FORAGING BEHAVIOR, TAXONOMY, AND MORPHOLOGY OF BEES
(HYMENOPTERA: APOIDEA), WITH AN EMPHASIS ON PERDITA
(HYMENOPTERA: ANDRENIDAE)

by

Zachary M. Portman

A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

Carol von Dohlen, Ph.D.
Major Professor

Terry Griswold, Ph.D.
Project Advisor

Nancy Huntly, Ph.D.
Committee Member

Karen Kapheim, Ph.D.
Committee Member

Luis Gordillo, Ph.D.
Committee Member

Mark R. McLellan, Ph.D.
Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2018
Several studies have been published previously and others remain to be submitted to peer-reviewed journals. As such, a disclaimer is necessary. All nomenclaturally relevant acts in this thesis have to be regarded as unpublished according to Article 8 of the International Code of Zoological Nomenclature, and will become available by separate publications.
ABSTRACT

Foraging behavior, taxonomy, and morphology of bees (Hymenoptera: Apoidea), with an emphasis on *Perdita* (Hymenoptera: Andrenidae)

by

Zachary M. Portman, Doctor of Philosophy

Utah State University, 2018

Bees are the most important pollinators of angiosperms, making them essential for the proper function of both agriculture and natural ecosystems. Bees are diverse, with approximately 20,000 species worldwide and 4,000 species in the United States. Despite their importance as pollinators, there are large gaps in our understanding of bee diversity and biology. In order to advance our knowledge of bee diversity and biology, I conducted three projects that help fill these gaps by addressing the taxonomy of a little-known bee group, exploring the evolution of pollen transport in two distantly-related bee genera, and then reviewing the pollen gathering behavior of bees as a whole. To expand scientific knowledge of bee diversity, I conducted a taxonomic revision of the *Perdita* subgenus *Heteroperdita* (Andrenidae). I described nine new species, described three previously unknown sexes, synonymized one species, and created a neotype for a species for which the holotype had been lost. This work increased the number of described species in *Heteroperdita* to 22 and increased the number of described *Perdita* species to 636. I then explored patterns of pollen transport in the distantly-related genera *Perdita* and *Hesperapis* (Melittidae). My results documented three different transport strategies: moist, dry, and glazed transport of pollen. Interestingly, the different ways that bees gather and transport pollen appear
to be associated with the morphology and adhesiveness of pollen that the bees specialize on. I then reviewed the pollen gathering strategies of bees, compiling previously disparate research on pollen gathering into a coherent framework. I documented a diverse array of seven types of pollen gathering strategies. I then explored the ecology, evolution, and prevalence of the different types of pollen gathering behaviors as well as provide an updated lexicon in order to facilitate continued research on pollen gathering. Overall, this dissertation advances our knowledge of the diversity and floral relationships of bees, which will support efforts to understand and conserve these important pollinators.

(330 pages)
PUBLIC ABSTRACT

Foraging behavior, taxonomy, and morphology of bees (Hymenoptera: Apoidea), with an emphasis on *Perdita* (Hymenoptera: Andrenidae)

Zachary M. Portman

Bees are the most important pollinators of flowering plants and are necessary for pollinating both wild plants and many of the crops that produce the food we eat. There are many different species of bees, with about 20,000 species worldwide and 4,000 species in the United States. Even though bees are important pollinators, there is still much we do not know about how many species there are and their biology. In order to better understand the species and their biology, I performed three projects that help fill these gaps by reviewing the species of a poorly known bee group, examining the different ways bees carry pollen, and then reviewing how bees gather pollen from flowers. To better understand bee diversity, I examined a group of species in the subgenus *Heteroperdita* in the genus *Perdita* (Andrenidae). I described nine species that were new to science, found the opposite sex of three species, and found that one species was a duplicate of a previously described species. This work increased the number of species in *Heteroperdita* to 22 and increased the number of species in the genus *Perdita* to 636. I then explored how pollen is carried back to the nest in two distantly-related bee groups, the genera *Perdita* and *Hesperapis* (Melittidae). I found that different species can carry pollen in one of three different ways: moist, dry, or glazed. Interestingly, how the bees carry pollen appears to depend on the shape and stickiness of the pollen grains that the bees prefer. I then reviewed how bees gather pollen from flowers. I combined previous research and my own observations of bees to classify the different pollen gathering behaviors into seven different types. I then examined why bees use different pollen gathering behaviors and provided a set terminology to refer to each
behavior. Overall, this dissertation advances our knowledge of the diversity of bees and their relationships with flowers, which will support efforts to understand and conserve these important pollinators.
To Theresa, who also loves bees.
ACKNOWLEDGMENTS

I would like to thank my committee for their contributions: Dr. Terry Griswold, my research adviser, Dr. Carol von Dohlen, my academic adviser, Nancy Huntly, Luis Gordillo, and Karen Kapheim.

