upon relatively few sources of pollen. These include only certain genera within the plant families Fabaceae, Solanaceae, and Zygophyllaceae. However, the males and females seek nectar from a comparatively wide variety of plants since the flowers of some of the preferred pollen sources produce little or no nectar and large quantities of nectar are required to meet the bioenergetic requirements of these fast-flying bees.

ACKNOWLEDGMENTS.—This investigation has been made possible and was carried out under the joint support of our respective institutions, the Smithsonian Institution, Washington, D.C. and the University of California, Berkeley. This arrangement accorded us not only the opportunity to pursue our program of research by working independently in Berkeley and Washington, but also allowed us to work jointly in Berkeley during the early part of 1975. We therefore express our appreciation to the authorities of our institutions for their support of the project and for the use of the requisite facilities and supporting staffs. For the sponsorship and financial support of our field and laboratory studies we acknowledge with gratitude the Leopold Edward Wrasse and Elvenia J. Slosson Endowment Funds of the Division of Agricultural Sciences, University of California, and grants from the Smithsonian Research Foundation (SRF-430039) and the Fluid Research Fund of the Smithsonian Institution.

Throughout the course of this investigation we have been ably assisted by Kathleen Sorensen in the transcription and recording of data, curation of specimens, preparation of maps, and assembly of bibliographic materials.

The illustrations which accompany this study...
were kindly prepared by Celeste Green, Senior Scientific Illustrator, Department of Entomological Sciences, University of California, Berkeley. The photographs in Plate 1 were taken by Dr. Edward S. Ross, California Academy of Sciences, San Francisco, at 2 miles north of Rodeo, New Mexico. Plates 2 and 3 are reproduced from photographs supplied by Ronald F. Shunk, Spring Valley, California, of a "sleeping" aggregation of males on Acacia constricta located at the Bagwell Ranch, 10 miles north of Rodeo, New Mexico.

We are indebted to Andrew R. Moldenke and John L. Neff, University of California, Santa Cruz, for providing us with much of the floral data pertaining to Notoxaea ferruginea that we have incorporated into Table 1.

We are grateful to Stanwyn G. Shetler, Department of Botany, Smithsonian Institution, Washington, D.C., for his advice, assistance, and review of the botanical names recorded in Tables 1 and 2. He is responsible for the arrangement of the plant families, genera, and species in these tables and has also compiled the information on botanical classifications embodied in this study. Accordingly he has materially enhanced the overall value and usefulness of these tables. Herbert G. and Irene Baker and Lincoln Constance, University of California, Berkeley, read the section on flower preferences and provided helpful comments.

Our investigations on the systematics of these bees have been most helpfully facilitated by a number of individuals who have generously given of their time and accorded us their much appreciated assistance. This has made it possible for us to examine the primary types of nearly all the North American oxaeids as well as those of the South American species described by Friese. Thus we are indebted to E. Königsmann, Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität zu Berlin, for the loan of the holotype of Oxaea rufa Friese as well as for providing us with specific information about the Friese type of O. nigerrima and for help in our attempts to locate the type repositories of O. texana Friese. In this latter regard we are also grateful to Willem N. Ellis, Zoologisches Museum, Universität van Amsterdam, Max Fischer, Naturhistorisches Museum, Vienna, and M. A. Lief tinck, Rhenen, the Netherlands, for their efforts to locate the type specimens of O. texana Friese. We are also grateful to Laszlo Moczar of the Zoological Institute of the University, Szeged, Hungary, who arranged with J. Papp of the Hungarian Natural History Museum, Budapest, for us to borrow the holotype of O. ferruginea Friese. Likewise we gratefully acknowledge E. Tortone se, Director of the Museo Civico di Storia Naturale "Giacomo Doria," Genoa, Italy, who kindly arranged with Delfa Guiglia to compare our notes and a specimen we sent of Protoxaea gloriosa (Fox) with the type specimens of O. tristis Gribodo. The results of her much appreciated assistance have contributed significantly to our studies. We are also indebted to Karl V. Krombein, National Museum of Natural History, Smithsonian Institution, Washington, D.C., who kindly examined for us the label data on the holotype of O. tachytiformis Cameron, and we also thank G. Knerer, currently in residence at the British Museum of Natural History, for additional information that he supplied in this regard.

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Historical Review

Klug (1807) proposed the genus Oxaea for a new species from Brazil, O. flavescens, of which he illustrated the male. He considered the genus unique in having three, rather than two-segmented labial palpi, a term which he apparently applied only to the short apical segments (in Oxaea and its immediate relatives, the first segment of the palpus is elongate and flattened, the last three segments short, cylindrical, together not as long as the first). He also noted that the maxillary palpi were absent, a condition he believed to be the case in Melecta, Melipona, and Acanthopus, although he did not attempt to assign Oxaea to a position near these or any other genus of bees.

Latreille (1810) was the first to attempt to place Oxaea in a classification. He presumably knew only the male, and included the genus among the parasitic bees near Melecta and Crocisa, as did Blanchard (1845). Many years later, Popov (1941, 1945, 1951) reported that the oxaeids, which he regarded as a distinct family, and the parasitic anthophorids of the genera Osiris, Pasites, Morgania, Schmiedeknechtia, and Neopasites (representing the tribes Osirini, Ammobatini and Neopasitini), resemble one another in having undifferentiated sagittae in the male genitalia (penis valves not separated from the penis). However, since this condition also occurs in the Andrenidae, Megachilidae, and Apidae (Snodgrass, 1941), Popov considered that the causes of morphological reduction in the sagittae were different in various groups. Rozen (1964) also found similarities between the third instar larvae of Protooxaea gloriosa and those of Nomada-like anthophorids. He wrote:

The similarities between the mature larva of P. gloriosa and those of the Nomada-like parasitic anthophorids (Nomada, Triepeolus, Oreopasites, etc.) are difficult to explain. Not only do the larvae of these two groups share the generalized features also encountered in the Colletidae, Andrenidae, Halictidae, and Melittidae, but they both also exhibit certain specialized characteristics, namely, the peculiar position of the posterior tentorial pits and the absence of antennal prominences and vertexal protuberances. Although, with the mature larvae, the long mandible of P. gloriosa contrasts with the short mandible of the parasitic bee, the long mandible of the first instar of P. gloriosa is somewhat similar to the extremely long mandible of the first stage parasitic forms. The mature larva of P. gloriosa is especially similar to that of Triepeolus sp. (I have examined the same series used by Michener, 1955). In addition to the characters referred to above, these taxa share: spiculated hypopharynx; attenuate mandibular apexes (though not blade-like in Triepeolus sp.); body without tubercles; spiracles on pigmented, sclerotized plates; and long atrial spines. Presumably the similarities result from convergent evolution, for the adults of Oxaeinae and the Nomada-like bees are too dissimilar to suggest a close relationship.

A number of authors have considered oxaeids (or at least Oxaea) related to the carpenter bees (Anthophoridae: Xylocopinae). For example, F. Smith (1854) placed them between Xenoglossa and Melitturga near Xylocopa and Lestis, Sichel (1865) considered their true position to be nearer the end of the tribe Xylocopites of Lepeletier (1841), and Blanchard (1845) and Ashmead (1899) assigned them to the Xylocopidae, stating that Oxaea and Lestis probably should be considered as a subfamily, the Oxaeinae.

Another relationship that has been suggested for Oxaea is with the diphaglossine colletids. Dalla Torre (1896) placed them in the Apidae, subfamily Podalirinae, between Diphaglossa and Lestis. Cockrell (1898) assigned the genus to the podalirine Anthophoridae between Centris and Megacilissa, and Friese (1898) in his monograph of the genera Megacilissa, Caupolicana, Diphaglossa, and Oxaea, considered the genus to be a derivative of the caupolicanine branch of the Diphaglossinae, related in particular to Megacilissa, which it resembles in habitus, coloration, and the extensive pollen-collecting apparatus. He also derived the Old World genus Melitturga from this group of colletids. Schrottky (1902) placed Oxaea next to Megacilissa (in the Andrenidae) but separated both genera from Caupolicana and Diphaglossa (Megacilissa is presently regarded as a synonym of Caupolicana). Strand (1910) placed Oxaea next to
**Figure 1.**—Phylogenetic relationships of Oxaeidae (Oxaea), after Schrottky (1913).

*Oxaea*, and Jürgensen (1912a, b) listed it in the end of the Colletidae following *Caupolicana* and *Ptiloglossa*. Ducke (1912) keyed out *Oxaea* next to the Diphaglossinae, but did not include it in that group. Schrottky (1913) discussed the interrelationships among the South American genera of Colletidae, but also excluded *Oxaea*, regarding it as a very aberrant genus, which to him apparently originated in tropical Brazil and was only slightly related to the colletids. His diagram of the relationships among the genera he discussed is reproduced in Figure 1. The most recent statement regarding a possible diphaglossine relationship is that of Roberts (1973) who comments:

The nests most similar architecturally to those of the Oxaeidae are those of the Diphaglossinae (Colletidae) such as *Ptiloglossa* (Roberts, 1971). Although similar in some aspects of adult morphology and behavior, fundamental differences in both adult and pre-imaginal morphology preclude attempts to link *Oxaea* and *Protoxaea* with the Diphaglossinae. My observations on pupal morphology and nest architecture of *Oxaea flavescens* corroborate the conclusions of Rozen (1965) based on *Protoxaea*, and indicate that the Oxaeidae have no close relatives within the Apoidea.

The more prevalent taxonomic view of the group has been that they are andrenids. This possibility was first suggested by Gerstaeker (1867), who rejected a close relationship with *Lestis*, as proposed by Sichel (1865), on the basis of differences in wing venation, mouthparts, pollen-collecting apparatus and form of the abdomen, emphasizing similarities in labial structure to the Andreninidae, and to *Andrena* in particular in the form of the cubital cell, the fringe on the sides and apex of the abdomen and the strongly developed coxal “curl.” Friese (1898) agreed in general with Gerstaeker and proposed assigning them to the Melittinidae behind *Megacilissa* and before *Systropha*. However, the strongest support for an andrenid relationship was the character analysis of Bischoff (1934) which revealed a similarity between *Oxaea* and genera of andrenine and panurgine bees through the possession of subantennal plates. This feature also impressed Michener who characterized the subfamily Oxaeininae in the Andrenidae for the reception of *Oxaea* and *Protoxaea*, noting some similarities to the Old World genus *Melitturga*. His treatment was endorsed by Graf (1966), who rejected separate family status for the group, in particular the interpretation of Rozen (see below). Graf, like Michener, relied heavily on the subantennal sutures, but discussed other characters, including the reduction of the sting, a feature shared with most andrenine and panurgine Andrenidae.

The most cogent arguments for regarding the oxaeids as a distinct family has been provided by Rozen (1965). We quote from him, in part, as follows:

Michener (1944) divided the andrenid subfamily Panurginae into two tribes, the Panurgini and Melitturgini, with the latter containing the single Old World genus *Melitturga*. This genus was relegated to tribal status apparently on the grounds that the adults, unlike those of other panurgines, bear certain striking resemblances to the essentially Neotropical Oxaeininae of the same family. In 1951 Rozen showed that the male genitalia of *Melitturga* are unlike those of the Oxaeininae and are not only typical of those of the Panurginae in general but quite like those of the *Camptopoeum-Panurgus-Panurginus-Epimethea* complex within the subfamily. On the basis of this information, Michener (1954) abandoned the idea that the genus *Melitturga* represents a distinct tribe of the Panurginae. Recently evidence in the form of the larva of *Protoxaea gloriosa* Fox (Rozen, 1964) suggested that the Oxaeininae were so unlike other Andrenidae that they should be removed from the family unless some form intermediate between the two subfamilies is found. In spite of the structure of the male genitalia, *Melitturga* is the only known possible intermediary . . . . As an adult, *M. clavicornis* and presumably the other members of the genus possess the following oxaeine-like features: body size large (though not so large as that of the Oxaeininae); compound eyes of male large and strongly converging above; ocelli, especially those of male, low on face first flagellar segment as long as scape; other antennal segments short; thorax robust and in male with dense pile; wings strongly papillate.

However, the Oxaeininae differ from all the Panurginae, including *Melitturga*, on the basis of numerous characters. The features of the larvae and the genitalia have already been mentioned. Michener (1944) gave the following signifi-
cantal characteristics of adult oxaeines: apex of posterior femur of female enlarged and forming a plate; scopula abundant from coxa to basitarsus; pterostigma absent; and marginal cell narrow and elongate. To these should be added: clypeus strongly protuberant; labrum as long as, or longer than, broad, and submentum fused into a single plate.

It is important to point out that the Oxaeinae differ from the Andreninae on the basis of all the characters indicated above except that the andrenine larvae lack conical tubercles (though the transverse ones on the anterior end of the body are more pronounced than those of the Oxaeinae). Also females of the Andreninae have the scopula distributed from the coxa to the basitarsus, as in the Oxaeinae. However, both of these characters are almost certainly plesiomorphic, for they are found in the Colletidae and are thus not significant for a judgment of phylogenetic relationships.

On these bases, Rozen reaccorded the oxaeids family status and we concur in this judgment.

Comparative Biology of the Family Oxaeidae

Flower Preferences.—The oxaeids, in so far as presently known, are narrowly polylectic, utilizing related or counterpart pollen sources in the northern and southern hemispheres, especially species of Cassia (Fabaceae) and Solanum (Solanaceae). These plants produce an abundance of pollen but no nectar, and are attractive only to pollen-gathering females which, like the males, must seek nectar elsewhere. Species in these taxonomically distant genera share convergent structural and functional similarities in the method of pollen presentation which are also approximated in such remote groups as Tibouchina, Rhynchanthera, and Tococa (Melastomataceae), (Laroca, 1970) and Pedicularis (Scrophulariaceae) and Dodecatheon (Primulaceae), vide Macior, 1971, 1974. Although morphological details differ, they all shed their pollen, which is dry, through terminal staminal pores which must be "buzzed" and vibrated or squeezed by the bee in order to release it. Perhaps because of the abundance of the pollen, which squirts out in clouds onto the venter of the abdomen and can be quickly gathered into the scopal hairs, most bee visitors are large forms whose weight inverts the flower, for example species of Bombus, Xylocopa, Centris, Caupolicana, and Ptiloglossa (see Linsley, 1962; Michener, 1962; Linsley and Cazier, 1963; Wille, 1963). In fact, Wille states that in the Province of Guanacaste, Costa Rica, Cassia biflora is called "abejon," meaning "large bee," presumably because of the large conspicuous bees which visit it. However, inversion of the flower, although facilitating the rapid capture of large amounts of pollen, is not necessary for the release of pollen, and these same authors have recorded small to medium-sized bees such as species of Exomalopsis, Psaeynthia, Augochloropsis, and Nomia, successfully gathering pollen. Not all bees, however, vibrate or squeeze the anthers. In addition to the "buzzing bees," which include oxaeids, Wille (1963) recorded "biting bees," which chew into the anthers and "gleaning bees," which pick up pollen left on the corolla by other bees. (For an informative discussion of the behavior of bees at flowers of Cassia, see Thorp and Estes, 1975).

Neither Cassia nor Solanum flowers produce nectar, and although Todd (1882) states that those of Solanum have no odor, Harris and Kuchs (1902) observed that "especially in the morning, the odor was decidedly pronounced." Other distinctions shared by at least some species of Cassia and Solanum are the production of both "right-handed" and "left-handed" flowers (Todd, 1882; Robertson, 1890; Harris and Kuchs, 1902) and two kinds of stamens, a single large stamen in addition to the four short ones in Solanum rostratum (but not all species of Solanum) and two long stamens in addition to the shorter ones in some species of Cassia. Although the functional interpretation of these two kinds of stamens has been subject to different interpretations (see Todd, 1882; Müller, 1883; Meehan, 1886, Robertson, 1890; Halsted, 1890; and Harris and Kuchs, 1902), the smaller anthers in Cassia are now known to produce viable pollen, the larger ones (the so-called "food anthers") smaller, sterile pollen grains (Meeuse, 1961). However, Bowers (1975) found that the dimorphic anthers in Solanum rostratum perform a different function: the primary role of the small anther is to provide pollen as an attractant to insect visitors and the larger anther functions in pollination. Linsley and Cazier (1972) reported that of a sample of 2565 pollen grains of Cassia bauhinioides removed from the scopal hairs of Protopaxa gloriosa, approximately 20 percent were large grains averaging about 80 microns in diameter and nearly 80 percent were small grains averaging about 27 microns, which, although not viable, contained protoplasm. Solanum also produces two sizes of pollen grains, but Bowers (1975) found no detectable dif-
ferences in the percentage of abortive grains between the large and small anthers within a flower, and hand-pollination experiments demonstrated no differences in pollen fertility between the two types of anthers. Stow (1927) found a correlation in *S. tuberosum* between their presence and high temperatures, and Joergensen (1928) reported a high proportion of "bad" pollen grains in experimentally produced euploid and aneuploid forms. However, since Heiser and Whitaker (1948) found that specimens of *S. elaeagnifolium* from California had the chromosome number \( n = 12 \), and were therefore diploid, it is possible that aborted pollen in this species results from hybridization, as in the *S. nigrum* complex (Stebbins and Paddock, 1949).

On the other hand, samples taken from bees gathering pollen from a pure stand of *S. elaeagnifolium* near Portal and a stand mixed with *S. rostratum* at Douglas, Cochise County, Arizona, each yielded about 35 percent viable grains averaging about 35 microns in diameter and 65 percent lacking protoplasm and averaging about 26 microns in diameter (Linsley, 1962; Linsley and Cazier, 1963). *Solanum rostratum* growing in the mixed stand at Douglas yielded about 85 percent viable pollen grains in bee-collected samples. However, these particular characteristics of pollen manufacture and presentation are not found in other plants known to be utilized as pollen sources by oxaeids, all of which also produce nectar.

Cazier and Linsley (1974) have commented on the fact that *Protoxaea gloriosa*, although polylectic as a species, either as individual females or as whole populations may be more or less regular polyleges constant to one of a variety of diverse plant species (during the course of the nesting season the preferences may change in response to sequential blooming of hosts). The species most commonly selected not only represent an array of plant families, e.g., Fabaceae (*Cassia, Prosopis, and Desmanthus*), Zygophyllaceae (*Kallstroemia* and *Larrea*), and Solanaceae (*Solanum*), but the flowers involved differ markedly in form, structure, and color (at least to the human eye). Further the average diameter of the pollen grains which they produce ranges from about 20 microns to 80 microns, a range which includes large numbers of plant species occurring in the territory of the bee which are not known to be utilized by the bee.

Cazier and Linsley (1974) have described some of the unique features of pollen and nectar presentation in *Kallstroemia grandiflora* and the following is extracted in part from their account:

[The flowers of *Kallstroemia grandiflora* produce an abundance of pollen and nectar, which is exploited in three ways by insects . . . including bees, wasps, flies and butterflies.

The plant is of special interest from the standpoint of pollination ecology, as both the plant and some of the insects have adaptations in behavior that are not always mutually beneficial. The flowers of *K. grandiflora* are allogamous for most of the daily flowering period and become autogamous as the flowers close. Thus, they can be either cross- or self-pollinated, with the former evidently favored. The flowers have little or no odor, a color range within "bee yellow" (500-650 \( \mu \)), and a strong ultraviolet reflective pattern on both upper- and under-surfaces. Insects are apparently attracted by the color and ultraviolet reflection, with the latter so arranged as to form non-reflective, dark target, "nectar guide" areas on both upper- and under-surfaces.

One group of bees and wasps gather pollen and nectar from the top of the flower, effecting both cross- and self-pollination in the process. A second group of smaller bees and wasps gather nectar from within the flower but avoid contact with the sexual portions and are therefore of no importance in pollination. The third group of honeybees and several other larger bees and wasps, extract nectar from the underside of the flower completely avoiding the sexual parts of the plant and therefore play no role in pollination. Even though the plant gains no direct benefit from this last group of insects it nevertheless provides them with a sepal nectar guide that directs them to the nectaries. It is proposed that these species may be contributing to the economy of the plant by reducing the quantity of available nectar so that pollinators have to visit more flowers to get their full nectar supply.

This conclusion is in line with that of Heinrich and Raven (1972) that "a flower must provide sufficient reward to attract foragers, but it must limit this reward so that the animals will go on to visit other plants of the same species," although the presumed method for accomplishing this in *Kallstroemia* is different from any which they describe or suggest.

Cazier and Linsley (1974) have reported on the method utilized by *Protoxaea gloriosa* for the collection of pollen and nectar from the flowers of *Kallstroemia*.

[Females] alight in the upturned flowers which droop downward with the bees weight, sometimes bending 180 degrees so that the bee is working upside down. As they land in the flowers, facing downward, they gather the style and all ten stamens into the venter, holding them there with all six legs. This places the anthers, which are abundantly covered with
Table 1.—Flower preferences of South American oxaeids

<table>
<thead>
<tr>
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<th>Nectar sources†</th>
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*Not including pollen sources also used for nectar.

large orange pollen grains, and the stigma, which is covered with stigmatic fluid, in contact with the abdominal venter and hind legs.