Vincent Tepedino has my heartfelt thanks for going above and beyond in his collaboration and guidance.

This work was supported by a National Science Foundation Graduate Research Fellowship under grant number DGE-1147384, a Utah State University Graduate Enhancement Award, a Utah State University Ecology Center Research Award, and a Desert Legacy Fund grant from the Community Foundation. The USDA-ARS Pollinating Insects Research Unit provided financial and material assistance. I acknowledge the support from the Microscopy Core Facility at Utah State University for the SEM work.

Zachary M. Portman
## CONTENTS

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>2.</td>
<td>TAXONOMIC REVISION OF <em>PERDITA</em> SUBGENUS <em>HETEROPERDITA</em> TIMBERLAKE (HYMENOPTERA: ANDRENIDAE), WITH DESCRIPTIONS OF TWO ANT-LIKE MALES</td>
<td>12</td>
</tr>
<tr>
<td>3.</td>
<td>CONVERGENT EVOLUTION OF POLLEN TRANSPORT MODE IN TWO DISTANTLY RELATED BEE GENERA (HYMENOPTERA: ANDRENIDAE)</td>
<td>221</td>
</tr>
<tr>
<td>4.</td>
<td>A REVIEW AND UPDATED LEXICON OF POLLEN GATHERING BEHAVIOR IN BEES (HYMENOPTERA: APOIDEA)</td>
<td>252</td>
</tr>
<tr>
<td>5.</td>
<td>SUMMARY AND CONCLUSIONS</td>
<td>306</td>
</tr>
</tbody>
</table>

**CURRICULUM VITAE** .................................................................................................................. 312
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Categorization of the different metasomal color patterns within <em>Perdita</em> (<em>Heteroperdita</em>)</td>
<td>167</td>
</tr>
<tr>
<td>3-I</td>
<td>The number of <em>Perdita</em> and <em>Hesperapis</em> species examined, categorized by host plant family and mode of pollen transport</td>
<td>243</td>
</tr>
<tr>
<td>3-II</td>
<td>Subgeneric and major species group breakdown of pollen transport mode in <em>Perdita</em> and <em>Hesperapis</em></td>
<td>245</td>
</tr>
<tr>
<td>3-III</td>
<td>The number of <em>Perdita</em> species falling into four categories of pollen transport mode and hair characters</td>
<td>246</td>
</tr>
<tr>
<td>4-1</td>
<td>Terminology used to refer to buzz pollination</td>
<td>293</td>
</tr>
<tr>
<td>4-2</td>
<td>Rubbing with the abdomen, scopae, and/or venter of the thorax</td>
<td>296</td>
</tr>
<tr>
<td>4-3</td>
<td>Tapping behavior in the literature</td>
<td>298</td>
</tr>
<tr>
<td>4-4</td>
<td>Rasping behavior in the literature</td>
<td>299</td>
</tr>
<tr>
<td>4-5</td>
<td>Panurgine bees known to temporarily accumulating pollen</td>
<td>300</td>
</tr>
<tr>
<td>4-6</td>
<td>Comparison of the repertoire of pollen gathering behaviors found in different bee species and groups</td>
<td>301</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>------------------------------------------------------------------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>2-1</td>
<td>Distribution of <em>Heteroperdita</em></td>
<td>169</td>
</tr>
<tr>
<td>2-2</td>
<td>Ventral view of the head of <em>Perdita coldeniae</em> females</td>
<td>170</td>
</tr>
<tr>
<td>2-3</td>
<td>Stiff, curved setae on the apex of the outer face of the mid tibia in females</td>
<td>170</td>
</tr>
<tr>
<td>2-4</td>
<td>Second submedial cell of forewing</td>
<td>171</td>
</tr>
<tr>
<td>2-5</td>
<td>Dorsal views of <em>Heteroperdita</em></td>
<td>172</td>
</tr>
<tr>
<td>2-6</td>
<td>Spotted male metasomas</td>
<td>173</td>
</tr>
<tr>
<td>2-7</td>
<td>Spotted female metasomas</td>
<td>175</td>
</tr>
<tr>
<td>2-8</td>
<td>Spotted male faces</td>
<td>176</td>
</tr>
<tr>
<td>2-9</td>
<td>Spotted female faces</td>
<td>177</td>
</tr>
<tr>
<td>2-10</td>
<td>Striped male metasomas</td>
<td>178</td>
</tr>
<tr>
<td>2-11</td>
<td>Striped female metasomas</td>
<td>179</td>
</tr>
<tr>
<td>2-12</td>
<td>Striped male faces</td>
<td>180</td>
</tr>
<tr>
<td>2-13</td>
<td>Striped female faces</td>
<td>181</td>
</tr>
<tr>
<td>2-14</td>
<td>Ant-like males</td>
<td>182</td>
</tr>
<tr>
<td>2-15</td>
<td>Amber male metasomas</td>
<td>183</td>
</tr>
<tr>
<td>2-16</td>
<td>Amber female metasomas</td>
<td>184</td>
</tr>
<tr>
<td>2-17</td>
<td>Amber male faces</td>
<td>185</td>
</tr>
<tr>
<td>2-18</td>
<td>Amber female faces</td>
<td>185</td>
</tr>
<tr>
<td>2-19</td>
<td>Miscellaneous male metasomas</td>
<td>187</td>
</tr>
<tr>
<td>2-20</td>
<td>Miscellaneous female metasomas</td>
<td>189</td>
</tr>
<tr>
<td>2-21</td>
<td>Miscellaneous male faces</td>
<td>190</td>
</tr>
</tbody>
</table>
2-22 Miscellaneous female faces ............................................................... 192
2-23 Male pygidial plates ........................................................................... 194
2-24 Female pygidial plates ....................................................................... 196
2-25 *Perdita arenaria* .................................................................................. 197
2-26 Distribution (males only) of *Perdita arenaria* and *P. yanegai* .......... 198
2-27 *Perdita bellula* ................................................................................... 199
2-28 Distribution of *Perdita bellula* and *P. coldeniae* ........................... 199
2-29 *Perdita coldeniae* ............................................................................. 200
2-30 *Perdita desdemona* female lateral habitus ..................................... 200
2-31 Distribution of *Perdita desdemona* and *P. vesca, P. exusta and P. frontalis* .... 201
2-32 *Perdita exusta* ................................................................................... 201
2-33 *Perdita frontalis* ............................................................................... 202
2-34 *Perdita hippolyta* ............................................................................. 202
2-35 *Perdita hooki* .................................................................................. 203
2-36 Distribution of *Perdita hippolyta* and *P. hooki* ............................ 203
2-37 *Perdita maculosa* ............................................................................. 204
2-38 *Perdita nuttalliae* ............................................................................. 204
2-39 Distribution of *Perdita maculosa, P. nuttalliae, and P. sycorax* ........ 205
2-40 *Perdita optiva* .................................................................................. 205
2-41 Distribution of *Perdita prodigiosa, P. optiva, and P. rhodogastra* ..... 206
2-42 *Perdita pilonotata* ............................................................................ 207
2-43 Distribution of *Perdita pilonotata and P. trifasciata* ....................... 207
2-44 *Perdita prodigiosa* .......................................................................... 208
2-45 *Perdita rhodogastra* ........................................................................ 208
4-4  *Ashmeadiella bucconis* tapping on Asteraceae .................................................. 304
4-5  *Osmia pilicornis* gathering pollen by rubbing the face ...................................... 305
4-5  Specialized ventral hairs ....................................................................................... 305
The estimated 20,000 species of bees are extremely diverse in terms of nesting behavior, social behavior, and diet (Michener 2007). However, despite the widely-recognized importance of bees as pollinators, the evolution of many basic aspects of their biology remain poorly understood. Particularly in the face of widespread fears of pollinator declines, building a broad base of knowledge about bees is critically important. Currently, large gaps in our knowledge exist concerning basic bee taxonomy, with numerous species undescribed, and/or lacking identification resources (Gonzalez and Griswold 2013). In addition, other basic aspects of bee biology remain poorly known, such as how bees transport and gather pollen from flowers.