As soon as the bees' hold on the style and stamens is secured, the mouthparts are inserted into the nearest nectary for from a fraction of a second to about one second, presumably dependent on the amount of nectar present. From one or two to all five nectaries are visited and on several occasions six mouthpart insertions are made, the first nectary being overlapped. After each nectary is sampled the bee shifts its hold on the style and stamens, shaking them rather violently, as its body moves around to a position from which the mouthparts can contact the next nectary. This shifting and shaking motion of the bee in rotating its position completely around the inside of the flower would account for the large amounts of loose pollen found throughout much of the body of the bee and occasionally in the bottom of the corolla. In Protoxaea each stop in the rotary movements is made at the juncture between two petals beneath which is a nectary. These are small, elongate (rectangular) dark green spongy-looking masses of tissue situated middorsal at the base on the elongate, narrow, hairy sepals issuing from beneath the area where the petals overlap.

By late morning the movements of females on exposed
### Table 2: Flower preferences of North American oxaeids

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<th>Nectar Sources</th>
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<td><strong>CAPPARACEAE</strong>&lt;br&gt;Koeberlinia spinosa</td>
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<td><strong>SOLANACEAE</strong>&lt;br&gt;Solanum elaeagnifolium&lt;br&gt;Solanum rostratum</td>
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Table 2.—Flower preferences of North American oxaeids—(Continued)

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**SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY**

**TABLE 2.—Flower preferences of North American oxaeids—(Continued)**

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<td>Vernonia texana</td>
</tr>
<tr>
<td></td>
<td>ZYGOPHYLLACEAE</td>
<td>Kallstroemia sp.</td>
<td>Eupatorium serotinum</td>
</tr>
<tr>
<td><em>Mesoxaea arizonica</em></td>
<td>ZYGOPHYLLACEAE</td>
<td><strong>LAMIACEAE</strong></td>
<td><strong>VERBENACEAE</strong></td>
</tr>
<tr>
<td></td>
<td>Kallstroemia grandiflora</td>
<td>Monarda sp.</td>
<td>Cassia sp.</td>
</tr>
<tr>
<td></td>
<td>FABACEAE</td>
<td><strong>LAMIACEAE</strong></td>
<td>Vitex pyramidata</td>
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<td><strong>LAMIACEAE</strong></td>
<td><strong>VERBENACEAE</strong></td>
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<td></td>
<td>ZYGOPHYLLACEAE</td>
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<td></td>
<td>Kallstroemia grandiflora</td>
<td><strong>LAMIACEAE</strong></td>
<td><strong>VERBENACEAE</strong></td>
</tr>
<tr>
<td><em>Mesoxaea clypeata</em></td>
<td>Unknown</td>
<td><strong>FABACEAE</strong></td>
<td>Sesbania macrocarpa</td>
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<td></td>
<td>FABACEAE</td>
<td><strong>FABACEAE</strong></td>
<td>Sesbania macrocarpa</td>
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*Not including pollen sources also used for nectar.

Flowers are very rapid because most of these blossoms have been already visited. Very often the bee then samples only one, two, or three of the nectaries before flying to the next flower. When an obscured, previously unvisited flower is found, either inside the plant or beneath another plant in the shade, females slow their flight and make a more complete visitation.

In southeastern Arizona, the principal pollen competitors of Protoxaea at Cassia, Larrea, and Solanum are large, fast-flying matinal colletids of the genera Caupolicana and Ptiloglossa. However, these bees start gathering pollen from this group of plants at dawn and only partially overlap the activity period of Protoxaea, which on a clear day starts about sunrise and continues for an hour or two after the colletids have completed pollen collecting, although in the later period there may be competition from species of Bombus, Xylocopa, and Centris. The caupolicane colletids do not visit Kallstroemia, the flowers of which do not open until an hour or more after sunrise, and we have not seen them at Desmanthus. On Kallstroemia Protoxaea is the largest pollen collector and dominates the flowers (Plate 1).

Protoxaea gloriosa is a matinal pollen gatherer, and unlike some early morning bees of the families Colletidae, Halictidae, and Anthophoridae, the females do not return to the flowers for pollen in the evening, even from plants such as Larrea tridentata, which make pollen available throughout the day (Hurd and Linsley, 1975).

It is interesting to note that some of the South American caupolicane colletids which occur
within the range of oxaeids presumably also take pollen from some of the same plant genera as those in North America, for example, Caupolicana ruficollis (Friese) and C. bicolor (Friese) from Larrea divaricata. Nectar plants from genera in common include Hoffmannseggia for Caupolicana ruficollis (Friese), C. lugubris (Friese), C. friesei Jörgensen, and C. bicolor, and Baccharis for C. lugubris. Caupolicana is best represented in warm temperate and subtropical regions of North and South America but is poorly represented or absent in the intervening zones (Michener, 1966). The genus is apparently best represented in Chile where oxaeids are absent.

On the other hand, although some Ptiloglossa in South America take pollen from Solanum, according to Schrottky (1908), in Paraguay Pt. matutina (Schrottky) visits Solanum balbisii and S. paniculatum, but not Cassia, which is visited by Oxaea flavescens in the same area.

The known flower preferences of oxaeid bees as interpreted from literature and supplemented with previously unpublished records are summarized in Tables 1 and 2. (For details of unpublished records for North American oxaeids, see the full data from specimens examined in the taxonomic accounts of each species.) In Tables 1 and 2, the plant families are arranged systematically according to the latest Englerian classification as revised by Hans Melchior (1964, Engler’s Syllabus der Pflanzenfamilien, II, 666 pages, Berlin-Nikolassee: Gebriider Borntraeger). The generic arrangement within families is alphabetical except in two cases. In the Fabaceae, the genera are alphabetical within their subfamilies, which are ordered systematically as follows: Mimosoideae, Caesalpinioideae, Faboideae. In the Asteraceae, the genera are alphabetical within their tribes, which are ordered systematically (according to Melchior, 1964) as follows: Vernonioeae, Eupatorieae, Astereae, Inuleae, Heliantheae, Helianoeae, Anthemideae, Senecioneae, Calenduleae, Arctoteae, Cardueae, Mutisieae, and Cichorieae. Inasmuch as the practice of using only regular endings on the names of families is gaining among plant taxonomists, the authors have elected to follow this trend and unlike Melchior, use the following regular names instead of the indicated irregular ones: Asteraceae for Compositae, Brassicaceae for Cruciferae, Fabaceae for Leguminosae, and Lamiaceae for Labiateae.

**Territoriality of Males.**—A behavioral activity which appears to be a biological characteristic of the Oxaeidae is male territoriality. Schrottky (1905) mentions the hovering flight of males of Oxaea in front of flowers in a manner suggestive of tabanids or syrphids. Roberts (1973) has reported that males of Oxaea flavescens Klug were aggressive in the vicinity of flowers. Linsley and Michener (1962) refer to territorial behavior in Protoxaea [P. gloriosa (Fox)] and Mesoxaea [M. nigerrima (Friese)] and fuller discussions are provided by Cazier and Linsley (1963) and Linsley and Cazier (1972). Essentially this behavior consists of guarding plants or groups of plants from all intruders except their own pollen-collecting females. At trees and shrubs the males hover in flight facing the plant at various levels depending upon its size, darting out to chase other insects and returning to the same territory immediately. When guarding annuals or low-growing plants they may poise above them or between them. In any case, periodically they leave the territory to obtain nectar to provide the energy to sustain the activity, usually from the plant or plants they are guarding if they are in bloom (Plate 1).

Cazier and Linsley (1963) speculated that the principal function of territoriality in these bees is to assure the immediate mating of newly emerged females through spacing and coverage of appropriate nectar plants. Because nesting females are ignored by males, they suggested that territorial belligerence toward other insects might reduce competitive pressure on females, although they noted that at least in some situations territorial activity of males is out of phase with pollen-collecting periods of females, especially at plants whose pollen is exploited early in the morning.

**Male “Sleeping” Aggregations.**—Sleeping aggregations of males are well known for Protoxaea gloriosa (see below) but do not appear to have been reported for other oxaeids. Thus it remains to be determined whether or not this is a family characteristic. Similar behavior has been recorded for many genera of colletids (see Rayment, 1935; Linsley and Cazier, 1972) and other bees.

**Nest Sites.**—In so far as known, oxaeids nest in flat or slightly sloping ground. Roberts (1973) found two nests of Oxaea flavescens in Colombia. They were about 10 meters apart in a sparsely grassy pasture a few hundred yards from an oxbow...
lake, each entrance being concealed by a small clump of grass. Bertoni (1911) also found the nest entrances of *Oxaea austera* Gerstäcker hidden at the bases of clumps of grass. On the other hand, *Mesoxaea texana* (Friese) apparently nests in areas of sparse vegetation with the entrances exposed (Cockerell, 1933). *Protoxaea gloriosa*, although sometimes nesting in grassy areas (Linsley and Cazier, 1972), usually also has the entrance exposed.

Robert (1973) found *Oxaea flavescens* nesting in homogeneous red, sandy clay devoid of rocks. According to Birkmann (Cockerell, 1933) the surface soil at a nesting site of *Mesoxaea texana* was sandy and deep grayish but the soil excavated from the burrows (presumably where the cells were located) was of a brick red color. The only known burrow of *Mesoxaea nigerrima* was in flat, hard soil (Linsley and Michener, 1962). *Protoxaea gloriosa* was found nesting in sandy soil with gravelly outcroppings (Linsley and Cazier, 1972).

*Oxaea fuscescens* Sichel is apparently a solitary nester as is *Mesoxaea nigerrima*. Truxal (1962) reported only seven burrows of an unidentified species of *Oxaea* in an area 25 by 30 feet. Burrows of *Protoxaea gloriosa* may be separated by less than a meter but concentrations usually reflect population pressure on limited suitable soil resources and not gregarious tendencies. However, Birkmann, 1932 (Cockerell, 1933), estimated that about 80,000 burrows of *Mesoxaea texana* were contained in an area about 700 feet in length by 230 feet in width.

**NEST ARCHITECTURE.**—The nest architecture of oxaeids is of the kind regarded by Michener and Lange (1957) as the basic primitive type of subterranean bee nest. It is most similar to that of diphaglossine Colletidae (Claude-Joseph, 1926; Janvier, 1932; Roberts, 1971). Typically, the burrows are vertical, more or less straight, apparently less so in *Mesoxaea texana* according to Birkmann (Cockerell, 1933), with horizontal laterals which are filled with soil when completed, each of which terminates in a single vertical cell. Cell provisions in *Mesoxaea nigerrima* were semiliquid and yellowish brown, filling the bottom one-third or one-fourth of the cell (Linsley and Michener, 1962).

The burrows are deep, 58 cm in the single known nest of *Mesoxaea nigerrima*, about 30–65 cm in several burrows of *Protoxaea gloriosa* (Cazier and Linsley, unpublished), and a remarkable 245 cm with laterals 20 to 50 cm long in a nest of *Oxaea flavescens* excavated over a two-day period by Roberts (1973). He speculated that the nest might be perennial:

The wings and mandibles of the female captured leaving the burrow showed very little wear. Thus, I cannot believe she excavated the burrow herself. Although the volume of soil removed from the nest amounts to 0.26 liters in compact form (probably twice that as excavated granules) there was no tumulus at the nest entrance. *Oxaea flavescens* is morphologically adapted for carrying especially small pollen grains. It seems unlikely that the female could have carried away the relatively large soil granules. Yet, it seems equally unlikely that wind and rain could have effectively dispersed so much soil within the short life of the female occupying the nest. Judging by her unbroken wings and mandibles, she was only 10–14 days old. Thus, she was probably the sister (not the mother) of the viable prepupa and pupa associated with the nest.

It would seem that the first, or one of the first, females to emerge at the beginning of the dry season claims her natal nest as her own. By so doing, she needs only to deepen the burrow a little and excavate a lateral burrow. Most of the soil excavated from each subsequent lateral is packed into the previous lateral. The small excess of soil which must be ejected from the nest is soon dispersed by wind and rain. After a few years the nest could easily attain a depth of 2.5 meters. Of course, new nests founded by females forced to leave their pre-empted natal nests should be much shallower. If fluctuations of soil moisture or greater susceptibility to parasitism increases pre-imaginal mortality in shallow nests, then selection should favor the tendency to re-occupy and deepen existing nests. Perhaps such a tendency explains why this nest of *O. flavescens* is the deepest bee nest on record.

**FEMALE AGGRESSIVENESS AT THE NEST SITE.**—

Truxal (1962) reported aggressiveness at a nest site of an unidentified species of *Oxaea* in eastern Peru as follows:

Each individual had apparently established a territory in the immediate vicinity of its burrow and was aggressively protecting this area. Individuals hovered about three feet above the burrow openings, and all flying objects that approached to within three or four feet would immediately be engaged and chased away at a very high rate of speed. They also engaged individuals of their own species in "combat." These encounters never lasted for more than 10 to 15 seconds; then the "owner" returned to its position above the burrow. Occasionally, upon returning to their burrows, the bees entered them and often remained below ground for several minutes. Seven specimens were easily taken because of their aggressive attitude toward the net. All specimens taken proved to be females.

Robert (1973) observed similar aggressive behavior in females of *O. flavescens*. Cockerell (1933)
records an experience of the Rev. G. Birkmann (1932) at a large nesting site of *Mesoxaea texana* where the “bees flew with such energy and speed that they would not try to avoid anyone standing in the way, but struck Mr. Birkmann’s body and hat.” At nest sites of *Protoxaea gloriosa*, Linsley and Cazier (1972) noted that females returning to their burrows with loads of pollen enter quickly, ignoring the presence of an observer, but when returning from midday nectar flights they commonly strike the observer about the face and head and enter the burrow less directly.

Since oxaeids have a reduced stinging apparatus, “bumping” invaders of their nesting area may be their principal means of defense.

**NEST PARASITES.**—Few positive data are available on the parasites of Oxaeidae. Schrottky (1904) reported finding *Thalestria smaragdina* Smith flying to flowers with males of *Oxaea* in Paraguay and Brazil and speculated that this species of *Thalestria* might be parasitic in the nests of *Oxaea* (he also commented on the similarity in coloration of the females). Subsequently, Bertoni (1911) observed *Thalestria smaragdina* flying about the nests of *Oxaea austera* in Paraguay.

A large and apparently undescribed species of *Tripeolus* commonly lays its eggs in cells of *Protoxaea gloriosa* in the San Simon Valley of southeastern Arizona and western New Mexico. Rozén (1966) has characterized the larva of this species and that of a closely related species from the nests of *Ptiloglossa jonesi* Timberlake at Portal, Cochise County, Arizona.

**IMMATURE STAGES.**—Rozén (1964) described the first stage and the post-defecating larva of *Protoxaea gloriosa* from a site one mile north of Rodeo, Hidalgo County, New Mexico, as follows (format slightly modified):

**First stage larva:** Head capsule and mouthparts apparently without setae though sensilla may be present, integument unpigmented except for mandibular apexes. Tentorium complete but very weak; posterior tentorial pits situated below posterior thickening and hypostomal ridge; anterior pits somewhat above epistomal groove; posterior thickening of head capsule well defined, similar in thickness to hypostomal ridge; pleurostomal ridge moderately broad but very weak, scarcely noticeable; epistomal ridge not evident but external groove present; parietal bands apparently absent.

Antennae moderately developed, perhaps a little more pronounced than those of mature larva. Labral tubercles large; labral apex cleft; labrum bearing spicules laterally but not apically nor on epipharyngeal surface. Mandibular corium non-spiculate; each mandible simple at apex, elongate, bearing small, sharp-pointed teeth scattered along upper and lower apical edges. Maxillae and labium greatly fused, reduced, and recessed; maxillary palpi evident but short; labial palpi evident but even shorter than those of maxillae; salivary opening a short transverse slit. Body form elongate, cylindrical, without tubercles but with intrasegmental lines at least anteriorly. Integument non-setose but minutely spiculate. Spiracular atrium not pigmented and not projecting above body wall, without elongate spines though perhaps with very short teeth near primary tracheal opening; peritreme apparently missing; primary tracheal opening not on collar and circular in outline, that is, not transverse as in mature larva; subatrium unpigmented, differing little in appearance from trachea. Abdominal segments 9 and 10 normal, without protuberances or ridges; anus apical.

**Postdefecating larva:** Head integument wrinkled, with scattered sensilla; epipharyngeal surface of labrum and hypopharynx spiculate; entire head including mandibular corium pigmented; parietal bands, all internal ridges, antennal rings and papillae, apex of labrum, apexes of mandibles, salivary gland opening, and palpi more darkly pigmented than other parts; coronal cleavage line and posterior part of labiomaxillary region less pigmented than other parts. Tentorium complete but weak; anterior and posterior arms darkly pigmented; remainder unpigmented; parietal bands, all internal ridges, antennal rings and papillae, apex of labrum, apexes of mandibles, salivary gland opening, and palpi more darkly pigmented than other parts; coronal cleavage line and posterior part of labiomaxillary region less pigmented than other parts. Tentorium complete but weak; anterior and posterior arms darkly pigmented; remainder unpigmented; each posterior tentorial pit lying below juncture of posterior thickening and hypostomal ridge but joined to posterior thickening by spur of former; anterior tentorial pits lying just above epistomal thickening; posterior thickening of head capsule moderately thin and resting slightly anterior to posterior margin of capsule; thickening
ridges, and epistomal ridges of about the same
gradually bending forward immediately above junc-
ture of spur to posterior teritorial pit and joining
hypostomal ridge; hypostomal ridges, pleurostomal
ridges, and epistomal ridges of about the same
thickness as posterior thickening; epistomal ridge
briefly interrupted medially; longitudinal thickening
of head capsule absent; parietal bands well
defined. Vertex nonprotuberant; clypeus somewhat
nearly straight but blunt, due
at least in part to somewhat telescoped abdominal
segments 8, 9, and 10 (the compression results from
the larva’s resting on the tip of its abdomen in a
vertical cell). Mesothorax and metathorax dorsally
fused, reduced, and recessed, so that only notable
features are palpi and salivary gland opening;
maxillary palpi conspicuous, a little longer than
basal diameter, and with some sensilla on small
prominences; labial palpi much smaller than max-
illary palpi; other sensilla on apex of labium on
small prominences; salivary opening a small curved
slit partly enclosing a low prominence. Body form
tapering and curving anteriorly to relatively small
head; posterior part nearly straight but blunt, due
to the compression effects from the larva’s resting on
its abdomen in a vertical cell). Mesothorax and metathorax
laterally divided into cephalic and caudal annules; other
segments not noticeably divided on postdefecating
form; tubercles very faint, transverse, presumably
on anterior part of caudal annules on prede
cating form. Integument rigid, nonspiculate, finely
wrinkled, and yellowish, with intersegmental lines
more darkly pigmented. Spiracles resting on ele-
vated, pigmented sclerites, peritreme flat; atrium
projecting above body wall, atrial wall darkly pig-
mented, beset with numerous hairlike spines, and
without rim; primary tracheal opening collarred and
slitlike, with slit at right angles to long axis of
body; collar with numerous short spines; subatrium
pigmented just below atrium and near attachment
of trachea but with area in between unpigmented;
subatrial wall bearing spines immediately below
atrium. Except for telescoping, abdominal segments
9 and 10 normal, without protuberances, or ridges;
anus a transverse slit located apically.

Roberts (1973) who found the larva of Oxaea
flavescens comments about it as follows:

Roben noted that the larva of Protoxiaeaeaeaeaeaeaeaeaeaeae
flavescens differs from all other bee larvae in possessing: (1) an apically cleft
labrum; (2) a reduced labiomaxillary region; (3) a long
mandible with a long blade-like apex; (4) a slit-like primary
tracheal opening. The larva of Oxaea flavescens possesses
these features and agrees in every detail with the description
of P. gloriosa. Thus, it seems that oxaeid larvae are as
similar morphologically as oxaeid adults.

The pupa of Oxaea flavescens has been de-
scribed and figured by Roberts (1973). Pupae of
other oxaeids are as yet unknown. Roberts’ descrip-
tion and comments follow:

Head: antenna with small tubercle (a) on outer surface
of pedicel. Mesosoma: pronotum with posterior lobes (b)
moderately produced; metanotum with small indistinct,
median tubercle (c). Each coxa and trochanter produced in
large apical spine (d); anterior femur with large basal spine
(e) and base of middle femur slightly produced; each femur
with rounded tubercle (f) anteriorly at apex, moderately
large on anterior femur to very large on posterior femur.
Metasoma: terga II-V each with small, irregular tubercles
(g) in sub-apical row; terminal spine (h) short and rounded
apically.

According to Yager and Rozen (1966), the pupae of the
Andrenidae possess mesoscutal tubercles, as do the pupae of
the Fideliidae (Rozen, 1970). The pupa of Oxaea flavescens
tacks mesoscutal tubercles. It may be distinguished from
pupae of the Colletidae by the presence of distinctive apical
tubercles on metasomal terga II-V, from the pupae of most
Megachilidae by its lack of setae, and from the pupae of the
Halictidae by the lack of tubercles on its wing. These dif-
frences, together with the unique apical tubercles on its
femora, support the decision to accord Oxaea and Protoxaea
familial rank.

Some Behavioral Characteristics of Adult
Protoxaea gloriosa (Fox)

Since the adult behavior of Protoxaea gloriosa is
better known at present than that of any other
Protoxaea, a few aspects are elaborated upon for future comparison with representatives of other genera as data become available. For more details see Linsley and Cazier 1972.

Emergence of Males, Establishment of Territories, and Other Premating Behavior.—At least in southeastern Arizona and western New Mexico, moisture from the first summer rains, which usually appear in the latter part of July or early August, appears to be the key factor stimulating emergence. As in most species of solitary bees, the males emerge for the season several days before the females. They immediately seek nectar, remaining at a single flower for several minutes if the supply is adequate. Favorable nectar sources both for newly emerged individuals and those in established territories are Koeberlinia spinosa, Baccharis glutinosa, and Asclepias subverticillata, as well as most pollen plants utilized by the female, including Kallstroemia grandiflora and Larrea tridentata.

Male territorial behavior has been described by Linsley and Michener 1962, Cazier and Linsley 1963, Linsley and Cazier 1972, and Hurd and Linsley 1975. The observations reported were made mostly in the San Simon Valley near Portal, Arizona, and Rodeo, New Mexico, or in the vicinity of Douglas, Arizona. In the San Simon Valley, the plant usually selected for the establishment of early season territories is Koeberlinia spinosa, in those areas where it is in bloom. This is a favored nectar source for newly emerging females during this period. Subsequently, such shrubs as Baccharis glutinosa and Larrea tridentata are sought out by later emerging females (the latter also an important pollen source for nesting females).

In open areas where females are active, territories are established near one or more low-growing plants, such as Cassia bauhinioideis and Kallstroemia grandiflora (both pollen plants for the female) and Ephedra trifurca, Lycium sp., Gutierrezia microcephala, and Cucurbita foetidissima (which are not pollen sources for the female; at C. foetidissima, territorial males keep away such regular pollen seekers as Peponapis pruinosa).

When guarding their territories, males attack and often tumble to the ground with other male Protoxaea but usually ignore pollen-collecting (mated, nonreceptive) females when guarding a pollen source. However, they fly out and pursue or attack larger insects, including butterflies, and even birds, but when small bees or wasps are abundant about the flowers they are usually not molested.

Male “Sleeping” Aggregations.—Massed nocturnal aggregations of males have been reported by Evans and Linsley 1960 and Cazier and Linsley 1963 and fully described by Linsley and Cazier 1972. The phenomenon is notable since the males which are strongly antisocial during that portion of the day in which they are attempting to establish or are occupying territories become highly social when congregating together for the night.

Male territorial behavior usually reaches a peak near midmorning when most newly emerged, receptive females leave their natal burrows for their first nectar flight. By midafternoon the males begin to gather in large masses on selected individual plants where they spend the night in a cluster (Plates 2, 3). The factors that influence the initial selection of the cluster site are unknown, but they include such diverse situations as the open empty valleys of the dried dehiscent pericarps of Datura quercifolia, the upright stems of such weedy plants as Heterotheca (telegraph-plant), and Amaranthus (pig-weed), the slender, jointed branches of Ephedra (Mormon tea), the horizontal leafy branches of Condalia spathulata (squaw bush), and Acacia constricta (white thorn) as well as deserted bird nests, especially those of the verdin (Auriparus flavipes).

Once the congregating site is selected, it is stained with a yellow excrement and has a distinctly noticeable odor. Linsley and Cazier 1972 reported that of 344 males from one aggregation which were marked with distinctive colors and released at various distances, five returned in the late afternoon from a release site one mile away, four from three miles distant, two from a distance of five miles, and one from ten miles.

Most aggregations contain several hundred males (Linsley and Cazier report one made up of more than 2000 individuals), but in some cases smaller separate clusters occur on the same plant near one another. The numbers are largest when the males first emerge and dwindle from attrition as the season progresses. Temperatures in the cluster fluctuate during the night (Linsley and Cazier report ranges from 20.5° to 25.5°C with air temperatures ranging downward from 23.5° to 18°C). When disturbed the cluster temperatures rise suddenly by 8° to 10°C.
EMERGENCE OF FEMALES, FEEDING AND MATING.—As mentioned above, as the season begins males emerge several days before the females and are established in territories by the time the first females appear. The females leave their natal burrows near midmorning (0830–1000 hrs.) and immediately seek nectar. Since on the initial flight they sip at the flower for several minutes, they are quickly found by males. Mating takes place on the flowers and lasts for several minutes. Linsley and Michener (1962) have described the action as follows:

At 8:47 a.m. on July 26, a mating pair of *P. gloriosa* was found hanging on the *Baccharis* blossoms, with a second (smaller) male on top of the pair and apparently trying to dislodge the first male to the accompaniment of a loud buzzing. The female was taking nectar and was apparently freshly emerged, since the wings were still soft and unfrayed and her pubescence showed no signs of wear. On each of the next two days, mating pairs were observed in the same situation; in each case the female was freshly emerged and in each there was an extra male atop the mating pair. During mating, the male forces the head between the propodeum and first metasomal segment, grasping the base of the latter with the mandibles. In one instance, mating was observed for 5 minutes and 30 seconds from the time the pair was discovered. When disturbed sufficiently, the female flies off with the male hanging on, even though not in sexual contact. In no case was the second male successful in dislodging the first, and in most instances there was a wide discrepancy in size between the two.

Mating has been observed on the flowers of *Koeberlinia spinosa* and *Kallstroemia grandiflora* as well as those of *Baccharis*.

**Systematics**

In the accounts that follow we have presented diagnoses of the family and genera with a revision of the North American species belonging to the genera *Protoxaea* and *Mesoxaea* which are centered in Mexico, but extend into the southwestern United States (Louisiana, Texas, New Mexico, and Arizona) and nearly to Central America (southwestern Chiapas, Mexico). The genus *Notoxaea* is monotypic and is known to occur from the Province of Mendoza, Argentina, into south-central Brazil (Mato Grosso). The species of the genus *Oxaea* are chiefly centered in the Guiano-Brazilian subregion, but one species (*Oxaea fuscescens* Sichel) evidently ranges from northern South Amer-ica well into Central America where it has been recorded from Guatemala.

Most of the members of this family are moderately large, robust bees, often with thick, pale pubescence on the thorax and in some species the metasomal terga are brilliantly metallic, while in others the terga are scarcely or not at all metallic. The wings (Figure 2) are frequently infuscated apically and in some species are entirely dark or nearly so.

**Family OXAEIDAE**


**Head:** Integument without metallic luster; antennal sockets distinctly below middle of eyes; antennae short, elbowed; flagellum much shorter than length of eye, first segment slender, elongated, about as long as, or longer than, scape, remaining segments enlarged broader than long except terminal segments longer than broad; eyes greatly en-
FIGURES 3-8.—Heads of Oxaeidae in frontal view, males: 3, *Protoxaea gloriosa* (Fox); 4, *P. australis* Hurd and Linsley; 5, *Mesoxaea clypeata* Hurd and Linsley; 6, *M. tachyiformis* (Cameron); 7, *Notoxaea ferruginea* (Friese); 8, *Oxaea flavescens* Klug.
larged in males (Figures 3–8); inner orbits of males converging strongly above (Figures 3–8); ocelli located low on face near antennal sockets, arranged in a broad triangle about twice as broad as long; epistomal suture biangularly arched, separated from antennal sockets by less than diameter of sockets; subantennal areas defined by an arched outer suture which is longer than inner suture and meets antennal socket near middle of side, and an inner nearly straight suture which meets antennal socket at lower inner margin; facial foveae absent; face above hind ocelli strongly differentiated (especially in female) from adjacent lateral areas by a vertical sulcus extending dorsally from each hind ocellus and face between sulci densely and confluently punctured to vertex or nearly so; clypeus strongly protuberant, projecting about as far as lower width of eye when seen in profile, lateral margins below torridal pits, more or less feebly concave, true dorsolateral angles situated at anterior torridal pits; lower lateral portions of clypeus strongly bent to rear, forming, as seen from below, an emargination for reception of labrum in repose; malar area not present; rear angle of mandibles behind posterior eye margin; labrum about as long as broad, or longer; mentum and submentum not represented by distinct sclerites; glossa short, slender, several times as long as broad, acutely pointed; labial palpi elbowed, basal segments elongated and broadly flattened, longer than remaining three subcylindrical, subequal segments together; stipites with posterior margins entire, without a row or comb of spines.

Thorax (including propodeum): Integument without metallic luster; preepisternal suture not evident below scrobal suture; scutellum gently rounded or nearly flat, almost horizontal in profile; propodeum declivous, without a well-defined basal area; wings (Figure 2) with pterostigma scarcely evident; marginal cell long and narrow, considerably longer than distance from apex to wing tip, apex bent away from wing margin; three submarginal cells, third largest and longest, first and second subequal in length along posterior margins, second not distinctly narrowed anteriorly; first recurrent vein interstitial with second transverse cubital vein; second recurrent vein received well beyond middle of third submarginal cell; wing surface with only a few large patches of hairs in basal area, distal area strongly papillate; jugal lobe of posterior wing long, more than three-fourths length of vannal lobe; intermediate coxae elongate but appearing short because basal portions are concealed by pleurae at least externally, much shorter than distance from summits to posterior wing bases; pollen-collecting hairs of female (see also abdomen) present on propodeum laterally, coxae, trochanters, femora, tibiae, and basitarsi; middle femora with a subtriangular, densely compacted brush of short orange bristles, basally on ventral surface and with a similar brush of matching bristles also at apex of middle trochanters ventrally in females; posterior femora of female enlarged and flattened to form a plate associated with, and similar to, basitibial plate; basitibial plates located at bases of posterior tibiae; posterior basitarsi shorter than tibiae; inner posterior tibial spurs longest; tarsal claws cleft, inner and outer rami of subequal length in the males, inner rami about half as long as outer ones in females; tarsal arolia present but reduced in males, scarcely evident in females.

Abdomen (metasoma): Tergal integument usually metallic (scarcey if at all in Notoxaea and without metallic luster in Protoxaea micheneri and Oxaea rufa), apical margins impunctate, glabrous and shining on terga I–V in males and I–IV in females; graduli present, laterally strongly bent posteriorly and passing above and behind spiracles; first sternum angularly emarginate at middle; pollen-collecting hairs of females present on ventral surfaces of first and second terga and medially on sterna I–III, although that on III very much smaller; pygidial plate present in female; male genitalia with capsule tapering basally so that gonobase is small, gonostyli incompletely differentiated from gonocoxites or not evident; penis valves not separated from penis (Figures 12, 16, 28, 60).

Discussion.—It is readily evident from the foregoing diagnosis that this family is distinguished from the other families of bees by a number of unique characteristics. Among these are the structure of the antennae, the position of the ocelli of the males in relation to the antennal sockets, the strongly differentiated face above the hind ocelli, the venation, the brushes of orange bristles located basally on the ventral surface of the middle femora, the apical modification of the hind femora of the female, and the structure of the male genitalia. On the other hand there are a number of features which are shared with one or more families of bees,
not the least of which is the presence of a sub-
antennal area defined by two subantennal sutures. However, to emphasize this condition or any other single character believed to be of fundamental importance in determining phylogeny, and hence the classification of the oxaeids, is to ignore the evidence obtained by viewing the constellation of all characters. Thus in retrospect it is quite apparent that in many previous classifications, as we have discussed elsewhere in this study, seemingly undue reliance upon one or only a few anatomical features has resulted in classifications in which the oxaeids have at one time or another been assigned to all the families of the Apoidea except the Halictidae and the Megachilidae.

Our analyses of the characters presented above reveal that apart from those unique to the oxaeids, the majority of characters are shared with the family Colletidae. It would thus appear to us from this indication as well as from the known overall similarities in their biologies that the oxaeids and the colletids were derived from a common ancestry.

It may be of some phylogenetic significance that among all the Apoidea only males of the colletid genus Ctenocolletes (Stenotritinae) and those of the Oxaeidae share an eighth metasomal sternum which has a large, exposed, hairy disc. These groups also share such other features as two sub-
antennal sutures below each antennal socket, elongated first flagellar segments of the antennae which are about as long or longer than the scape, the lack of preepisternal sutures below the scrobal sutures, and the ocelli are situated low on the face, much nearer the antennal sockets than to the posterior margin of the vertex.

The family is composed of four genera, which may be distinguished in the following key.

**Key to the Genera of the Family Oxaeidae**

1. Maxillary palpi present, six-segmented; gonostyli evident, partially differentiated from gonocoxites (Figures 16, 20, 28, 40, 44, etc.) .............................. 2
   Maxillary palpi absent; gonostyli not evident (Figure 12) ........................................ Oxaea
2. Mandibles simple apically (Figures 3-6, 8); metasomal terga brownish-black or black, not partly or largely reddish .................................................. 8
   Mandibles bidentate apically (Figure 7); metasomal terga I-III and sometimes IV at least partly or largely reddish ........................................... Notoxaea
3. Eighth metasomal sternum of male entire, not emarginate medially on apical margin (Figures 19, 23, 27, 31, 35, 39); metasomal terga VI (males) and V (females) without long, conspicuous tufts of white hairs at sides ........................................... Protoxaea
   Eighth metasomal sternum of male deeply emarginate medially on apical margin (Figures 43, 47, 51, 55, 59, 67); metasomal terga VI (males) and V (females) with long, conspicuous tufts of white hairs at sides ........................................... Mesoxaea

**Genus Oxaea Klug**

**Figures 8–12**


**DIAGNOSIS.**—Males usually with pale maculations on clypeus, labrum, mandibles, and basal segments of antennae; mandibles simple apically (Figure 8); maxillary palpi absent; metasomal terga brownish black, black or partly or largely reddish; metasomal terga VI (males) and V (females) with long, conspicuous tufts of white or black hairs at sides; eighth metasomal sternum of male deeply emarginate medially on apical margin (Figure 11); gonobase greatly reduced, ringlike, much wider than long, not tapering basally and gonostylus not evident (Figure 12).

**DISCUSSION.**—The lack of maxillary palpi and the absence of partially differentiated gonostyli in the male (Figure 12) uniquely serve to distinguish the genus Oxaea from the other genera of the Oxaeidae. These features and others clearly indicate that
Oxaea has departed more from the ancestral archetype than have the genera Mesoxaea, Notoxaea, and Protoxaea, all of which have retained the six-segmented maxillary palpi and have the gonostyli of the males partially differentiated from the gonocoxites (Figures 16, 28, 60). It may be significant that while Oxaea is centered in the Guiana-Brazilian subregion (Moure and Seabra, 1962:235) and occurs as far north as Central America (Moure and Urban, 1963:361), the other genera of the family occupy peripheral ranges either well to the north of Oxaea in North America (Mesoxaea and Protoxaea) or chiefly to the south of it in South America (Notoxaea). Since these genera, as is dis-
cussed elsewhere in this study, are more nearly related to one another than they are to *Oxaea*, it may be that the ranges of their precursors were ecologically preempted by the evolutionary events which have led to the formation of *Oxaea*. If so, this could explain why *Mesoxaea*, *Notoxaea*, and *Protoxaea* occupy ranges peripheral to that of the genus *Oxaea*.

In coloration, the integument of several metasomal terga in some species of *Oxaea* is largely reddish and nearly without metallic green reflections (e.g., *O. rufa* Friese), while in other species the terga of the females are largely metallic green and their males have only the marginal depressions of the terga either brilliantly metallic green (e.g., *O. flavescens* Klug) or black and nearly without metallic reflections (e.g., *O. schwarzi* Moure and Seabra). In some species the eyes of the males approximate closely on the vertex (e.g., *O. alvarengai* Moure and Urban), but in other species (e.g., *O. flavescens*) the eyes are widely separated dorsally (Figure 8). Unlike the females of *Mesoxaea*, *Notoxaea*, and *Protoxaea* which have the surfaces of the mesoscutum, scutellum, and metanotum closely punctured and dull, these sclerites in the females of several species of *Oxaea* are broadly impunctate and shining.

As mentioned previously, only one of the eight species now included in the genus *Oxaea* is known to be present in Central America. This species, *O. flavescens* Sichel (1865:342), was originally described from Caracas, Venezuela, and has subsequently been reported from the Guianas (Cockerell, 1917a:135) and Guatemala (Moure and Urban, 1963). It is easily recognized from the original description and the color illustration provided by Sichel (1865:342).

**Notoxaea, new genus**

*Figures* 7, 13-16

*Oxaea.*—Friese, 1898:78-85 [in part; not Klug, 1807:261].


**Type-species.**—*Oxaea ferruginea* Friese, 1898, present designation.

**Diagnosis.**—Males with pale maculations on clypeus and mandibles; mandibles bidentate apically (Figure 7); maxillary palpi present, six-segmented; metasomal terga I–III and sometimes IV at least partly or largely reddish; metasomal terga VI (males) and V (females) with long, conspicuous tufts of white hairs at sides; eighth metasomal sternum of male deeply emarginate medially on apical margin (Figure 15); gonobase greatly reduced, ringlike, much wider than long, not tapering basally and gonostyli evident, partially differentiated from gonocoxites (Figure 16).

**Discussion.**—The correct name for the single included species has presented some problems because although Schrottky (1907:19) placed his earlier described *Oxaea versicolor* Schrottky (1903:45) as a junior synonym of *Oxaea ferruginea* Friese (1898:83), he did so believing that these were the sexes of the species as it occurred in Asuncion, Paraguay (*ferruginea*, the male and *versicolor*, the female). However, this association has been open to some question since *ferruginea* is “... known from Mendoza, Argentina to southern Mato Grosso, Brazil,” and since the type locality of *ferruginea* given by Friese (1898:83) lies well to the northeast of this, then three possibilities exist: (1) the species ranges or occurs farther northward in Brazil than Moure and Seabra (1962:235) indicate; (2) the species described by Friese (1898:83) from the Brazilian State of Piaui (Piauhy) is dif-
ifferent from that which occurs in Argentina, Paraguay, and northward into Mato Grosso, Brazil, and (3) the type locality cited by Friese (1898:83) for *ferruginea* is erroneous.

Our examination of the Friese type specimen of *ferruginea* reveals unequivocally that it represents the same species that Schrottky (1907:17) and subsequent investigators believed it to be. However, the type specimen bears a locality label (hand printed in black ink) which reads: "Tianhy, Brasilia 1889." In addition, there are three other labels, a Friese identification label and two labels which contain hand-printed, black ink arabic numbers: 856/22 and 9, respectively. The identification label
is lowermost on the pin and reads: Oxaea ferruginea $\delta$ (in Friese's handwriting in black ink) followed by det Friese 1897 (machine printed) and below which Friese has written in black ink: "Piauhy-Brasilia." Clearly Friese is responsible for making the decision that "Tianhy, Brasilia" equals "Piauhy-Brasilia." We have been unable to discover the reason which prompted Friese to make this change and likewise we have been unable to locate "Tianhy" in any of the geographic place name sources available to us. It may be of some significance that among the 25 other specimens of oxaeid bees loaned to us for study from the collections of the Hungarian Natural History Museum by Dr. J. Papp, there are three specimens bearing identical Tianhy, Brasilia, 1889 locality labels. These have been identified by Friese as: Oxaea austera Gerstaecker (1 $\delta$) and O. flavescens Klug (2 $\delta$). There is also another specimen of ferruginea ($\delta$) in that collection which has the same locality label as the type specimen (Tianhy, Brasilia), but it lacks a Friese identification label. Presumably this specimen, which is only about 13 mm in length, was not seen by Friese since he cites only a single male, 15 mm in length.

Conclusions.—From the foregoing discussion we conclude that while Schrottky (1907:17) correctly associated the sexes of ferruginea, it is still doubtful whether or not the species occurs in northeast Brazil. It may be that there existed in 1889 a "Tianhy" or equivalent geographic place name in that region, but it also appears equally, if not more probable, that such a place name may have existed in southern Brazil. If so then the type specimen could well have been collected within the currently known range of the species as defined by Moure and Seabra (1962:285).

The single known specimen ($\varphi$) of Oxaea rufa Friese (1899:244) from northeast Brazil (Para) has the metasoma almost entirely reddened and thus bears a somewhat similar appearance to ferruginea. However, our examination of this specimen not only confirms the conclusion of Schrottky (1907:17) that it is a larger and different species, but unlike ferruginea it lacks maxillary palpi and belongs to the genus Oxaea.

The synonymy of Notoxaea ferruginea has been reviewed by Moure (1944:4-5; 1947:226), who assigned the species to the North American genus Protoxaea primarily because the maxillary palpi are six-segmented. Although Notoxaea shares a number of characteristics with the North American genera Mesoxaea and Protoxaea, including the six-segmented maxillary palpi, it is readily separated from these, as well as from the genus Oxaea, by its apically bidentate mandibles.