**Introduction to Perdita**

*Perdita* Smith is a species-rich genus in the family Andrenidae (Hymenoptera). With 634 species, and 127 subspecies, it is the most species-rich genus in North America (Portman and Griswold, in press). Despite being one of the most species-rich bee genera, *Perdita* is limited to the Nearctic region, with most species concentrated in the arid regions of the United States and northern Mexico (Michener 2007). The collective range of *Perdita* extends from coast to coast in the United States, as well as north into Canada and south to Guatemala (Michener 2007).

*Perdita* was originally described by F. Smith in 1853 from *Perdita halictoides* (Smith 1853). A number of species were described by Cockerell in the late 1800’s and early 1900’s, though almost all taxonomic work since then was accomplished by P. H. Timberlake, who

---

2 This chapter is written in the style of the journal Zootaxa.

**Perdita Nesting Biology**

All *Perdita* (and all bees within the subfamily Panurginae) so far explored are non-social. The species range from completely solitary to communal, meaning many different females sharing the same nest but provision their own nest cells. This condition is not very far from primitive sociality, and there is a possibility that social species exist in the numerous species whose nesting behavior remain unexplored (Rozen 1967). Of the species that are solitary with no sharing of nests, most appear to be gregarious (nesting in close proximity) though this could be forced by limitations in suitable habitat or be an artifact of detection.

All of the *Perdita* whose biology are known have been found to nest in sand, either loose or packed (Rozen 1967, Torchio 1975, Norden et al. 1992, Norden et al. 2003). However, given the small proportion of species that are the basis of this observation, as well as the fact that a bee in the sister genus, *Macrotera* (*Cockerellula* *opuntiae*) Cockerell, nests in solid sandstone (Custer 1928, Bennett and Breed 1985), the potential for different nesting substrates remains a possibility. Known nesting occurs in in ground devoid of vegetation, and ranging anywhere from completely...
horizontal surfaces to near-vertical surfaces (Rozen 1967). The nest depths range from less than 10 cm, to almost a meter, but are generally shallow (Michener 1963, Rozen 1967). The number of nest cells per nest is also quite variable, ranging from the extreme of one cell per nest in *Perdita maculigera maculipennis* (Michener and Ordway 1963) to at least 65 cells in a communal-nesting species, *Perdita lingualis* (Michener 1963). The nest architectures are largely similar in form, with a vertical or near-vertical main shaft and horizontal branches of varying length off of this main stem ending in a single nest cell.

**Floral Specialization in Perdita**

Perdita are notable for their floral specialization, with different Perdita species collectively specialized on plants from numerous different host families, meaning that a given species only gathers pollen from a related group of floral hosts or a single species of floral host (Danforth 1996, Michener 2007). Many species of Perdita often utilize the same floral hosts, and multiple species often coexist together on the same host plant. For example, Hurd et al. (1980) documented 21 species of *Perdita* that are specialists on Asteraceae. One particularly interesting species is *Perdita hurdi* Timberlake, which is oligolectic on the flowers of the Unicorn plant (*Proboscidea arenaria* and *P. althaeafolia*, in the family Pedaliaceae). Females obtain pollen by piercing through the corolla of the unopened flowers (Hurd and Linsley 1963).

*Perdita* have two adaptations that allow them to specialize on a preferred host: extended diapause and synchrony with environmental cues. Torchio (1975), followed populations of *Perdita (Perdita) nuda* Cockerell over a course of five years. The populations were discovered in 1970 and the bees gathered pollen exclusively from the gum plant, *Grindelia squarrosa* (Pursh) Dunal (Asteraceae). In the following two seasons of 1971 and 1972, the host plant failed to bloom and the bees failed to emerge. Excavations of nest sites during both years discovered larvae that
had remained in diapause. In 1973 and 1974, *G. squarrosa* bloomed normally, and the populations of *P. nuda* emerged in synchrony. This demonstrated that the *Perdita* larvae were able to remain in diapause for at least 35 months and that some kind of cues served to synchronize the bees with their floral host. Nests excavated in 1973 also showed old diapaused larvae, indicating that even when the bees emerge normally, some proportion still remained in diapause. While it is not known how long bees can remain in diapause, theoretically there is an upper limit, as diapause is associated with a metabolic cost (Danforth 1999). This delayed emergence, or bet-hedging behavior has also been recorded from another *Perdita* species, *Perdita (Alloperdita) floridensis* Timberlake as well as in a species in a sister genus, *Macrotera portalis* (Danforth 1999, Norden et al. 2003). It seems likely that the majority of *Perdita* species practice bet-hedging and delayed emergence.