Names Currently Applied in Notoxaea.—Listed below are the names applied in the genus Notoxaea and, except for argentina which was first assigned to the genus Ptiloglossa, were originally proposed in Oxaea. Only the name ferruginea is currently considered valid since the others have been shown to be junior synonyms.

argentina (Jörgensen, 1909:221), new combination
ferruginea (Friese, 1898:88), new combination
haematura (Cockerell, 1918:222), new combination
versicolor (Schrotky, 1903:45), new combination

Genus Protoxaea Cockerell and Porter

Figures 2-4, 17-40; Map 1; Plates 1, 2

Megacilissa.—Fox, 1893:421 [in part; not Smith, 1854:123].
Oxaea.—Authors [not Klug, 1807:261]—Cockerell, 1896:42.

Type-Species.—Megacilissa gloriosa Fox, monotypic and original designation.

Diagnosis.—Males without pale maculations on clypeus, labrum, mandibles, and antennae; mandibles simple apically (Figures 3, 4); maxillary palpi present, six-segmented; metasomal terga brownish black or black, not partly or largely reddish; metasomal terga VI (males) and V (females) without long, conspicuous tufts of white hairs at sides; eighth metasomal sternum of male entire, not emarginate medially on apical margin (Figures 19, 27, 39); gonobase elongate, not ringlike, much longer than wide, tapering basally and gonostyli evident, partially differentiated from gonocoxites (Figures 20, 28, 40).

Discussion.—Unlike the genus Oxaea which lacks maxillary palpi, the genus Protoxaea, like the genera Mesoxaea and Notoxaea, possesses six-segmented maxillary palpi. Also the males of Protoxaea, like those of Mesoxaea and Notoxaea, have the gonostyli partially differentiated from the gonocoxites while they are not evident in Oxaea (Figure
Thus in these and other characters Protoxaea appears to be more closely related to Mesoxaea and Notoxaea than it is to Oxaea. However, since the mandibles of Notoxaea are uniquely bidentate apically, we conclude that although Protoxaea, Mesoxaea, and Notoxaea were derived from the same ancestry, Protoxaea is more closely related to Mesoxaea. It is noteworthy that while Protoxaea and Mesoxaea occupy partly sympatric ranges, these genera occur in North America, well to the north of both Oxaea and Notoxaea.

As now understood, Protoxaea is composed of three species, two of which (P. australis and P. micheneri) occur in Mexico below the elevation of Mexico City and well to the south of the disjunct from the third (P. gloriosa), which is widely distributed across northern Mexico and adjacent southwestern United States (Map 1).

Key to the Species of the Genus Protoxaea

1. Males .............................................................................................................................................. 2
   Females .............................................................................................................................................. 4
2(1). Sixth metasomal tergum entirely pale pubescent, chiefly yellow or yellowish white, hairs at sides frequently white; discal pubescence of metasomal terga III-V mostly or entirely pale ......................................................... 3
   Sixth metasomal tergum mostly or entirely dark pubescent, reddish to brownish black, occasionally a few hairs at extreme sides white; discal pubescence of metasomal terga III-V mostly or entirely dark .......................... 1. P. australis
3(2). Eyes less strongly convergent above, separated on vertex by more than distance between rims of antennal sockets; middle and hind femora bright reddish yellow apically ............................... 2. P. gloriosa
   Eyes more strongly convergent above, separated on vertex by less than distance between rims of antennal sockets; middle and hind femora black ......................................................... 3. P. micheneri
4(1). Fifth and sixth metasomal terga chiefly pale pubescent, mostly yellow or yellowish white ................................................................................................................................. 5
   Fifth and sixth metasomal terga dark pubescent, reddish brown to brownish black, at most with a few white hairs on extreme sides .................................................. 1. P. australis
5(4). Vertex evenly rounded, not modified as below; pronotal collar emarginate mediadly .......................................................................................................................... 2. P. gloriosa
   Vertex carinate posteriorly, medially emarginate, and as seen from in front bilobate in outline; pronotal collar elevated mediadly .......................................................................... 3. P. micheneri

1. Protoxaea australis, new species

Figures 4, 17-24; Map 1

Protoxaea sp. nr. gloriosa.—Linsley and Michener, 1962:388

Geographic Range (Map 1).—South-central and southwestern Mexico (Guerrero, Morelos, and Puebla).

Male.—Length 15-18 mm. Length of forewing, including tegula, 14-17 mm. Head and body black; metasomal terga faintly metallic blue green in bright light, most evident on impunctate, apical margins; antennae brownish black above, reddish brown on some flagellar segments below; mandibles black, reddened apically; clypeus black, narrowly reddened on medioapical margin; wings dissimilar in coloration, forewings hyaline basally, rather contrastingly infuscated with brown black apically and weakly violaceous in bright light, hind wings nearly hyaline throughout, faintly stained with brownish black infuscation narrowly along costal margin; wing veins dark reddish brown, nearly black apically; tegulae reddish brown to dark mahogany, darkening basally to black; legs dark reddish brown to nearly black basally, tarsi usually somewhat redder; tibial spurs pale reddish brown; claws deep mahogany red, banded medially with black.

Vestiture of head chiefly ochraceous to nearly white on hind margins and face below antennal sockets; pubescence on face above antennal sockets fulvo-ochraceous to fulvous, paling to ochraceous or white on vertex behind; thorax thickly clothed dorsally with fulvous pubescence, paling posteriorly to nearly white on propodeum and to fulvo-ochraceous on lower sides and ventrally; legs chiefly...
pale pubescent, mostly whitish or cinereous basally, darkening on tibiae and tarsi to reddish brown; pubescence of first metasomal tergum consisting of long, erect white plumose hairs, thickest laterally and on ventrally exposed surfaces; metasomal terga II–V without apical bands of pale pubescence, mostly clothed with short, posteriorly directed, brownish black pubescence, longest and thickest at sides, and basal discal surface of tergum II with erect whitish or cinereous pubescence; metasomal tergum VI with pubescence much longer than that on preceding terga, longest at sides and entirely brownish black; metasomal tergum VII with pubescence disposed laterally as posteriorly projected tufts of plumose hairs, similar in size and color to that on tergum VI; metasomal sterna thickly clothed with rather long plumose hairs, usually mostly or entirely white on sterna I–III and reddish brown on succeeding sterna, which in some specimens may display variable amounts of pale pubescence apically and usually laterally at extreme sides.

Eyes moderately converging above, separated on vertex by considerably more than minimum distance between hind ocelli and also by more than minimum distance between rims of antennal sockets, but by much less than distance across hind ocelli; clypeus densely and confluentely punctate,
punctures on sides much smaller than those on median surface; supraclypeal area about as finely and densely punctate as on upper sides of clypeus; frontal carina short, narrowly triangular in outline, about as long as maximum diameter of median ocellus, weakly excavated basally; middle tibiae and basitarsi of equal length; punctation of metasomal terga I and II dense, crowded, about equal size, that on tergum II more crowded, usually separated by less than their diameters, and extending well posteriorly onto marginal depression; punctation on terga III–V of similar size to that on tergum II, but becoming sparser on each tergum and with larger impunctate areas medially, al-
though punctures extend well onto marginal depressions; structure of seventh metasomal tergum (Figures 17, 21), seventh and eighth metasomal sterna (Figures 18, 19, 22, 23), and genitalia (Figures 20, 24) as illustrated.

**Female.**—Length 16–18 mm. Length of forewing, including tegula, 15–16 mm. Head and body black, somewhat paler on metasomal sterna; metasomal terga faintly metallic blue green in bright light, most evident on impunctate, apical margins; antennae brownish black above, somewhat paler below and scape reddened at apex; mandibles black, reddened apically and often medially; clypeus black; wings dissimilar in coloration, forewings hyaline basally, apically lightly infuscated with brownish black, hind wings nearly entirely hyaline, scarcely infuscated apically; wing veins dark reddish brown; tegulae reddish brown, darker basally; legs dark reddish brown, blacker on coxae, and trochanters, redder on tarsi; tibial spurs pale reddish brown, nearly testaceous; claws dark mahogany red, blackish medially.

Vestiture of head moderately long and pale ochraceous or white on clypeus, becoming fulvo-ochraceous about antennal sockets and above posterior ocelli; hind margins of head thickly clothed with long pubescence, mostly white or pale ochraceous, becoming intermixed dorsally near vertex with fulvo-ochraceous hairs; thorax thickly clothed with fulvous pubescence dorsally, paling to ochraceous or white on scutellum, metanotum propodeum and on lower sides and ventrally; legs chiefly white pubescent, but external surfaces of fore and middle tibiae and tarsi reddish brown pubescent; scopal hairs of hind legs entirely white or nearly so; discal surface of first metasomal tergum with a few long, erect, whitish or ochraceous hairs basally, and apically with some similarly colored, but shorter and posteriorly projecting hairs situated laterally and forming a medially incomplete transverse band; similar medially interrupted bands of pale pubescence present on discs of metasomal terga II–V, which at extreme sides consist of longer hairs; otherwise discal surfaces clothed only basally at sides with very short, inconspicuous brownish hairs; scopal hairs of terga I and II white or nearly so; metasomal tergum V apically transversed by a thick fringe of long, posteriorly directed, plumose hairs characteristically reddish brown, but at extreme sides sometimes with a few intermixed white hairs; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long reddish brown hairs; scopal hairs of metasomal sterna I–III white, other surfaces of metasomal sterna II–VI thickly clothed with rather short to long, posteriorly directed, reddish brown hairs; extreme sides of metasomal sterna II–V with long tufts of white plumose hairs projecting posteriorly from under overlapping tergal surfaces.

Eyes scarcely diverging below (48:52); clypeus densely, coarsely, and confluent punctate on sides, punctures on median surface larger and nearly confluent, not separated by their diameters; supra-clypeal area with punctures about as coarse and crowded as on upper surface of clypeus; frontal carina narrowly triangular in outline, deeply excavated, longer than maximum diameter of median ocellus; metasomal tergum I with discal surface basal to marginal depression nearly impunctate medially, but with large punctures laterally, separated by less than their diameters at extreme sides; discal surfaces of metasomal terga II–IV sparsely impunctate medially, more crowded laterally, but mostly separated by their diameters or more; fifth metasomal tergum rather densely punctured throughout, medially punctures separated by about or less than their diameters.

**Types.**—Holotype male and allotype female were collected at Mexcala, Guerrero, Mexico, on 29 June 1951 by P. D. Hurd, Jr., and are deposited in the collections of the California Academy of Sciences, San Francisco. Additional specimens (paratypes) were collected at the type locality on the same date by H. E. Evans (1♀, 1♂) and P. D. Hurd, Jr. (1♀) and are, respectively, on deposit in the collections of the California Insect Survey, Essig Museum of Entomology, University of California, Berkeley, and the Snow Entomological Museum, University of Kansas. Other specimens examined (paratypes) include: 1♀, 3.7 miles north of the Rio Balsas (Highway 95), Guerrero, Mexico, 5 August 1963 (G. W. Byers, and party, KU); 9♀, 2♂, 4 miles southwest of Yautepec (3800 feet), Morelos, Mexico, 2 July 1961, from flowers of an unidentified species of Cassia (C. D. Michener, KU); 1♀, 10 miles west of Cuautla, Morelos, Mexico, 22 July 1962 (H. E. Milliron, CNC); and 2♀, Petalcingo, Puebla, Mexico, 23 July 1962 (H. E. Milliron, CNC).

**Discussion.**—Like P. micheneri, this species ap-
pears to inhabit the upland areas of south-central Mexico below the lower limits of the pine forest. As will be noted in the accompanying illustrations, the paratype male from Petlalcingo, Puebla, Mexico, has a somewhat broader eighth metasomal sternum with a more slender apex (Figure 23) than that exhibited by the holotype male from Mexcala, Guerrero, Mexico (Figure 19). In addition, the pubescence on the seventh metasomal tergum of the Puebla specimen (Figure 21) is noticeably longer than that of the holotype male (Figure 17).

In spite of these differences and some others evident in these structures, as well as the genitalia (Figures 20, 24), we interpret them as individual variations and regard the specimens as conspecific.

To judge by the overall similarities in structural features, *P. australis* is more nearly related to *P. micheneri* than it is to *P. gloriosa*. Doubtless these species were derived from a common ancestry since they share so many characters.
2. Protoxaea gloriosa (Fox)

Figures 2, 3, 25-36; Map 1; Plates 1-3

Megacilissa gloriosa Fox, 1893:421:422 ♀ [New Mexico: Las Cruces].

Oxaea gloriosa.—Cockerell, 1898:70 [New Mexico: Mesilla Valley].—Friese 1896:85; 86, ♀♀ ♂♂ [New Mexico: Las Cruces, Mesilla].


Location of Types.—Protoxaea gloriosa, Academy of Natural Sciences, Philadelphia; P. gloriosa pallida, American Museum of Natural History, New York; P. tristis, Museo Civico di Storia Naturale, “Giacomo Doria,” Genoa, Italy.

Geographic Range (Map 1).—Southwestern United States (Arizona, New Mexico, and Texas) and adjacent northern Mexico (Baja California, Chihuahua, Coahuila, Durango, Nuevo Leon, Sinaloa, Sonora, and Tamaulipas).

Male.—Length 14-18. Length of forewing, including tegula, 13-16 mm. Head and body black, metasomal terga feebly metallic blue green, most evident on impunctate apical margins; antennae dark reddish brown above, redder below on apical flagellar segments; mandibles mahogany red, nearly black apically; clypeus black, narrowly edged with red apically; wings dissimilar in coloration, forewings hyaline basally, heavily infuscated apically with brownish black, which reflect violaceous tints in bright light, hind wing hyaline scarcely infuscated apically; wing veins reddish brown, darker apically; tegulae testaceous; legs black on coxae, trochanters, femora, and much of tibiae; tibiae apically and tarsal segments yellow or reddish yellow; tibial spurs testaceous; claws dark mahogany red, blackened medially.

Vestiture of head chiefly ochraceous, paler and whiter on hind margins, turning to fulvo-ochraceous on face above ocelli and on vertex (older specimens chiefly or entirely whitish or white); thorax thickly clothed dorsally with fulvo-ochraceous to fulvous pubescence (whiter in older specimens), paling to ochraceous or white on thorax behind and to ochraceous on sides and ventrally (whiter in older specimens); legs entirely pale pubescent, mostly ochraceous basally turning to fulvous on tarsi; pubescence of first metasomal tergum consisting of very long, erect, ochraceous to whitish plumose hairs, thickest laterally and on ventrally exposed surfaces; pubescence on second metasomal tergum similar in color to that on first tergum, but shorter, chiefly erect, and pale ochraceous or whitish on basal surface of disc medially, much shorter, mostly decumbent, directed posteriorly and situated laterally, forming a subapical transverse band of ochraceous pubescence; metasomal terga III-V clothed with short, ochraceous to yellowish pubescence (whitish or white in older specimens), chiefly disposed laterally, but forming subapical band, which at sides consists of much longer and frequently whitish hairs; pubescence on metasomal tergum VI much longer than that on preceding terga, chiefly yellow, ochraceous, or yellowish white (white in older specimens), hairs at sides becoming white or nearly so; metasomal tergum VII with pubescence disposed laterally as posteriorly projecting tufts of plumose hairs, similar in size and color to that on tergum VI; metasomal sternum thickly clothed with moderately long ochraceous or yellowish hairs (whitish in older specimens), those situated apically on sternum longer...
and disposed mainly as transverse bands of pubescence.

Eyes moderately converging above, separated on vertex by much more than minimum distance between hind ocelli and also by more than minimum distance between rims of antennal sockets, but less than distance across hind ocelli; clypeus densely and confluently punctured on sides, punctures on median surface larger and coarser, and well separated; supraclypeal area densely, finely, and confluently punctured, punctures much smaller and more crowded than those on adjacent median surface of clypeus; frontal carina short, narrowly triangular in outline, nearly as long as maximum diameter of median ocellus, deeply excavated throughout its length; middle tibiae longer than basitarsi (65:60); punctuation on metasomal terga I–VI dense, crowded, separated by about puncture width or less, extending posteriorly well onto marginal depressions with punctures on tergum I larger than those on succeeding terga; structure of seventh metasomal tergum (Figures 25, 29, 33), seventh and eighth metasomal sterna (Figures 26, 27, 30, 31, 34, 35), and genitalia (Figures 28, 32, 36) as illustrated.

**FEMALE.**—Length 17–22 mm. Length of forewing, including tegula, 15–17 mm. Head and body black; metasomal terga scarcely to feebly metallic blue green with some purplish tints evident in bright light and most evident on impunctate apical margins; antennae dark reddish brown to brownish black, somewhat paler below, and apex of scape narrowly reddened; mandibles chiefly mahogany red to nearly red basally, darkening to black apically; clypeus black, occasionally reddened somewhat apically; wings dissimilar in coloration, forewings hyaline tinged with yellowish on basal third, heavily infuscated with brownish black on apical two-thirds and rather strongly violaceous in bright light, hind wings mainly hyaline except for some slight infuscation apically; wing veins reddish brown to black; tegulae testaceous; legs mostly reddish yellow, but coxae and trochanters black and femora stained or marked in part with black; tibial spurs reddish yellow; claws dark mahogany red, medially marked with black.

Vestiture of head chiefly moderately long and mostly ochraceous on face, sometimes paler about antennal sockets and above ocelli near vertex: hind margins of head thickly clothed with ochraceous pubescence, paling to white on propodeum; legs entirely pale pubescent, chiefly ochraceous, somewhat paler on hind femora; scopal hairs of hind legs mostly ochraceous, usually intermixed with some paler, nearly white hairs; discal surface of first metasomal tergum clothed with long, erect pale (mostly white) plumose hairs; discal surfaces of metasomal terga II–IV before glabrous margins, clothed with very short, erect, ochraceous hairs, thickest and longest at sides, which are replaced on extreme sides and ventrally exposed surfaces of terga I and II by scopae consisting of long, densely plumose, mainly whitish hairs and ventroapically on terga III and IV with long tufts of ochraceous plumose hairs; metasomal tergum V apically traversed by a thick fringe of long, posteriorly directed, plumose hairs, characteristically and uniformly ochraceous or yellowish, but occasionally turning to white on extreme sides; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long, reddish yellow hairs, rarely turning to white at extreme sides; scopal hairs of metasomal sterna I–III ochraceous, other surfaces of metasomal sterna II–VI thickly clothed with rather short to long, posteriorly directed, ochraceous pubescence; extreme sides of metasomal sterna II–V with long tufts of ochraceous to whitish plumose hairs projecting posteriorly from under overlapping tergal surfaces.

Eyes scarcely diverging below (55:57), clypeus closely and finely punctate on sides, punctures on median surface larger and somewhat less crowded; supraclypeal area densely and confluently punctured except at sides and above; frontal carina narrowly triangular in outline, short, longer than diameter of median ocellus, deeply excavated throughout length; discal surfaces before marginal depressions of metasomal terga I–V densely and finely punctured, those on tergum I separated by mostly twice or more their diameters and those on succeeding terga by less or about their diameters.

FIGURES 25–28.—Protoxaea gloriosa (Fox), male (Douglas, Arizona): 25, seventh metasomal tergum (left half ventral); 26, 27, seventh and eighth metasomal sterna (left halves dorsal); 28, genitalia (left half ventral).

FIGURES 29–32.—Protoxaea gloriosa (Fox), male (Las Delicias, Chihuahua, Mexico): 29, seventh metasomal tergum (left half ventral); 30, 31, seventh and eighth metasomal sterna (left halves dorsal); 32, genitalia (left half ventral).
27–55 (H. A. Scullen, GEB). Patagonia angustissima (UA). Pena Blanca Lake, \( \delta \), VIII–17–74, on flowers of *Acacia angustissima* (UA). Penas Blancas Lake, \( \delta \), VIII–17–74, on flowers of *Acacia angustissima*, 0930–0945 MST (T. J. Zavortink, TJ2); 6 \( \delta \), 8 \( \delta \), VIII–18–74, on flowers of *Kallstroemia grandiflora*, 0845–1150 MST (T. J. Zavortink, TJ2); 4 \( \delta \), 3 \( \delta \), VIII–20–74, on flowers of *Kallstroemia grandiflora*, 0850–1145 MST (T. J. Zavortink, TJ2). Pena Blanca Lake, 5.3 mi W, 4700 ft, VII–29–72, on flowers of *Acacia angustissima*, 1115–1215 MST (T. J. Zavortink, TJ2); 4 \( \delta \), VIII–15–75, on flowers of *Cassia leptocarpa*, 0700–0730 MST (E. G. and J. M. Linsley, CIS). Ruby, \( \delta \), VIII–15–61 (J. C. Bequaert, UA); 8 \( \delta \), VIII–16–61 (J. C. Bequaert, UA). Sonora, 7.6 mi E, \( \delta \), VIII–15–55, on flowers of *Croton corymbosus* (P. H. Timberlake, PHT).


Texas: Pecos River, 2 \( \delta \), \( \varphi \) (J. C. Bequaert, MCZ). Bexar County: \( \delta \), VII–18–30 (H. B. Parks, USNM); \( \delta \), Vl–19–50 (H. B. Parks, USNM); \( \delta \), VII–21–50 (H. B. Parks, TAM); \( \delta \), VI–24–50 (H. B. Parks, TAM); \( \delta \), VI–26–50 (H. B. Parks, TAM); \( \delta \), IX–25–30 (H. B. Parks, TAM); \( \delta \), VI–25–41 (H. B. Parks, TAM); \( \delta \), VI–26–50 (H. B. Parks, MCZ, TAM, U Colo); \( \delta \), VII–10–51 (H. B. Parks, TAM); \( \delta \), IX–10–51 (H. B. Parks, TAM); \( \delta \), IX–15–51 (H. B. Parks, TAM); \( \delta \), IX–25–52 (H. B. Parks, TAM); \( \delta \), IX–21–52 (H. B. Parks, TAM); \( \delta \), IX–16–56 (TAM). Ft. Sam Houston, \( \varphi \), VII–19–52 (M. S. Wasbauer, AMNH). San Antonio, \( \varphi \), (USNM). Brewster County: 2 \( \delta \), VII–27–55, on flowers of *Larrea tridentata* (A. H. Alex. TAM). Alpine, \( \delta \), VI–3–42 (E. C. Van Dyke, CAS); \( \delta \), VII–1–42 (E. C. Van Dyke, CAS). Big Bend National Park, \( \delta \), VII–16–50 (R. F. Smith, AMNH). Chisos Mountains, Big Bend National Park, 3 \( \delta \), 2 \( \varphi \), on flowers of *Aloysia lycoidea* (J. C. Bequaert, MCZ). Cov. Springs (6 mi W) Big Bend National Park, \( \delta \), VII–16–50 (R. F. Smith, AMNH). Lajitas, 5 mi W,
Figures 33–36.—Protoxaea gloriosa (Fox), male (8 mi S Canutillo, Durango, Mexico): 33, seventh metasomal tergum (left half ventral); 34, 35, seventh and eighth metasomal sternae (left halves dorsal); 36, genitalia (left half ventral).

DISCUSSION.—Of the three species of the genus Protooxaea as now understood, P. gloriosa is the most widely distributed (Map 1). It occurs disjunctly well to the north of its congeners and is the only species of the family Oxaeidae known to inhabit the Mexican Plateau. However, in the northeastern part of its range (Texas and Nuevo Leon, Mexico) and also in a portion of its northwestern range (Arizona, Sonora, and Sinaloa, Mexico) it has been found at a number of localities with several species of the genus Mesoxaea (viz., M. texana, M. arizonica, and M. rufescens). It has also been collected on one occasion in Baja California (Canipole) somewhat to the north of the Cape Region where M. vagans is evidently endemic.

Protooxaea gloriosa was first described by Fox (1894:421–422) from Las Cruces, New Mexico, from a single female specimen. In the following year, Gribovo (1894:278–280) described the same species as Oxaea tristis, n. sp., on the basis of two males collected in Durango, Mexico. Apart from the independent views of these authors whose aesthetic impressions differed on the appearance of this species, our initial studies revealed that only one species of the family Oxaeidae known is found on the Mexican Plateau, namely P. gloriosa. With this in mind we reexamined the original descriptions provided by Fox and Gribovo and concluded that these authors had characterized the same species even though the names they had used suggested otherwise (gloriosa versus tristis). To confirm the suspected synonymy, a male specimen of P. gloriosa from Durango (8 miles south of Canutillo) was compared for us with the type of the Gribodo spe-
cies by Dott. Delfa Guiglia who communicated that the last visible metasomal sternum (VIII) is, as we suspected, not deeply emarginate (cf. Figures 27, 31, and 35 with the same structure in the genus *Mesoxaea*, e.g., Figures 43, 47, 51, etc.). Accordingly, we have placed *Oxaea tristis* Gribodo as a synonym of *P. gloriosa*. A reexamination of the specimens recorded by Cockerell (1906:314; 1934b:153) as *tristis* from Arizona (Douglas and San Bernardino Ranch) reveals that these represent *Mesoxaea rufescens*, which is described as a new species elsewhere in this study.

There is a great deal of individual variation in the size of the body as well as in the coloration of the vestiture of this species. Almost certainly much of the variation in body size is directly attributable to the amount of food available to the larva during development. Presumably small-sized adults result from larvae that have fed upon less than the average amounts of pollen and nectar stores, although doubtless other factors are involved and should be investigated experimentally. Older adult specimens (e.g., wings markedly frayed, mandibles of females worn apically) tend to possess paler and sometimes largely whitish pubescence. This suggests that certain nesting colonies, such as those observed by H. B. Parks in Bexar County, Texas (Cockerell 1934b:153), likely differ in their relative ages. Perhaps this sort of variation prompted Cockerell (1934b:153) to characterize *P. gloriosa pallida* as a subspecies. As he points out the observed differences among nesting colonies are interesting and deserve further study. However, since we have been unable to detect geographic, size or colorational differences within the species, we have relegated *P. gloriosa pallida* to synonymy.

There is, as would be expected, a certain degree of individual variation in the structure of the male genitalia as well as in the associated metasomal terga and sterna. To indicate the extent and nature of this variation, we have selected and illustrated these structures in males from Douglas, Arizona (Figures 25–28), Las Delicias, Chihuahua, Mexico (Figures 29–32), and Canutillo, Durango, Mexico (Figures 33–36).

*Protoxaea gloriosa* is the most well-known species of the family and much of our current knowledge about behavior and comparative biology of these bees is based upon studies of this species.

### 3. *Protoxaea micheneri*, new species

*Protoxaea* sp.—Linsley and Michener, 1962:388.

**Male.**—Length 17 mm. Length of forewing, including tegula, 15 mm. Head and body black; metasomal terga without metallic luster; antennae dark reddish brown above, somewhat paler on apical flagellar segments below; mandibles black, stained above apically and near middle with dark mahogany red; clypeus black; wings similar in coloration, hyaline basally, lightly infuscated with brownish black apically, more noticeably so on forewings; wing veins chiefly dark reddish brown, somewhat darker apically and along costal margin; tegulae testaceous; legs chiefly brownish black, apical tarsal segments reddish brown; tibial spurs pale reddish brown; claws deep mahogany red, banded medially with black.

Vestiture of head chiefly ochraceous, paler, and whiter on hind margins, turning to fulvo-ochraceous on face above ocelli and on vertex; thorax thickly clothed dorsally with mostly fulvo-ochraceous pubescence, paling to nearly white on thorax behind and to ochraceous on lower sides and ventrally; legs entirely pale pubescent, chiefly fulvo-ochraceous, paling to nearly white especially on hind trochanters and coxae; pubescence of first metasomal tergum consisting of long, erect white plumose hairs, thickest laterally and on ventrally exposed surfaces; metasomal terga II-V clothed (except on tergum II with long, erect whitish hairs medially at base) with golden, posteriorly directed, simple hairs, shortest basally, much longer and denser over marginal depressions imparting the appearance of apical bands, which on ventrally exposed sides pale to white; pubescence on metasomal tergum VI much longer than that on preceding terga, mostly pale yellow, turning to white on sides; metasomal tergum VII with pubescence disposed laterally as posteriorly projecting tufts of plumose hairs, similar in size and color to that on tergum VI; metasomal sterna thickly clothed with rather long, white plumose hairs.

Eyes rather strongly converging above, separated on vertex by more than minimum distance between hind ocelli, but by much less than minimum distance between rims of antennal sockets; clypeus densely and conflually punctate, punctures on...
sides much smaller than those on median surface; supraclypeal area about as finely and densely punctate as on upper sides of clypeus; frontal carina short, scarcely evident, about as long as maximum diameter of median ocellus, scarcely excavated basally; middle tibiae shorter than basitarsi; punctation of metasomal terga I and II extending well posteriorly onto marginal depressions, rather dense, and fine laterally, larger and sparser medially, and separated there by much more than their diameters; punctation of terga III–V similar in size to that on tergum II but much sparser and with some impunctate areas medially, although punctures extend well onto marginal depressions; structure of seventh metasomal tergum (Figure 37), seventh and eighth metasomal sterna (Figures 38, 39), and genitalia (Figure 40) as illustrated.

FEMALE.—Length 16–19 mm. Length of forewing, including tegula, 13–14 mm. Head and body black, metasomal terga scarcely with metallic blue green reflections in bright light, observable only in certain positions on impunctate areas; antennae dark brownish black above, somewhat paler below, and scape reddened at apex; mandibles black, reddened somewhat above and apically; clypeus black; wings dissimilar in coloration, forewings hyaline
basally, apically lightly infuscated with brownish black, hind wings nearly entirely hyaline, scarcely infuscated apically; wing veins mostly reddish brown, darker on costal and outer veins; tegulae testaceous; legs dark reddish brown, blacker on coxae, trochanters, and femora; tibial spurs pale reddish brown; claws dark mahogany red, irregularly mottled with black.

Vestiture of head moderately long and ochraceous or white on clypeus, becoming fulvo-ochraceous about antennal sockets and above posterior ocelli; hind margins of head thickly clothed with long pubescence, mostly pale ochraceous to white, becoming intermixed dorsally near vertex with fulvo-ochraceous hairs; thorax thickly clothed with bright fulvous, pubescence dorsally, becoming ochraceous or whitish posteriorly on propodeum and on lower sides and ventrally; legs chiefly white pubescent, but external surfaces of fore and middle tibiae ochraceous to fulvo-ochraceous pubescent; scopal hairs of hind legs entirely white pubescent or nearly so; discal surface of first metasomal tergum with a few long, erect whitish or ochraceous hairs dorsally, otherwise nearly devoid of pubescence; discal surfaces of metasomal terga II–IV before glabrous margins, clothed with very short, mostly decumbent, posteriorly directed whitish hairs mostly or entirely situated laterally, which at extreme sides and on ventrally exposed surfaces are replaced on terga I and II by scopae consisting of long, densely plumose, mainly whitish hairs and ventroapically on terga III and IV with long tufts of chiefly whitish plumose hairs; metasomal tergum V apically traversed by a thick fringe of long, posteriorly directed, plumose hairs characteristically white at sides and ochraceous or yellowish on medial tergal surface; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long, yellowish hairs, which at sides are replaced by small tufts of whitish pubescence; scopal hairs of metasomal sternum I–III white, other surfaces of metasomal sternum II–VI thickly clothed with rather short to long, posteriorly directed, whitish or yellowish hairs; extreme sides of metasomal sternum II-V with long tufts of white plumose hairs projecting posteriorly from under overlapping tergal surfaces.

Eyes scarcely diverging below (43:45); clypeus densely, coarsely, and confluentely punctate on sides, punctures on median surface larger and separated by about their diameters; supraclypeal area with punctures smaller and more crowded than those on adjacent median surface of clypeus; frontal carina narrowly triangular in outline, deeply excavated, longer than maximum diameter of median ocellus; vertex carinate posteriorly, medially emarginate, and as seen from in front bilobate in outline; pronotal collar tuberculately elevated medially; discal surface basal to marginal depression of metasomal tergum I nearly impunctate except for a few well-separated punctures basally and at extreme sides; discal surface of metasomal tergum II medially nearly impunctate, with only a few widely scattered punctures, which laterally become denser and crowded; discal surfaces of terga III and IV with punctation similar to that on tergum II, but impunctate medial area much reduced; fifth metasomal tergum densely and confluentely punctured throughout.

**Geographic Range (Map 1).**—South-central Mexico (Morelos and Puebla).

**Types.**—Holotype male, allotype female, and 3 paratypes (3♀) were collected at 3 miles northwest of Tequesquitengo, Morelos, on 16 August 1962, from the flowers of an unidentified species of *Kallstroemia* (Zygophyllaceae) by Radclyffe B. Roberts and Norman B. Marston. These specimens are the property of the University of Kansas and are deposited in the Snow Entomological Museum. One additional paratype (♀) was collected at 15 miles southeast of Acatlan, Puebla, Mexico, on 10 July 1952, by E. E. Gilbert and C. Don MacNeill and is located in the collection of the California Insect Survey, Essig Museum of Entomology, University of California, Berkeley.

**Discussion.**—Protoxaea micheneri, named in honor of Dr. C. D. Michener for his outstanding contributions to the classification of bees, is one of the most distinctive species not only of this genus, but also of the family Oxaeidae. The peculiarly carinate and medially emarginate vertex of the female is unique among the oxaeids and one can only speculate on the possible adaptive significance of this unusually modified head. It seems unlikely that it represents an adaptive response stemming from its intrarfloral relationships and equally unlikely that it is specialized for some unusual nesting requirements. *Protoxaea micheneri* is more closely related to *P. gloria* than it is to *P. australis*, but differs from both in many characteristics.
Mesoxaea, new genus
FIGURES 5, 6, 41-68; MAPS 2, 3
Oxaea.—Authors [in part; not Klug, 1807:26].
Protoxaea.—Authors [in part; not Cockerell and Porter, 1899:
410].

Type-Species.—Oxaea nigerrima Friese, present designation.

Diagnosis.—Males without pale maculations on clypeus, labrum, mandibles, or antennae; mandibles simple apically (Figures 5, 6); maxillary palpi present, six-segmented; metasomal terga brownish black or black, not partly or largely reddish; meta-

somal terga VI (males) and V (females) with long, conspicuous tufts of white hairs at sides; eighth metasomal sternum of male deeply emarginate medially on apical margin (Figures 43, 47, 51, 55, 59, 67); gonobase greatly reduced, ringlike, much wider than long, not tapering basally and gonostyli evident, partially differentiated from gonostytes (Figures 44, 48, 52, 56, 60, 64, 68).

Discussion.—As presently understood the genus Mesoxaea is composed of seven species which occupy much of the Mexican mainland to the northeast, south, and west of the Mexican Plateau. Although none of the species is known to inhabit

MAP 2.—Known occurrence of Mesoxaea vagans (Fox), *M. rufescens* Hurd and Linsley, *M. tachytiformis* (Cameron), and *M. texana* (Friese).
the Mexican Plateau north of the Valley of Mexico (Maps 2, 3), it is possible that one or more may eventually be found in some of the deep barrancas that originate in the Plateau and drain into the Pacific. Two of the species occupy isolated ranges with *M. vagans* apparently restricted to the Cape Region of Baja California (Map 2) and *M. texana* confined to western Louisiana, southern Texas, and adjacent northeastern Mexico (Map 3). The other species of the genus are centered primarily in southwestern and western Mexico with two of the species, *M. arizonica* and *M. rufescens*, ranging northward along the west coast of Mexico into extreme southern Arizona (Maps 2, 3). *Mesoxaea tachytiformis* is known from the Valley of Mexico and westward from several localities in Morelos, Guerrero and Colima (Map 2). *Mesoxaea clypeata* thus far has been collected only at a few localities in the State of Nayarit, Mexico (Map 3), and *Mesoxaea nigerrima* occupies the southernmost range of the genus from Veracruz and Chiapas northwestwardly to Colima and Jalisco (Map 3). No species of the genus has been found in the Gulf Coast region of Mexico between Vera Cruz and Nuevo Leon. Almost surely one or more species of *Mesoxaea* occur in this area and we interpret the apparent absence of the genus to the lack of collecting.

*O arizonica* • *clypeata* • *nigerrima*

**MAP 3.**—Known occurrence of *Mesoxaea arizonica* (Cockerell), *M. clypeata* Hurd and Linsley, and *M. nigerrima* (Friese).
Key to the Species of the Genus Mesoxaea

1. Males .......................................................................................................................... 2
   Females .......................................................................................................................... 8

2(1). Metasomal terga II–V black pubescent apically, without transverse bands of white
      pubescence; eyes moderately to strongly convergent above, separated on vertex by
      less than distance between rims of antennal sockets ................................................. 3
   Metasomal terga II–V pale pubescent apically, provided with transverse bands of white
      pubescence; eyes less strongly convergent above, separated on vertex by more than
      distance between rims of antennal sockets ............................................................... 1. *M. tachytiformis*

3(2). Clypeus nearly punctate throughout ........................................................................... 4
   Clypeus, except on sides, nearly impunctate, at most with a few widely scattered
      punctures medially ......................................................................................... *M. clypeata*

4(3). Forewings heavily infuscated with brownish black, at most with cells R and first Cu
      hyaline or nearly so ......................................................................................... 5
   Forewings hyaline or nearly so on basal half or more, only apical third or so infuscated
      with brownish black ....................................................................................... *M. rdgerritna*

5(4). Forewings heavily and nearly uniformly brownish black, somewhat paler near base,
      but not hyaline or nearly so; eyes moderately convergent above, separated on vertex
      by about or more than distance between hind ocelli ............................................. 5. *M. nigerrima*
   Forewings heavily infuscated with brownish black, but hyaline in cells R and first Cu;
      eyes more strongly convergent above, separated on vertex by much less than distance
      between hind ocelli ..................................................................................... 6. *M. arixonka*

6(4). Face above antennal sockets to hind margin of head at least in part and often chiefly
      pale pubescent; hind margins of head mostly pale pubescent ..................................... 7
   Face above antennal sockets to hind margin of head entirely dark, pubescent; hind
      margins of head, except pale pubescence on cheeks below, dark reddish-brown to
      nearly black pubescent .................................................................................... 4. *M. texana*

7(6). Eyes strongly convergent above, separated on vertex by less than distance between
      hind ocelli .............................................................................................................. 3. *M. vagans*
   Eyes less strongly convergent above, separated on vertex by at least and usually much
      more than distance between hind ocelli .................................................................. 2. *M. rufescens*

8(1). Dorsum of thorax pale pubescent, chiefly ochraceous, fulvo-ochraceous or fulvous, often
      paler posteriorly ................................................................................................. 9
   Thorax wholly dark pubescent, dark brown to brownish black pubescent ................. 12

9(8). Second metasomal tergum punctate across much of discal surface before marginal
      depression; clypeus flat or somewhat depressed on median surface, not furrowed
      mediolongitudinally ............................................................................................. 10
   Second metasomal tergum impunctate except at extreme sides; clypeus conspicuously
      furrowed mediolongitudinally ........................................................................... 1. *M. tachytiformis*

10(9). Hind margins of head and thorax below chiefly or entirely pale pubescent; second
      metasomal tergum basal to marginal depression not densely punctate, with large
      impunctate areas extending across discal surface .............................................. 11
   Hind margins of head and thorax below chiefly or entirely dark brown or brownish
      black pubescent; second metasomal tergum basal to marginal depression densely
      punctate, without large impunctate areas extending across discal surface .......... 4. *M. texana*

11(10). Punctures on second metasomal tergum just before marginal depression well scattered
       and much of surface impunctate ........................................................................... 2. *M. rufescens*
   Punctures on second metasomal tergum just before marginal depression more densely
   punctate, surface punctured more or less continuously across disc ....................... 3. *M. vagans*

12(8). Clypeus nearly punctate throughout ....................................................................... 13
   Clypeus, except on sides, nearly impunctate, at most with a few widely scattered
   punctures medially ............................................................................................... *M. clypeata*

13(12). Scopal hairs of hind femora chiefly or entirely white .............................................. 5. *M. nigerrima*
   Scopal hairs of hind femora brownish black ............................................................. 6. *M. arixonka*
Mesoxaea is more closely related to Protoxaea and Notoxaea than it is to Oxaea as indicated by a number of structural features including the presence of six-segmented maxillary palpi and the partly differentiated gonostyli of the males. Since among other features, the mandibles of Notoxaea are bidentate apically, it would appear that because of the simple mandibles Mesoxaea is more nearly related to Protoxaea, although it may well have been derived from the same ancestry that also led to the formation of Notoxaea. Curiously these three genera occupy allopatric ranges to the south (Notoxaea) and north (Mesoxaea, Protoxaea) of the genus Oxaea.

It should be noted that while the eyes in the males of Mesoxaea converge above and sometimes markedly so, there is individual variation in the expression of this character so that some caution must be exercised when using the degree of convergence for identification purposes. Thus, for example, individual variation in the minimum upper interorbital distance ranges in 42 specimens of M. vagans from 7 to 13 units with the mode at 8, while in 53 specimens of M. arizonica this distance ranges from 5 to 10 units with the mode at 7.

1. Mesoxaea tachyiformis (Cameron), new combination

FIGURES 6, 41-44, MAP 2


GEOGRAPHIC RANGE (Map 2).—South-central and southwestern Mexico (Colima, Distrito Federal, Guerrero, and Morelos).

MALE.—Length 20-22 mm. Length of forewing, including tegula, 16-18 mm. Head and body black; metasomal terga faintly metallic blue green with some purplish reflections in bright light, most evident on impunctate apical marginal depressions; antennae dark brownish black above, reddened on some flagellar segments below; mandibles deep mahogany red with some black usually at base and subapically; clypeus black or noticeably reddened on medial surface; wings similar in coloration, hyaline basally, infuscated with brownish black apically, mostly beyond closed cells; wing veins reddish brown, somewhat darker apically; tegulae testaceous externally, darkening to brownish black basally; legs chiefly dark reddish brown or brownish black, tarsi not appreciably darker than tibiae; tibial spurs reddish brown; claws deep mahogany red, usually marked irregularly with black.