As a result of the diversity of floral hosts used by the genus, *Perdita* provides a natural laboratory that can help us understand which characteristics of their biology are due to specialization on particular floral hosts and which characteristics potentially share a common evolutionary origin.

**Pollen transport**

Bees provision their young with pollen that they collect from flowers and transport back to the nest (Thorp 2000). The various methods of pollen transport can be subdivided into a few main categories. At the broadest level, bees can transport pollen from flowers to the nest either internally in the crop or externally on specialized structures. The external structures come in a diverse array of forms, and they are composed of specialized hair brushes called scopa or flattened plates called corbiculae (Thorp 1979). In most bees, the scopa are located on the hind tibia and basitarsi, but they are also found on other areas of the hind legs, the thorax, the
abdomen, or various combinations of these locations (Roberts and Vallespir 1978, Thorp 1979).
The location of these hairs is generally consistent in related bees, with the greatest amount of
variation seen between different bee families and tribes.

In addition to differences in the location of scopal hairs, bees also show a difference in
how they carry pollen in the scopa. While a slight majority of bees transport pollen in a dry state,
many bees, including the economically vital honey bees and bumble bees, carry pollen that has
been stuck together by moistening it with nectar (Thorp 1979, Michener 2007). Bees using both
dry and moist transport strategies co-occur everywhere bees are known to exist, and it is unknown
which state is ancestral in bees and what advantages, if any, the two transport strategies have.

**Pollen gathering**

Pollen transport and pollen gathering are complementary behaviors that bees use to
provision their young. While pollen transport refers to the act of bringing pollen back to the nest,
pollen gathering refers to the initial act of taking up pollen from flowers. Some bees use the same
specialized structures to both gather and transport pollen (Thorp 2000), however, most bees use
separate for pollen gathering and pollen transport. It is well-recognized that pollen gathering
behavior evolved from ancestral grooming behavior (Jander 1976, Grinfel’d 1962). However,
these basic behaviors have diversified into a number of different forms that often utilize
behavioral patterns that have no analogous grooming function. In addition, the diversity of
behaviors that bees use to gather pollen and bees often have specialized morphological structures
that aid in gathering pollen (Thorp 1979, 2000).

With the increased prevalence of high-quality electronic recording devices, as well as
advanced in rearing bumblebee colonies for scientific study, the amount of research and number
of observations of bee behavior have rapidly multiplied. However, the terminology used to
describe pollen gathering behavior in bees has not been set. As a result, many behavioral observations are published in isolation, often using disparate terms to describe identical behaviors. As a result, it is clear that bee use a variety of pollen gathering behaviors, but it difficult to compare these observations in order to identify broader patterns. For example, some important outstanding questions include whether specialist and generalist bees use different behaviors, whether generalist bees have a broader breadth of behaviors, or whether certain behaviors are associated with particular host plants. Currently, there is a clear need to organize the existing literature on pollen gathering behavior, provide a clear lexicon, and present this information in a way that is clearly understood by other researchers.

Dissertation overview

The following chapters make up a wide-ranging exploration of the biodiversity, evolution, and behavior of bees. They primarily converge around the theme of the relationship between bees and their floral hosts. Chapter two presents a taxonomic revision of the *Perdita* subgenus *Heteroperdita*, a group of minute bees that are all strictly specialized on plants in the genus *Tiquilia*. Chapter three examines the evolution of pollen transport in two distantly-related genera: *Perdita* and *Hesperapis* and suggests that the evolution of pollen transport mode may be driven by pollen morphology. Lastly, chapter four reviews the different ways in which bees gather pollen and provides an updated lexicon and definitions that delineate the different types of pollen gathering behavior.

References


Portman, Z.M. & Griswold, T. In Press. Review of *Perdita* subgenus *Procockerellia* Timberlake (Hymenoptera, Andrenidae) and the first *Perdita* gynandromorph. *Zookeys*.