Vestiture of head chiefly pale ochraceous, paler and whiter on face below antennal sockets and on hind margins of head; pubescence on face above antennal sockets fulvo-ochraceous, darkening to brownish black on upper part of face and vertex; thorax thickly clothed with mostly ochraceous to fulvo-ochraceous pubescence, paling to nearly white on thorax behind, at sides, and below; legs pale pubescent, chiefly ochraceous to white basally, turning to bright fulvous on exterior surfaces of tibiae and tarsi; pubescence of first metasomal tergum consisting of long, erect ochraceous to whitish plumose hairs, thickest at sides and on ventrally exposed surfaces; metasomal terga II-V with apical bands of long, white plumose hairs, which extend onto ventroapical margins, otherwise clothed with short, posteriorly directed, brownish black pubescence except on basal discal area of tergum II, which is densely clothed with erect, moderately long white pubescence; metasomal tergum VI with numerous long, posteriorly directed, white plumose hairs arising just before impunctate apical margin, which are longest and somewhat tuftlike laterally and usually are intermixed on ventral margins with posteriorly projecting tufts of plumose hairs, which are densest in the middle region and extend to the middle of the tergum; metasomal tergum VII with brownish black pubescence becoming white at extreme sides, disposed posteriorly on median metasomal tergum surface with brownish black hairs; metasomal tergum VII with brownish black pubescence becoming white at extreme sides, disposed laterally as posteriorly projecting tufts of plumose hairs, which are short and somewhat tuftlike laterally and usually are intermixed on the apical margins of other tergum regions; metasomal tergum VII with brownish black pubescence becoming white at extreme sides, disposed laterally as posteriorly projecting tufts of plumose hairs, which are short and somewhat tuftlike laterally and usually are intermixed on the apical margins of other tergum regions;

Eyes moderately convergent above, separated on vertex by considerably more than minimum distance between hind ocelli and also by more than minimum distance between rims of antennal sockets, but by much less than distance across hind ocelli: clypeus depressed mediolongitudinally.
coarsely and nearly confluent punctures on sides and above, punctures becoming much less crowded medially and nearly impunctate on somewhat smoothed and reddened apical margin; supraclypeal area about as coarsely and densely punctate as on upper sides of clypeus; frontal carina triangular in outline, very short, much less than diameter of median ocellus, deeply excavated basally; middle tibiae and basitarsi of equal length; punctation on discs of metasomal terga I and II extending well posteriorly onto apical depressions, dense, rather fine with punctures separated by mostly less than their diameters, on terga III and IV similarly extending well onto apical depressions, punctures somewhat larger and less crowded, especially medially, and with some impunctate or sparsely punctate areas extending across terga on and basal to raised submarginal areas; fifth metasomal tergum
with discal punctures similar in size and disposition, but larger and less densely crowded medially; structure of seventh metasomal tergum (Figure 41), seventh and eighth metasomal sterna (Figures 42, 43), and genitalia (Figure 44) as illustrated.

**Female.**—Length 20–22 mm. Length of forewing, including tegula, 16–18 mm. Head and body black, reddened on metasomal terga and sterna; metasomal terga feebly metallic blue green with some purplish tints in bright light and most noticeable on impunctate surfaces; antennae dark brownish black, reddened below and at apex of scape and apex of pedicel; mandibles deep mahogany red, black subapically; clypeus black, somewhat reddened apically; wings dissimilar in coloration, forewings rather uniformly infuscated throughout and feebly violaceous in bright light, hind wings mainly hyaline except for some blackish infuscation apically and posteriorly; wing veins dark reddish brown to black; tegulae testaceous, somewhat darkened basally; legs dark reddish brown dorsally, extensively reddened below; tibial spurs nearly testaceous, apically darker; claws dark mahogany red basally, black apically.

Vestiture of head chiefly moderately long and ochraceous or white on face from clypeus nearly to vertex where it becomes brownish black; hind margins of head thickly clothed with long pubescence, mostly pale ochraceous to white, becoming brownish black on top of head; thorax thickly clothed with bright fulvous pubescence dorsally, becoming ochraceous or whitish posteriorly on metanotum, propodeum, and on lower sides and ventrally; legs chiefly white pubescent basally, darker pubescent, usually reddish brown on external surfaces and on tarsi; scopal hairs of hind legs entirely pale, mostly white or nearly so; discal surfaces of metasomal terga I–IV devoid of pubescence except for very short, posteriorly directed brownish black hairs situated laterally, which on terga I and II at extreme sides and on ventrally exposed surfaces are replaced by scopae consisting of long, densely pubescent hairs, mainly whitish hairs and ventroapically on terga III and IV with long tufts of chiefly whitish pubescent hairs: metasomal tergum V apically traversed by a thick fringe of long, posteriorly directed, pubescent hairs characteristically white at sides and brownish black on median tergal surface; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long, brownish black hairs, which at extreme sides are replaced by small tufts of white pubescence; scopal hairs of metasomal sterna I–II white, other surfaces of metasomal sterna II–V (except at extreme sides) and VI thickly clothed with rather short to moderately long, posteriorly directed, reddish brown to brownish black hairs; extreme sides of metasomal sterna II–V with long tufts of white plumose hairs projecting from under overlapping tergal surfaces.

Eyes weakly diverging below (61:66); clypeus mediolongitudinally depressed, closely, coarsely, and rugosely punctate, except narrow impunctate mediolateral apical corners and roughly formed apical margin, supraclypeal area about as coarsely and rugosely punctured as adjacent clypeal areas; frontal carina narrowly triangular in outline, deeply excavated, slightly longer than maximum diameter of median ocellus; discal surfaces basal to marginal depressions of metasomal terga I–IV impunctate except for a few large punctures at sides; fifth metasomal tergum densely and confluently punctured.

**Specimens Examined.**—Mexico. Colima: Colima, 1 ♂, X (T. Conradt, USNM).
Distrito Federal: Mexico, 1 ♂ (J. R. Inda, USNM).
Morelos: Amacuzac, 6 mi S, 6, X-8-63 (A. E. and M. M. Michelbacher, CIS).
Guerrero: Venta de Zopilote, 2800 ft, 1 ♂, X (H. H. Smith, USNM).

**Discussion.**—Although this species is known only from a few specimens, we have no hesitancy in associating the sexes which were described as different species. The male, which was named first by Cameron (1901), is indeed reminiscent of a large wasp of the genus *Tachytes*, but as Cockerell (1920:177) has pointed out the type locality given by Cameron (Santa Fe Mountains, New Mexico) is erroneous. The holotype was examined for us by Dr. Karl V. Krombein, who reports that there are three labels affixed to the pin—a handwritten label: "(17a547) Oxaea tachytiformis Cam. type New Mexico," a small machine-printed label: "Cam. Coll. 1902–105," and a third label: "B. M. TYPE HYM. (machine printed), 17.2.547 (handwritten)."

Dr. G. Knnerer subsequently looked further into this matter for us and writes:

The records for this number (Cam. Coll. 1902–105) reveal that the insects in this shipment came from "diverse localities." Then I had a look at the original description of *Oxaea tachytiformis* and checked the other types of new species.
In a report on the bees from San Miguel County, New Mexico, Cockerell (1904:8,9) writes:

It seems advisable here to make some statement regarding the species of Oxaea, Nomia, &c., which Mr. Cameron has described (Trans. Am. Ent. Soc.), purporting to come from the region about Santa Fé, New Mexico. The character of the species is Mexican, and I am quite confident that the locality assigned is entirely wrong. I wrote Mr. Cameron about it, and he kindly informed me that the material was collected years ago by a person who was known to have visited the Santa Fé region, but who might very well have obtained the insects elsewhere. The collection included some species of Bombus which might have come from near Santa Fé.

The female of M. tachytiformis was described by Cockerell (1920:178) as a new species (Protoxaea implexata) from the Federal District of Mexico. The collections of the National Museum of Natural History, Smithsonian Institution, contain both sexes from this locality. Consequently, there is scarcely any doubt that these specimens represent the sexes of the same species because this is the only Mesoxaea known to occur in the Valley of Mexico.

Mesoxaea tachytiformis is structurally a uniquely distinctive species as is evident from the key to species. To judge from the structure of male genitalia (Figure 44) it occupies an annexant position between those species represented by M. arizonica, M. clypeata, M. nigerrima, and M. texana on the one hand and by M. rufescens and M. vagans on the other. Conceivably M. tachytiformis was derived from the same ancestry that led to the formation of these two groups of species and is the sole representative of its group.
without apical bands of pale pubescence, mostly clothed with short, posteriorly directed, brownish black pubescence, longest and thickest at sides; tergum II tufted with white pubescence on ventrally exposed sides and with shorter and less conspicuous, erect white hairs on discal surface medially at base; metasomal terga III and IV tufted with long, whitish pubescence on extreme ventrally exposed sides; metasomal tergum V entirely brownish black or black pubescent, shortest on punctate surface basally, much longer and forming a transverse band of simple hairs arising just before impunctate apical margin, projecting posteriorly and terminating in thick tufts of plumose hairs laterally; metasomal tergum VI with numerous long, posteriorly directed, white plumose hairs arising just before impunctate apical margin, longest and somewhat tuftlike laterally, usually intermixed on median tergal surface with brownish black or black hairs; metasomal tergum VII with pubescence chiefly white and disposed laterally as posteriorly projected tufts of plumose hairs; metasomal sterna thickly clothed with rather long, plumose hairs, usually white or cinereous on sterna I—III, and on terga IV—VI brownish pubescent basally, but apical hairs white or nearly so.

Eyes moderately convergent above, separated on vertex by about or more than minimum distance between hind ocelli, but always by much less than minimum distance between rims of antennal sockets; clypeus densely, finely and confluently punctured on sides, punctures on median surface larger, coarser, and separated by shining interspaces on lower half, except medial margin impunctate, smooth, and reddened; supraclypeal area, except above, densely and confluentely punctured, without shining interspaces; frontal carina somewhat triangular in outline, deeply excavated basally, nearly as long as diameter of median ocellus; middle tibiae and basitarsi of equal length; punctuation on discs of metasomal terga I and II dense, rather fine with punctures separated by mostly less than their diameters, that on terga III and IV similar, but larger and much less densely disposed, especially medially, and with large impunctate or sparsely punctate areas extending across terga and basal to submarginal depressions; fifth metasomal tergum with discal punctures similar in size and disposition to those on tergum II, but larger and less densely crowded especially medially; structure of seventh metasomal tergum (Figure 45), seventh and eighth metasomal sterna (Figures 46, 47), and genitalia (Figure 48) as illustrated.

FEMALE.—Length 16–20 mm. Length of forewing, including tegula, 14–15 mm. Head and body black, not much paler on metasoma below; metasomal terga feebly metallic blue green with some purplish tints in bright light and most noticeably so on impunctate surfaces; antennae dark brownish black, somewhat reddened at apex of scape, pedicel, and variably below on usually apical flagellar segments; mandibles black, reddened usually at base and occasionally apically; clypeus brownish black to black, not reddened on medial surface; wings dissimilar in coloration, forewings hyaline on about basal two-thirds, apical third darkly infuscated with brownish black, hind wings nearly hyaline throughout, scarcely and only faintly infuscated apically; wing veins mostly reddish brown, apical veins beyond closed cells darker; tegulae testaceous externally, darkening to brownish black basally; legs mostly brownish black to black, somewhat reddened on tarsi and below; tibial spurs dark reddish brown; claws deep mahogany red, banded medially with black.

Vestiture of head chiefly long and white on face, especially that about ocelli antennal sockets, clypeus at sides, becoming brownish black on upper part of face and on vertex; hind margins of head rather thickly and mostly clothed with long whitish pubescence, sparsest and shortest on cheeks, intermixed with and sometimes replaced by dark brownish black pubescence dorsally near and on vertex; thorax thickly clothed with fulvous pubescence dorsally, paling to ochraceous on metanotum, propodeum, and on lower sides and ventrally; legs chiefly white pubescent basally, darker pubescent, usually reddish brown on exterior surfaces and on tarsi; scopal hairs of hind legs entirely pale, mostly white or nearly so; discal surfaces of metasomal terga I–IV devoid of pubescence except for very short, posteriorly directed, brownish black hairs situated laterally, which at extreme sides and on ventrally exposed surfaces are replaced on terga I and II by scopae consisting of long, dense plumose, mainly whitish hairs and ventroapically on terga III and IV with long tufts of chiefly whitish plumose hairs; metasomal tergum V apically traversed by a thick fringe of long, posteriorly di-
Figures 45-48.—*Mesoxea rufescens* Hurd and Linsley, male (5.3 mi W Pena Blanca Lake, Santa Cruz County, Arizona): 45, seventh metasomal tergum (left half ventral); 46, 47, seventh and eighth metasomal sterna (left halves dorsal); 48, genitalia (left half ventral).

Rected, plumose hairs characteristically white at sides and brownish black on median tergal surface; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long, mostly brownish black plumose hairs, sometimes at extreme sides with a few white hairs; scopal hairs of metasomal sterna I–III white; other surfaces of metasomal sterna II–V (except at extreme sides) and VI thickly clothed with rather short to moderately long, posteriorly directed, reddish brown to brownish black hairs; extreme sides of metasomal sterna II–V with long tufts of white plumose hairs projecting posteriorly from under overlapping tergal surfaces.

Eyes weakly diverging below (46:51); clypeus, except narrowly impunctate mediolateral corners, coarsely, rugosely, and nearly confluent punctate throughout; supraclypeal area, except narrowly
impunctate sides, about as coarsely punctate as clypeus; frontal carina narrowly triangular in outline, deeply excavated, slightly longer than maximum diameter of median ocellus; discal surfaces of metasomal terga I–V basal to marginal depressions deeply and coarsely punctured, punctures well separated medially, crowded laterally, sparsest on tergum I and closest and densest on tergum V.

**Types.**—Holotype male was collected 5.3 miles west of Pena Blanca Lake, Santa Cruz County, Arizona, on 29 July 1972 from the flowers of *Acacia angustissima* (Fabaceae) between 1000–1100 (Mountain Standard Time) by T. J. Zavortink, and is deposited in the collections of the California Academy of Sciences, San Francisco. The allotype female was collected one mile east of Douglas, Cochise County, Arizona, and 20 August 1962, from the flowers of *Verbesina encelioides* by M. A. Cazier and is deposited in the collections of the California Academy of Sciences.


**Discussion.**—This species inhabits the northwestern Mexican mainland from Nayarit to southern Arizona (Map 2) and has been collected on a number of occasions with *M. arizonica*, which occupies a similar geographic range (Map 3). While
the female of *M. rufescens* is readily distinguished by the pale pubescent thorax from that of *M. arizonica*, whose thorax is darkly pubescent, the males of these species are quite similar in general appearance. However, they may be easily separated owing to the less heavily infuscated forewings of *M. rufescens* as noted in the accompanying key. *Mesoxaea rufescens* is most closely related to *M. vagans*, which is apparently endemic in the Cape Region of Baja California.

3. *Mesoxaea vagans* (Fox), new combination

**Figures 49–52; Map 2**


**LOCATION OF TYPE.**—California Academy of Sciences, San Francisco.

**GEOGRAPHIC RANGE** (Map 2).—Mexico (Cape Region of Baja California).

**MALE.**—Length 15–19 mm. Length of forewing, including tegula, 12–16 mm. Head and body chiefly black; metasomal terga feebly metallic blue green, most evident on apical marginal depressions in bright light; antennae brownish black above, mahogany red below; mandibles dark brownish black or black, usually reddened on basal half; clypeus dark brownish black, sometimes somewhat reddened apically; wings similar in coloration, chiefly or entirely hyaline basally, infuscated with black apically; wing veins dark reddish brown; tegulae testaceous externally, darkening to brownish black basally; legs chiefly dark brownish black, tarsi dark reddish brown; tibial spurs reddish brown; claws deep mahogany red, banded medially with black.

Vestiture of head chiefly ochraceous, somewhat paler, and often turning to white on hind margins of head and genae below; pubescence on face usually pale ochraceous or white below antennal sockets, darkening to brownish black on upper part of face and vertex; thorax thickly clothed with fulvo-ochraceous pubescence throughout (becoming white or nearly so in older specimens); legs chiefly reddish brown pubescent, darkest basally and on ventral surfaces, usually paling to fulvous on exterior surfaces and on tarsi; pubescence of first metasomal tergum mostly consisting of long, erect, whitish plumose hairs, thickest at sides and ventrally, darkening to nearly black over raised submarginal areas laterally; metasomal tergum II–IV without apical bands of pale pubescence, mostly clothed with short, posteriorly directed, brownish black pubescence, longest and thickest at sides; tergum II tufted with white pubescence on ventrally exposed sides and with shorter and less conspicuous erect, white hairs on discal surface medially at base. Metasomal tergum III and IV tufted with long, whitish pubescence on extreme ventrally exposed sides; metasomal tergum V entirely black pubescent, shortest on punctate surface basally, much longer and forming a transverse band of simple hairs arising just before impunctate apical margin, projecting posteriorly and terminating in thick tufts of plumose hairs laterally; metasomal tergum VI with numerous, long, posteriorly directed, white plumose hairs arising just before impunctate apical margin, projecting posteriorly and terminating in thick tufts of plumose hairs laterally; metasomal tergum VII with pubescence chiefly white and disposed laterally as posteriorly projecting tufts of plumose hairs; metasomal sterna thickly clothed with rather long, plumose hairs, usually white or cinereous on sterna I–III and reddish brown or brownish black thereafter.

Eyes strongly convergent above, separated on vertex by less than distance between hind ocelli and always by less than distance across hind ocelli or that between rims of antennal sockets; clypeus coarsely and nearly confluentely punctured throughout, except almost impunctate, on somewhat smoothed and reddened, narrow, apical margin; suprafrontal area, except above, densely and confluentely punctured, without shining interspaces; frontal carina somewhat triangular in outline, deeply excavated basally, nearly as long as diameter of median ocellus; middle tibiae and basitarsi of equal length; punctures on discs of metasomal terga I and II dense, rather fine with punctures separated by mostly less than their diameters, that on terga III and IV primarily, but larger and much less densely disposed, especially medially and with large impunctate or sparsely punctate areas extending across terga basal to raised submarginal areas; fifth metasomal tergum with discal punctures similar in size and disposition to those on
Figures 49-52.—Mesoxaeta vagans (Fox), male (6 mi N Santa Anita, Baja California, Mexico): 49, seventh metasomal tergum (left half ventral); 50, 51, seventh and eighth metasomal sterna (left halves dorsal); 52, genitalia (left half ventral).

Tergum II, but larger and less densely crowded especially medially; structure of seventh metasomal tergum (Figure 49), seventh and eighth metasomal sterna (Figures 50, 51), and genitalia (Figure 52) as illustrated.

Female.—Length 16–19 mm. Length of forewing, including tegula, 15–16.5 mm. Head and body black, not paling perceptibly on ventrally exposed surfaces; metasomal terga feebly metallic blue green with some purplish tints in bright light, most noticeably so on impunctate surfaces; antennae dark brownish black, somewhat reddened at apex of scape, pedicel, and variably below on usually apical flagellar segments; mandibles black, red-
dened usually basally and sometimes apically; clypeus brownish black to black, not reddened on medial surface; wings similar in coloration, chiefly or entirely hyaline basally, infuscated with black apically; wing veins dark reddish brown, irregularly blackened; tegulae testaceous; legs mostly brownish black to black, somewhat reddened on tarsi and below; tibial spurs dark reddish brown; claws deep mahogany red, banded medially with black.

Vestiture of head chiefly moderately long and white on face, especially that about ocelli, antennal sockets, clypeus at sides, becoming brownish black on upper part of face, and on vertex; hind margins of head thickly clothed with long pubescence, mostly white, but intermixed with and replaced by dark brownish and black pubescence dorsally near and on vertex; thorax thickly clothed with fulvous pubescence dorsally, usually becoming ochraceous or whitish posteriorly on metanotum, propodeum, and on lower sides and ventrally; legs chiefly white pubescent basally, darker pubescent, usually reddish brown on exterior surfaces and on tarsi; scopal hairs of hind legs entirely pale, mostly white or nearly so; discal surfaces of metasomal terga, the genitalia of the males, especially vagans only by the more densely punctured metasomal sterna I—III. In addition to these differences, this species differs from Mesoxa
clypeus: frontal carina narrowly triangular in outline, deeply excavated, slightly longer than maximum diameter of median ocellus; discal surfaces basal to marginal depressions of metasomal terga I—V deeply and coarsely punctured, punctures well separated medially, crowded laterally, sparsest on tergum I medially, and closest and densest on tergum V.


**Discussion.**—Mesoxaea vagans is evidently endemic to the Cape Region of Baja California. It is closely related to, and very similar in appearance to M. rufescens, which inhabits the adjacent Mexican mainland from Nayarit to southern Arizona (Map 2). It is also similar in colorational features to M. texana, which was considered to be the same as this species by Fox (1894). Even though the females of M. rufescens differ principally from those of M. vagans only by the more densely punctured metasomal terga, the genitalia of the males, especially the structure of the penis valves and the volsellae, are strikingly different (Figures 48, 52). In addi-
tion, the eyes of the male in *M. vagans* are usually more strongly convergent above than those of *M. rufescens*.

Fox (1894:119–120) named the species from specimens which had been collected in Baja California (El Taste, west side and at 3400 ft. San Jose del Cabo, October) and Texas (Cypress Mills). However, as we have noted elsewhere in this study, the material from Texas represents another species, viz., *M. texana*. Since Fox (1894:119–120) did not select a type specimen for *vagans* and since the collections of the California Academy of Sciences contain the Fox specimens of *vagans* from El Taste, we select the male labeled *Oxaea vagans*, #286 as the lectoholotype and the female labeled as *Oxaea vagans*, no number, as the lectoallotype.

4. *Mesoxaea texana* (Friese), new combination

**Figures 53–56; Map 2**

*Oxaea texana* Friese, 1898:85, ♂ [Texas: Dallas].


*Oxaea vagans*—Authors [not Fox 1894:119]—Fox 1894:120 [Texas: Cypress Mills; Baja California record applies to *Mesoxaea vagans*, q.v.].—Friese 1898:80, 85, ♂.—Cameron 1901:316 [Mexico].

**Location of Type.**—Unknown.

**Geographic Range** (Map 2).—Southern United States (Louisiana and Texas) and adjacent northeastern Mexico (Nuevo Leon).

**Male.**—Length 17–24 mm. Length of forewing, including tegula, 15–20 mm. Head and body black, metasomal sternum usually somewhat reddened; metasomal terga feebly metallic blue green with purplish tints, most evident on impunctate apical depressions; antennae brownish black above, brightly reddened below; mandibles deep mahogany, reddened basally and apically; clypeus dark brownish black, reddened apically; wings nearly similar in coloration, forewings hyaline basally, apical half or more heavily infuscated with brownish black and violaceous in strong light, hind wings hyaline basally in area of closed cells, beyond these lightly infuscated with brownish black and somewhat violaceous in bright light; wing veins chiefly reddish brown, stained irregularly with black; tegulae testaceous, darkening basally to reddish brown; legs dark reddish brown, tarsi and ventral surfaces redder; tibial spurs deep reddish yellow; claws mahogany red, irregularly banded, or marked with black.

Vestiture of head chiefly cinereous or whitish on face below antennal sockets, and on cheeks below; pubescence of face above antennal sockets and hind margins of head, except cheeks below, dark reddish brown to nearly blackish brown; thorax thickly clothed with mostly fulvo-ochraceous to fulvous pubescence (becoming whitish in older specimens) darkening on sides and below (variably) to dark reddish brown or brownish black; legs entirely dark reddish brown pubescent, not paling on exterior surfaces; pubescence of first metasomal tergum mostly consisting of long, erect whitish or ochraceous plumose hairs, thickest at sides and ventrally, darkening to black over raised submarginal areas laterally; metasomal terga II–IV without apical hands of pale pubescence, mostly clothed with short, posteriorly directed, reddish brown or brownish black pubescence, longest and thickest at sides; tergum II usually tufted with at least some white pubescence on ventrally exposed sides and with shorter and less conspicuous white hairs on discal surface medially at base; terga III and IV without long tufts of white pubescence on ventrally exposed sides, rarely and at most with only a few white hairs on one or more of these terga; metasomal tergum V entirely black pubescent, shortest on punctate surface basally, much longer and forming a transverse band of simple hairs arising just before impunctate apical margin, projecting posteriorly and terminating in thick tufts of plumose hairs laterally; metasomal tergum VI with numerous long, posteriorly directed, white plumose hairs, usually intermixed on median tergal surface with brownish black or black hairs; metasomal tergum VII with pubescence chiefly white and disposed laterally as posteriorly projecting tufts of plumose hairs; metasomal sternum thickly clothed with rather long plumose hairs, usually white or cinereous on sterna I–II and sometimes also on apical margins of sterna III and IV, otherwise chiefly or entirely reddish brown pubescent.
Eyes moderately convergent above, usually separated on vertex by at least minimum distance between hind ocelli and always by less than distance across hind ocelli or that between rims of antennal sockets; clypeus coarsely and confluent punctated at sides and above, becoming less strongly punctate on slightly depressed anterior half medially and almost impunctate on smoothed and reddened apical margin; supracylpeal area punctured about as strongly as adjacent clypeal surface, except above where almost impunctate, frontal carina narrowly triangular in outline, deeply excavated basally, nearly as long as diameter of median ocellus; middle tibiae slightly longer than basitarsi (75:70); punctation on discs of metasomal terga I and II dense, rather fine with punctures separated by mostly less than their diameters, that on terga III and IV similar, but larger and much less densely disposed, especially medially and with larger impunctate or sparsely punctate areas extending across terga on and basal to submarginal areas; fifth metasomal tergum with discal punctures similar in size and disposition to those on tergum II, but larger and less densely crowded especially medially; structure of seventh metasomal tergum (Figure 53), seventh and eighth metasomal sterna (Figures 54, 55), and genitalia (Figure 56) as illustrated.

**Female.**—Length 20-24 mm. Length of forewing including tegula, 16-18 mm. Head and body black, not paling perceptibly on ventrally exposed surfaces; metasomal terga feebly metallic blue green with some purplish tints in bright light and most noticeable on impunctate surfaces; antennae dark reddish brown to brownish black, reddened below and at apex of scape, pedicel, and basal flagellar segments; mandibles chiefly black, reddened basally and apically; clypeus black, sometimes reddened medially; wings somewhat similar in coloration, chiefly or entirely hyaline basally, infuscated with black apically, especially heavily so on forewings, violaceous in bright light; wing veins dark reddish brown, tinged irregularly with black; tegulae testaceous externally, dark yellowish brown basally; legs dark reddish brown, tarsi and ventral surfaces redder; claws deep mahogany red, mottled with black.

Vestiture of head chiefly cinereous or whitish on face below antennal sockets and on cheeks below; pubescence of face around antennal sockets and above including vertex and hind margins of head, except lower genal areas, dark reddish brown to nearly blackish brown; thorax thickly clothed with mostly fulvo-ochraceous to fulvous pubescence (whitish in older specimens), darkening on sides and below (variably) to dark reddish brown or brownish black; pubescence on thorax behind usually paler, ochraceous to nearly white; legs entirely dark reddish brown pubescent, not paling on exterior surfaces; scopal hairs on hind femora entirely pale, mostly white or nearly so, those on hind coxae, trochanters, and tibiae largely or entirely dark fuscous; discal surfaces of metasomal terga I–IV devoid of pubescence except for very short, posteriorly directed, brownish black hairs situated laterally, which at extreme sides and on ventrally exposed surfaces are replaced on terga I and II by scopae consisting of long, densely plumose, mainly whitish hairs and ventroapically on terga III and IV with moderately long tufts of reddish brown plumose hairs; metasomal tergum V apically traversed by a thick fringe of long, posteriorly directed, plumose hairs characteristically white at sides and brownish black on medial tergal surface; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long, brownish black plumose hairs; scopal hairs of metasomal sterna I–III white or chiefly so; other surfaces of metasomal sterna II–V (except extreme sides) and VI thickly clothed with rather short to moderately long, posteriorly directed, reddish brown to brownish black hairs; extreme sides of metasomal sterna II–V with long tufts of white hairs projecting posteriorly from under overlapping tergal surfaces.

Eyes weakly diverging below (58:60); clypeus, except narrowly impunctate mediolateral corners, coarsely and rather rugously punctate, although punctures medioapically separated and with some shiny interspaces; supracylpeal area for the most part with punctures well separated and largely absent on sides and above; frontal carina narrowly triangular in outline, deeply excavated, slightly longer than maximum diameter of median ocellus; discal surfaces basal to marginal depressions of metasomal terga I–V, deeply and coarsely punctured, punctures well separated medially, crowded laterally, sparsest on tergum I medially, and closest and densest on tergum V.

FIGURES 53-56.—Mesoxaea texana (Friese), male (Falfurrias, Brooks County, Texas): 53, seventh metasomal tergum (left half ventral); 54, 55, seventh and eighth metasomal sterna (left halves dorsal); 56, genitalia (left half ventral).

Texas, Bastrop County: $\varphi$, VIII-31-51, on flowers of perennial Monarda sp. (A. H. Alex, TAM). Bexar County: $\varphi$, VII-20-31 (H. B. Parks, TAM); 4$\varphi$, X-12-31 (H. B. Parks, TAM); $\varphi$, same data (H. B. Parks, U. Colo.); $\varphi$, IX-6-36 (TAM); 2$\varphi$, 4$\varphi$, no date (TAM). Brazos County: $\varphi$, VII-18-51, on flowers of Gossypium sp. (A. H. Alex, TAM); $\varphi$, VII-31-51, on flowers of Sesamum indicum (A. H. Alex, TAM); 2$\varphi$, VII-1-51, on flowers of Sesamum indicum (A. H. Alex, TAM); $\varphi$, VIII-3-51, on flowers of Sesamum indicum (A. H. Alex, TAM); $\varphi$, VIII-5-54, on flowers of Eupatorium serotina (A. H. Alex, TAM); $\varphi$, VII-22-55, on flowers of Vernonia texana (A. H. Alex, TAM). College Station: $\varphi$, VIII-31-39 (USNM). Millican, $\varphi$, VI-17-56 (H. E. Evans and E. G. Mathews, CU). Brooks County: Falfurrias, $\varphi$, VII-7-65 (J. E. Gillaspy, GEB); &$, VI-23-66 (J. E. Gillaspy, GEB); 2$\varphi$, VI-3-67, on flowers of Monarda sp. (J. E. Gillaspy, GEB). Burleson Co.: $\varphi$, IX-24-56, on flowers of Solanum rostratum (A. H. Alex, TAM). Harris Co.: $\varphi$, VIII-15-28 (L. D. Beamer, KU). Dickinson, 2$\varphi$, VI-1929 (F. M. Hull, TAM). Rose Hill, $\varphi$, VIII-20-32 (R. Birk-

DISCUSSION.—Superficially this species closely resembles Mesoxaea vagans and M. rufescens in colorational features, but is structurally most closely related to M. nigerrima. The amount of pale vestiture on the head and thorax is subject to some variation in both the males and the females. In some specimens there is much pale pubescence on the face above the antennae and on the sides and venter of the thorax, while in others this pubescence is largely or entirely dark in coloration.

Mesoxaea texana has been observed nesting in very large numbers in Hufsmith, Harris County, Texas, by the Reverend Birkmann (1932), who published a newspaper article about his observations in The Giddings News. These observations were subsequently summarized in part by Cockerell (1933), who identified the species, and by Rayment (1935), who mentioned these observations. Since the original information contained in the Reverend Birkmann’s article has never been reproduced and has entailed a special effort through the Library of Congress to obtain the article, it is presented verbatim below so that it will be conveniently available for use by future investigators:

I will write now of a novel experience in natural history which I had some few days ago right here in Harris County.

Ten days ago we had a storm, a hurricane they called it in the papers. We however suffered no damage. Hufsmith is in the northern part of the county, and we were only skirted by the storm. We were fortunate in getting rain after a pretty long drought. The rain brought new life to plants and animals, even the insects in the ground got busy and began to come out and breathe some fresh air.

I am especially referring to a great swarm of wild bees that for several days had a holiday in the air and, for a change, made their burrows in the sand.

Now, wild bees are not honey bees that are occasionally found in the woods, but by this term are meant all species of insects that are related to the honeybees, for instance, the humble bees and the carpenter bees and many others. In Lee County there are several hundred different species of wild bees. The humble bees are the only ones of the “wild bees” that live in colonies, all the rest live in pairs, each pair has its own burrow or nest. Some burrow in wood, or in stems or weeds, others dig into the ground, where they lay their eggs and have their brood, some once a year, others twice.

Now I am coming to my subject more closely. Some days ago my son, with whom I am now staying, tells me that he has seen a lot of bees or wasps in the air and they are making a great ado and hubbub flying in all directions, and not only over a small area, but for quite a distance the noise is heard and the ground is full of newly dug holes. Next morning when the day grows warm we go out and I found all this to be true, and not the half told. I could not see the insects on account of my poor eyesight, but my son tells me all I want to know. He tells me the bees are flying, some of them only a half foot from the ground, others fly higher, so as to get over the weeds, still others are pretty high up, all of them flying fast and like so many little furies, making all the noise possible [sic] to them. You could hear them at some distance, the sound was similar to that heard in the telegraph wires at times, but much louder, and to listen to them for a while would make me a little nervous. The question was: What is all that about? What are these hundreds of thousands of bees after? And the ground was as stated, full of holes. Fresh earth was lying beside these holes, you could see the bees had just opened them. My grandson Roger caught about a dozen of these bees for me and I have sent specimens for determination to Prof. Cockerell of Boulder, Col., who is a great scholar and student of the bees, knows all of the thousands of bees in the world, and has collected and described many of them in scientific books and periodicals. I suppose that the species of which I am writing is one new to science, at least, I have never before observed it in Lee County. And if it should prove to be a known species, I think that their habit of building so many homes near one another, and of swarming in such great numbers, and with so much noise and fury has not been observed before. I have never before seen anything like such a great area occupied by the bees, and never before heard such sounds produced by thousands and thousands of these insects.

I stepped off the ground, it was about 700 feet in length, and 250 feet in width. I counted (or rather Roger did) 29 holes in ten feet square (100 sq. ft.) and 46 holes in another ten feet square. According to this reckoning there were about 80,000 holes and counting one pair of bees for each
hole, there would have been one hundred thousand individual bees. All of the same kind.

This spectacle lasted for about four or five days, according to my observation. After that time, there were only a few specimens [sic] to be noticed. They are in their burrows now and the females will come out occasionally to gather food for their offspring.

What food? I don’t know, I don’t think that anyone knows. Bees don’t collect animal food like the wasps do, but I suppose their subsistence is on sweets which they get from plants and flowers.

G. Birkmann

(This is a very interesting article, and the editor is glad Rev. Birkmann is yet able to find delight in nature, as he did for so many years at Fedor.)

Friese (1898:85) cites two males with his original description of this species and we have not been able to locate their whereabouts.

5. *Mesoxaea nigerrima* (Friese), new combination

FIGURES 57–60; MAP 3

*Oxaea nigerrima* Friese, 1912:199, ♀ [Mexico: Vera Cruz].

*Protaxaea nigerrima*—Linsley 1951:1086.—Linsley and Michener, 1962:386, fig. [Mexico: 14 miles south of Cuernavaca].

**LOCATION OF TYPE.**—Zoologisches Museum, Humboldt-Universität, Berlin.

**GEOGRAPHIC RANGE** (Map 3).—Southwestern to southern Mexico (Chiapas, Colima, Guerrero, Jalisco, Michoacan, Morelos, Oaxaca and Vera Cruz).

**MALE.**—Length 16–22 mm. Length of forewing, including tegula, 15–17 mm. Head and body chiefly or entirely black; metasomal terga feebly metallic blue green, most evident on impunctate apical marginal depressions; antennae dark reddish brown to brownish black above, deep reddish brown basally, becoming deep mahogany red or black apically; clypeus black, reddened along apical margin; wings dissimilar in coloration, forewings nearly uniformly and heavily infuscated throughout with black, feebly violaceous in bright light, hind wings much paler, hyaline basally and lightly infuscated with black apically and posteriorly; wing veins dark reddish brown; tegulae dark reddish brown, black basally; legs brownish black to black on coxae to femora, tibiae and tarsi reddish brown; tibial spurs pale reddish brown; claws deep mahogany red, irregularly marked with black.

Vestiture of head chiefly ochraceous to nearly white on face below antennal sockets and on lower hind margins of head (variable); pubescence on face above antennal sockets chiefly brownish black to black, sometimes pubescence just above antennal sockets intermixed with some fulvous hairs; vertex and hind margins of head dorsally (variable) chiefly or entirely brownish black; thorax thickly clothed with fulvo-ochraceous to fulvous pubescence, usually paling to ochraceous, somewhat posteriorly and usually darkening partly on lateral and ventral surfaces (variably) to brownish black; legs with chiefly brownish black to fulvous pubescence basally, paling to bright fulvous on tarsi; pubescence of first metasomal tergum consisting of long, erect whitish plumose hairs, thickest at sides and on ventrally exposed surfaces; metasomal terga II–IV, without apical bands of pale pubescence, mostly clothed with short, posteriorly directed, brownish black pubescence, (except basal discal surface of tergum II with some erect white hairs), longest and thickest at sides; metasomal tergum V mostly clothed with brownish black pubescence, turning to white at extreme sides, shortest on punctate surface basally, much longer and forming a transverse band of long simple hairs arising just before impunctate apical margin, projecting posteriorly and terminating in small tufts laterally; metasomal tergum VI with numerous long, posteriorly directed, mostly or entirely white plumose hairs arising just before apical margin, longest and somewhat tuftlike laterally and usually intermixed medially with some brownish black or black hairs; metasomal tergum VII with pubescence chiefly or entirely white (sometimes intermixed or replaced medially with brownish black or black hairs) and disposed laterally as posteriorly projecting tufts of plumose hairs; metasomal sternum thickly clothed with rather long plumose hairs, usually white on sternum I–III and brownish black on succeeding sternum, which in some specimens may display variable amounts of pale pubescence apically and laterally.

Eyes moderately convergent above, separated on vertex by nearly or more than minimum distance between hind ocelli, but by less than distance between rims of antennal sockets; clypeus with a rather broad, reddened, impunctate, apical margin medially, otherwise densely and confluent punctured on sides, median surface somewhat depressed and with punctures larger and well separated,
interscapylcal area densely, finely, and confluent punctured; frontal carina triangular in outline, very short, much shorter than diameter of median ocellus, deeply excavated especially basally; middle tibiae slightly longer than basitarsi (70:65); punctuation on discs of metasomal terga I and II dense, rather fine, with punctures mostly separated by less than their diameters, those on terga III and IV similar but less densely punctate, especially medially and laterally over and basad to raised submarginal areas; fifth metasomal tergum with punctures similar in size and disposition to those on tergum II, but less densely crowded especially medially; structure of seventh metasomal tergum (Figure 57), seventh and eighth metasomal sternum (Figures 58, 59), and genitalia (Figure 60) as illustrated.

**FEMALE.**—Length 18–23 mm. Length of forewing, including tegulae, 16–17.5 mm. Head and body black, somewhat paler on metasomal sternum; metasomal terga feebly metallic blue green with some purplish tints evident in bright light and most visible on impunctate apical margins; antennae dark reddish brown to brownish black, somewhat reddened at apex of scape and pedicel and to a variable extent on flagellar segments, especially below; mandibles chiefly deep mahogany red to black, especially basally and sometimes apically; clypeus black, narrowly reddened apically; wings dissimilar in coloration, forewings weakly violaceous, nearly uniformly infuscated throughout with brownish black, but slightly less so basally, hind wings hyaline or nearly so, slightly violaceous in bright light; wing veins chiefly brownish black, sometimes somewhat reddened; tegulae dark reddish brown; legs mostly blackish brown dorsally, usually reddened below on femora, tibiae, and tarsi; tibial spurs deep reddish brown; claws reddish basally, blackened apically.

Vestiture of head chiefly moderately long and white on face about antennal sockets and clypeus at sides; face above antennal sockets rather thickly clothed with long pubescence, mostly white pubescence on cheeks at sides, becoming intermixed with and replaced by dark brownish and black pubescence dorsally; thorax thickly clothed with dark brownish black pubescence; legs, except whitish scopal hairs on hind femora, clothed with rather long brownish to blackish pubescence; discal surfaces of metasomal terga devoid of pubescence except for very short, posteriorly directed, brownish black hairs situated laterally, which at extreme sides and on ventrally exposed surfaces are replaced on terga I and II by scopae consisting of long, densely plumose, mostly whitish hairs and ventroapically on terga III and IV with tufts of brownish black plumose hairs usually intermixed with some white hairs; metasomal tergum V apically traversed by a thick fringe of long, posteriorly directed, plumose hairs characteristically white at sides and brownish black on medial tergal surface; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long, brownish black, plumose hairs; scopal hairs of metasomal sternum I medially white, laterally brownish black, those on sternum II and median tuft on sternum III largely or entirely white; other surfaces of metasomal sternum II–V (except extreme sides) and VI thickly clothed with rather short to moderately long, posteriorly directed, reddish brown to brownish black hairs; extreme sides of metasomal sternum II–V with long tufts of white plumose hairs projecting posteriorly from under overlapping tergal surfaces.

Eyes weakly diverging below (51:56); clypeus densely and rather rugosely punctured throughout, punctures on median surface larger than those on sides, and with rugae polished and shining; supra-clypeal area densely and nearly confluent punctured except at sides and above; frontal carina narrowly triangular in outline, short, longer than maximum diameter of median ocellus, deeply excavated and polished; discal surfaces before marginal depressions of metasomal terga I–V deeply punctured virtually throughout, punctures well separated medially, crowded laterally, sparsest on tergum I medially and closest and densest on tergum V.

FIGURES 57-60.—Mesoxaea nigerrima (Friese), male (21 mi W Tehuantepec, Oaxaca, Mexico):
57, seventh metasomal tergum (left half ventral); 58, 59, seventh and eighth metasomal sterna
(left halves dorsal); 60, genitalia (left half ventral).


Discussion.—This species, which occurs in the southernmost area occupied by the genus Mesozaea (Map 3), shares many characters with M. arizonica and M. texana. As presently known these species are allopatric in distribution and it appears they were derived from a common ancestry. In colorational features M. nigerrima closely resembles M. arizonica from which it may be readily distinguished by the accompanying key. Although the geographic ranges of M. nigerrima and M. arizonica are nearly contiguous in southwestern Mexico there is a large geographic hiatus separating the ranges of M. texana and M. nigerrima in the Gulf coast region of eastern Mexico (Maps 2, 3). Most likely this comparatively wide separation of their known ranges is due to a lack of collecting.

6. Mesoxaea arizonica (Cockerell),
new combination and new status

Figures 61–64; Map 3


Location of Type.—American Museum of Natural History, New York.

Geographic Range (Map 3).—Southwestern United States (Arizona) and adjacent northwestern Mexico (Nayarit, Sinaloa, and Sonora).

Male.—Length 16–20 mm. Length of forewing, including tegula, 14–16 mm. Head and body chiefly or entirely black; metasomal terga faintly metallic blue green, most evident on impunctate, apical, marginal depressions; antennae dark reddish brown to brownish black above, reddened below and scape usually somewhat reddened also; mandibles dark reddish brown basally, becoming deep mahogany red or black apically; clypeus black, reddened along apical margin; wings dissimilar in coloration, forewings, except pale basal cells (R and 1st Cu), uniformly and heavily infuscated throughout with black, feebly violaceous in bright light, hind wings entirely hyaline or nearly so; wing veins dark reddish brown; tegulae reddish brown to nearly testaceous; legs brownish black to black on coxae and femora, tibial and tarsi dark reddish brown; claws deep mahogany red, irregularly blackened.

Vestiture of head chiefly pale ochraceous to white on face below antennal sockets and on hind margins of head; pubescence on face above antennal sockets ochraceous to fulvous (variable) turning to brownish black to black on top of face and vertex; pubescence on hind margins of head adjacent to vertex chiefly or entirely white, sometimes intermixed with a few brownish black or black hairs; thorax thickly clothed with ochraceous to fulvous pubescence (variable), usually paling to white or pale ochraceous posteriorly on propodeum and sometimes darkening partly on lateral and ventral surfaces (variable) to brownish black; legs with chiefly brownish black pubescence basally, paling to fulvous or ochraceous on tarsi, sometimes also on hind femora; pubescence of first metasomal tergum consisting of long, erect whitish plumose hairs, thickest at sides and on ventrally exposed surfaces; metasomal terga II–IV, without apical bands of pale pubescence, mostly clothed with short, posteriorly directed, brownish black pubescence (except basal discal surface of tergum II with some erect white hairs), longest and thickest at sides; metasomal tergum V mostly clothed with brownish black pubescence, turning to white at extreme sides, shortest on punctate surfaces basally, much longer and forming a transverse band of long simple hairs arising just before impunctate apical margin, projecting posteriorly and terminating in small tufts laterally; metasomal tergum VI with numerous long, posteriorly directed, mostly or entirely white plumose hairs arising just before apical margin, longest and somewhat tuftlike laterally and usually intermixed medially with some brownish black or black hairs; metasomal tergum VII with pubescence chiefly or entirely white (sometimes intermixed or replaced medially with brownish black or black hairs) and disposed laterally as posteriorly projecting tufts of plumose hairs, usually white on at least sterna I–III and brownish black on succeeding sterna, which in some specimens may display variable amounts of pale pubescence apically and laterally.

Eyes moderately to strongly convergent above, separated on vertex usually by much less than minimum distance between hind ocelli and always by
considerably less than distance between rims of antennal sockets; clypeus with a rather broad, reddened, impunctate, apical margin medially, otherwise densely and confluentely punctured on sides, median surface somewhat depressed and with punctures much larger, well separated and with interspaces smooth and shining; supraclipeal area densely, finely, and confluentely punctured; frontal carina narrowly triangular in outline, short, about as long or longer than maximum diameter of median ocellus, deeply excavated virtually throughout its length; middle tibiae and basitarsi of equal length; punctuation on discs of metasomal terga I and II dense, rather fine with punctures separated by mostly less than their diameters, those on terga III and IV similar, but less densely punctate especially medially and laterally over and basal to raised submarginal areas; fifth metasomal tergum with punctures similar in size and disposition to those on tergum II, but less densely crowded especially medially; structure of seventh metasomal tergum (Figure 61), seventh and eighth metasomal sterna (Figures 62, 63), and genitalia (Figure 64) as illustrated.

**FEMALE.**—Length 18-23 mm. Length of forewing including tegula 15-17 mm. Head and body black, metasomal sterna somewhat paler, dark brownish black; metasomal terga feebly metallic blue green with some purplish tints evident in bright light and most visible on impunctate apical margins; antennae dark reddish brown, scape and pedicel reddened narrowly at apices and to some extent on ventral surfaces of flagellar segments; mandibles dark brownish black, reddened basally and at apex; clypeus black, narrowly margined with red; wings dissimilar in coloration, forewings weakly violaceous, nearly uniformly and heavily infuscated with brownish black, slightly less so in basal cells (R and 1st Cu); hind wings hyaline basally, faintly infuscated apically and scarcely violaceous in bright light; wing veins brownish black; legs mostly brownish black dorsally, somewhat paler below; tibial spurs bright reddish brown; claws chiefly black, reddened basally.

Vestiture of head short to moderately long, and mostly white on face about antennal sockets and clypeus at sides; face above antennal sockets rather thickly clothed with erect reddish brown pubescence; hind margins of head thickly clothed with long pubescence mostly white on cheeks at sides, usually becoming intermixed with and replaced by brownish black pubescence dorsally (variable); thorax thickly clothed with brownish black pubescence, that on metanotum sometimes paler marginally to a fringe of fulvous hairs; legs, including scopal hairs, clothed entirely with rather long, brownish black pubescence; discal surfaces of metasomal terga devoid of pubescence except for a very few, short, posteriorly directed, brownish black hairs situated laterally, which at extreme sides and on ventrally exposed surfaces are replaced on terga I and II by scopae consisting of long, densely plumose reddish brown hairs (often intermixed with some white hairs) and ventroapically on terga III and IV with tufts of brownish black plumose hairs sometimes intermixed with white hairs; metasomal tergum V apically traversed by a thick fringe of long, posteriorly directed, plumose hairs characteristically white at sides and brownish black on median tergal surface; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long, brownish black, plumose hairs; scopal hairs on sternum I brownish black, those on sternum II and median tuft on sternum III variably either chiefly whitish or mostly brownish, but with some whitish hairs; other surfaces of metasomal sterna II–V (except extreme sides) and VI thickly clothed with rather short to moderately long, posteriorly directed, reddish brown to brownish black hairs; extreme sides of metasomal sterna II–V with long tufts of white plumose hairs projecting posteriorly from under overlapping tergal surfaces.

Eyes weakly diverging below (48:54); clypeus densely and rugosely punctured especially on sides, punctures on median surface larger than those at sides and much less crowded and with interspaces shining; supraclipeal area densely and nearly confluentely punctured, except at sides and above; frontal carina narrowly triangular in outline, short, longer than maximum diameter of median ocellus, deeply excavated basally; discal surfaces before marginal depressions of metasomal terga I–V deeply punctured, punctures well separated medially, crowded laterally and closest and densest on tergum V.

**Figures 61-64.** *Mesoxaea arizonica* (Cockerell), male (Sonoita, Santa Cruz County, Arizona): 61, seventh metasomal tergum (left half ventral); 62, 63, seventh and eighth metasomal sterna (left halves dorsal); 64, genitalia (left half ventral).

(W. J. Hanson, GEB). Pena Blanca Lake, 9.5 mi WNW of Nogales, 4000 ft, 55 $\delta$, $\varphi$, VIII-18-74, on flowers of *Kallstroemia grandiflora* from 0830 to 1200 MST (T. J. Zavortink, TJZ); $\delta$, VIII-19-74, on flowers of *Tephrosia leiocarpa*, 1515-1530 MST (T. J. Zavortink, TJZ); 29 $\delta$, VIII-20-74, on flowers of *Kallstroemia grandiflora* from 0830-1145 (T. J. Zavortink, TJZ); 5 $\delta$, VIII-20-74, on flowers of *Tephrosia leiocarpa*, 1145-1200 (T. J. Zavortink, TJZ). Pena Blanca Lake, 5.3 mi W, 2 $\delta$, VII-29-72, on flowers of *Acacia angustissima*, between 1000-1215 MST (T. J. Zavortink, TJZ). Sonoita, 6 mi SE, $\delta$, VIII-27-68 (R. W. Thorp, UCD). Tumacacori Mountains, 5 $\varphi$, no date, on flowers of *Lotus* sp. (I. Wilson, AMNH, CAS, KU). Nayarit: Acaponete, $\delta$, IX-29-66 (G. E. & A. S. Bohart (GEB). Acaponete, 8 mi SE, $\varphi$, X-19-64 (A. E. Michelbacher, CIS). Navarrete, 2 $\varphi$, VII-28-53 (C and P. Vaurie, David Rockefeller Mexican Expedition, 1953). Tepic, 44 mi NW Tepic, $\delta$, VIII-30-71 (W. J. Hanson, GEB). Sinaloa: Arroyo del Saucillo, 4 mi NW of Choix, 2 $\delta$, VIII-
7. Mesoxaea clypeata, new species

MALE.—Length 16–21 mm. Length of forewing, including tegula 16–18 mm. Head and body chiefly or entirely black; metasomal terga feebly metallic blue green, most evident on impunctate apical marginal depressions; antennae black or brownish black above, deep reddish brown or mahogany below; mandibles dark reddish brown basally, becoming deep mahogany red or black apically; clypeus black laterally, paling to deep mahogany red on medial surface; wings dissimilar in coloration, forewings nearly uniformly infuscated throughout with black, somewhat darker apically, hind wings hyaline; wing veins dark reddish brown; tegulae dark reddish brown, irregularly mottled with yellow; legs chiefly dark reddish brown, tarsi usually redder; tibial spurs pale reddish brown; claws deep mahogany red, banded medially with black.

Vestiture of head chiefly ochraceous to nearly white on hind margins of head and face below antennal sockets; pubescence on face above antennal sockets bright fulvo-ochraceous darkening to brownish black on upper part of face and vertex; thorax thickly clothed with mostly ochraceous to fulvo-ochraceous pubescence, usually paling posteriorly to nearly white and sometimes darkening on lateral and ventral surfaces (variably) to brownish black; legs with chiefly brownish black to fulvous pubescence basally, paling to bright fulvous on tibiae and tarsi; pubescence of first metasomal tergum consisting of long, erect whitish plumose hairs, thickest at sides and on ventrally exposed surfaces; metasomal terga II–IV, without apical bands of pale pubescence, mostly clothed with short, posteriorly directed, brownish black pubescence, longest and thickest at sides, sometimes terga II and IV tufted with whitish pubescence at extreme ventrally exposed sides and usually basal discl surface of tergum II with erect whitish or cinereous pubescence; metasomal tergum V mostly or entirely clothed with brownish black pubescence (sometimes becoming whitish laterally), shortest on punctate surface basally, much longer and forming a transverse band of long simple hairs arising just before impunctate apical margin, projecting posteriorly, and terminating in thick tufts of plumose hairs laterally; metasomal tergum VI with numerous long, posteriorly directed, white plumose hairs arising just before impunctate apical margin, longest and somewhat tuftlike laterally and occasionally intermixed medially with brownish black or black hairs; metasomal tergum VII with pubescence chiefly white and disposed laterally as posteriorly projecting tufts of plumose hairs; metasomal sternum thickly clothed with rather long plumose hairs, usually mostly or entirely white on sternum I–III and brownish black on succeeding sternum, which in some specimens may display variable amounts of pale pubescence apically and laterally.
Eyes strongly convergent above, separated on vertex by less than transverse diameter of median ocellus (Figure 5); clypeus, except at sides, nearly impunctate, at most with a few, well-separated large punctures on depressed median surface; supraclypeal area densely punctured, without shining interspaces; frontal carina triangular in outline, very short, much shorter than diameter of median ocellus, deeply excavated basally; middle tibiae and basitarsi of equal length; punctuation on discs of metasomal terga I and II dense, rather fine with punctures separated by mostly less than their diameters, those on terga III and IV similar, but less densely punctate especially medially and laterally over and basal to raised submarginal areas; fifth metasomal tergum with discal punctures similar in size and disposition to those on tergum II, but less densely crowded especially medially; structure of seventh metasomal tergum (Figure 65), seventh and eighth metasomal sterna (Figures 66, 67), and genitalia (Figure 68) as illustrated.

**FEMALE.**—Length 18–20 mm. Length of forewing, including tegula, 18–21 mm. Head and body chiefly black, paling somewhat ventrally to very dark mahogany; metasomal terga feebly metallic blue green with some purplish tints evident in bright light and most evident on impunctate apical margins; antennae dark brownish black, somewhat reddened at apex of scape and pedicel and to a variable extent on flagellar segments; mandibles chiefly deep mahogany red to black, usually near bases and apices; clypeus black laterally, paling to deep mahogany on medial surface; wings dissimilar in coloration, forewings rather uniformly infuscated throughout and violaceous in bright light, hind wings mainly hyaline except for some blackish infuscation apically and posteriorly; wing veins dark brownish black; tegulae dark mahogany, somewhat reddened externally; legs mostly blackish brown dorsally, usually much reddened on tarsal segments and below; tibial spurs deep reddish brown; claws deep mahogany red, banded medially with black.

Vestiture of head chiefly moderately long and white on face, especially that about ocelli, antennal sockets and clypeus at sides; hind margins of head thickly clothed with long pubescence, mostly white on lower genae, becoming intermixed with and replaced by dark brownish and black pubescence dorsally; thorax thickly clothed with dark brownish black pubescence at least dorsally, usually paling irregularly at sides and below to dark brown; legs mostly clothed with rather long brownish pubescence, sometimes paling to reddish brown on tarsal segments; scopal hairs of hind legs mostly reddish brown, sometimes with intermixture of brownish black or black hairs; discal surfaces of metasomal terga I–IV devoid of pubescence except for very short, posteriorly directed, brownish black hairs situated laterally, which at extreme sides and on ventrally exposed surfaces are replaced on terga I and II by scopae consisting of long, densely plumose, chiefly cinereous to whitish hairs and ventro-apically on terga III and IV with long tufts of chiefly whitish plumose hairs; metasomal tergum V apically traversed by a thick fringe of long, posteriorly directed, plumose hairs characteristically white at sides and brownish black on medial tergal surface; metasomal tergum VI densely clothed on either side of pygidial plate with moderately long, brownish black plumose hairs; scopal hairs of metasomal sternum I brownish black; those on sternum II and median tuft on sternum III largely or entirely white; other surfaces of metasomal sterna II–V (except extreme sides) and VI thickly clothed with rather short to moderately long posteriorly directed, reddish brown to brownish black hairs; extreme sides of metasomal sterna II–V with long tufts of white plumose hairs projecting posteriorly from under overlapping tergal surfaces.

Eyes weakly diverging below (49:55), clypeus, except at sides, nearly impunctate, at most with a few, well-separated large punctures on smoothed and reddened median surface; supraclypeal area densely and nearly confluent punctured except at sides and above; frontal carina triangular in outline, short, distinctly less than diameter of median ocellus, deeply excavated and polished; discal surfaces before marginal depressions of metasomal terga I–V deeply punctured, well separated medially, crowded laterally, sparsest on tergum I medially, and closest and densest on tergum V.

**GEOGRAPHIC RANGE** (Map 3).—Southwestern Mexico (Nayarit).

**TYPES.**—Holotype male, allotype female, and 9 paratypes (♂, 8 ♀) were collected 4 miles south of Acaponeta, Nayarit, Mexico, on 2 September 1962, by D. H. Janzen. Additional paratypes (7 ♀, 4 ♂) are from the following localities in Nayarit: Acaponete, ♀, 29 September 1966 (G. E. and A. S.
FIGURES 65–68.—Mesoxaea clypeata Hurd and Linsley, holotype male (4 mi S Acaponeta, Nayarit, Mexico): 65, seventh metasomal tergum (left half ventral); 66, 67, seventh and eighth metasomal sternum (left halves dorsal); 68, genitalia (left half ventral).

Bohart, GEB); 8 miles southeast of Acaponete, 9, 19 October 1964 (A. E. Michelbacher, CIS); Navarrete, 6♂, 28 July 1953 (C. and P. Vaurie, 1953 David Rockefeller Mexican Expedition, AMNH); 18 miles north of Tepic, 2♀, 16 August 1960 (P. H. Arnaud, Jr., E. S. Ross, and D. C. Rentz, CAS) and 4.5 miles southeast of Tuxpan, 9, 9 September 1965, on flowers of Sesbania macrocarpa (R. D. Sage, CIS). The primary types are deposited in the collections of the California Academy of Sciences, San Francisco.

DISCUSSION.—The sparsely punctate and shining clypeus distinguishes Mesoxaea clypeata from all its congeners. Structurally it is most closely related
to *M. nigerrima*, which is very similar in colorational features. At present this species is known only from a few localities in the State of Nayarit, Mexico, and has been collected at some localities there with *M. arizonica* and *M. rufescens*. Nothing is known about its nesting habits or its pollen sources.

### Literature Cited

**Ashmead, William H.**


**Bertoni, A. de Winkelried**


**Birkmann, G.**

1932. [Habits of *Protoxaea texana.*] *Giddings News* (Giddings, Texas), 2 September 1932: page 7, columns 6 and 7.

**Bischoff, H.**


**Blanchard, Émile**


**Bowers, Karen A. W.**


**Cameron, P.**


**Cazier, M. A., and E. G. Linsley**


**Claude-Joseph, F.**


**Cockerell, T. D. A.**


**Crawford, J. C.**


**Dalla Torre, C. G. de**


**Ducke, A.**


Evans, Howard E., and E. Gorton Linsley


Fox, William J.


Friese, H.


Gerstaecker, A.


Graf, Vinalto


Gribodo, Giovanni


Halsted, Byron D.


Harris, J. Arthur, and Oscar M. Kuch


Heinrich, Bernd, and Peter H. Raven


Heiser, C. B. Jr., and T. W. Whitaker


Hurd, Paul D., Jr., and E. Gorton Linsley


Iliger, Karl

1806. William Kirby's Familien der Bienenarten Insekten mit Züsatzten, Nachweisungen und Bemerkungen. Magazin für Insekten (Braunschweig, Reichard), 5:28-175.

Janvier, H.


Joergensen, C. A.


Jörgensen, P.


Klug, J. C. F.


Laroca, Sebastián


Latrille, P. A.


Lepetieter de Saint-Fargeau, M. le Compe Amédec Louis Michel


Linsley, E. Gorton


Linsley, E. Gorton, and Mont A. Cazier


Linsley, E. Gorton, and Charles D. Michener


Macior, Lazarus Walter


Meehan, Thomas


Meeuse, B. J. D.


Michener, Charles D.


Michener, C. D., and R. D. Lange


Mitchell, Theodore B.


Moure, Jesús S.


Moure, Jesús S., and B. Lucas de Oliveira


Moure, J. S., and C. A. C. Seabra


Moure, J. S., and D. Urban


Müller, Fritz


Olivier, M.


Popov, V. V.


Raymont, Tarlton

Roberts, Radclyffe B.


Robertson, Charles
1890. Flowers and Insects, V. Botanical Gazette, 15:199-204.

Rozen, Jerome G., Jr.


Sandhouse, Grace A.

Schrottky, C.


1913. La Distribución Geográfica del los Hymenópteros Argentinos. Anales de la Sociedad Científica Argentina, 75:114-115, 180-286.

Sichel, J.

Smith, Frederick

Snodgrass, Robert Evans


Stephen, W. P., G. E. Bohart, and P. F. Torchio

Stow, I.

Strand, Embrik

Thorp, Robbin, and James R. Estes

Todd, J. E.

Truxal, F. S.

Wille, Alvaro

Yager, Karen, and Jerome G. Rozen, Jr.
Plates 1–3
PLATE 1.—Protoxaea gloriosa (Fox): male (above) hovering in territorial flight; female (below) in flower of Kallstroemia grandiflora (Torrey) Gray.
PLATE 2.—"Sleeping" aggregation of males of Protoxaea gloriosa (Fox).
PLATE 3.—Closeup details of “sleeping” aggregation of males.
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