Abstract

*Perdita* subgenus *Heteroperdita* Timberlake, a distinctive subgenus of 22 species from the southwestern United States and adjacent Mexico, all specialists on *Tiquilia* (Boraginaceae), is revised. Nine new species are described: *Perdita (Heteroperdita) desdemona* Portman, sp. n., *P. (H.) exusta* Portman & Griswold, sp. n., *P. (H.) hippolyta* Portman & Griswold, sp. n. (male previously incorrectly described as *P. pilonotata* Timberlake), *P. (H.) hooki* Portman & Neff, sp. n., *P. (H.) nuttalliae* Portman, sp. n., *P. (H.) prodigiosa* Portman & Griswold, sp. n., *P. (H.) sycorax* Portman, sp. n., *P. (H.) titania* Portman & Griswold, sp. n., and *P. (H.) yanegai* Portman, sp. n. The following sexes are associated and described for the first time: the male of *P. (H.) frontalis* Timberlake, 1968, the female of *P. (H.) optiva* Timberlake, 1954, and the true male of *P. (H.) pilonotata* Timberlake, 1980. *Perdita (H.) fasciatella* Timberlake, 1980 is proposed as a junior synonym of *P. (H.) sexfasciata* Timberlake, 1954. A neotype is designated for *P. (H.) pilonotata* Timberlake, 1980. Two species in particular, *P. prodigiosa* and *P. pilonotata*, are sexually dimorphic with distinctive ant-like males. Information is presented on floral relationships, phenology, and geographic distribution. Identification keys for males and females are provided.

---

3 This chapter is written in the style of the journal Zootaxa where it has been published.
Introduction

_Perdita_ Smith, 1853 is a species-rich genus that is limited to North America with both abundance and diversity concentrated in the arid southwestern United States and adjacent northern Mexico (Michener 2007). While few species have had their nesting biology explored, all known species are solitary or communal and nest in sandy or partially-sandy soil (Rozen 1967; Eickwort 1977; Danforth 1989; Norden _et al._ 2003). Their floral habits are better known, with the vast majority of species strictly specialized on floral hosts across a diverse array of plant families (Cockerell 1896; Eickwort 1977; Minckley _et al._ 2000; Neff 2003).

The vast majority of taxonomic work performed on the genus was accomplished by P. H. Timberlake (1953–1980), who published a massive multi-volume work in which he described over 500 species. Since then, 31 species were moved from _Perdita_ to the genus _Macrotera_ Smith, 1853 and taxonomic work has been limited to scattered species descriptions and synonymies, and a revision of the small subgenus _Xerophasma_ Cockerell, 1923 (Griswold & Parker 1988; Griswold 1993; Danforth 1996; Neff 2003, 2010; Michener 2007; Griswold & Miller 2010; Portman _et al._ 2016). Including the work contained herein, _Perdita_ encompasses 637 described species and an additional 127 subspecies, divided amongst 17 subgenera. With numerous undescribed taxa and the majority of species (over 400) assigned to one paraphyletic subgenus, _Perdita_ (s. str.) (Danforth 1996), it is clear that much more work remains to be done on the genus at both the specific and subgeneric levels.

The purpose of this revision is to further the knowledge of the taxonomy of the subgenus _Heteroperdita_ Timberlake, 1954 and facilitate identification of the species. Towards this end, a key is provided, as well as images and range maps of every species. In addition, information on the biology and morphology of the subgenus is compiled. This represents an important step in our understanding of the subgenus, but work still remains to be done on the taxonomy of
*Heteroperdita*, as evidenced by the large spatial and temporal gaps in sampling, disjunct ranges, and high level of variation in multiple species, which suggest the presence of cryptic species.

**Taxonomic history**

The first species of *Heteroperdita, Perdita trifasciata* Timberlake, was described in 1953 without assignment to a subgenus. The following year Timberlake (1954) described the subgenus *Heteroperdita* to contain *P. trifasciata* and six additional new species. Further species were added over the years by Timberlake (1958: 1 species, 1960: 1 species, 1962: 1 species, 1968: 2 species, 1980: 1 species). *Perdita pilonotata* Timberlake, (1980) was originally erroneously placed in the subgenus *Macroterella* Timberlake, 1954 (then *Perdita*, but now in *Macrotera*); it was later correctly placed in subgenus *Heteroperdita* by Danforth (1996). Including *P. pilonotata*, Timberlake described all of the 14 species of *Heteroperdita*. One new species — *Perdita exusta* — was reported from Clark County, Nevada in an unpublished report by Griswold *et al.* (1999) but the species was not described.

**Phylogenetics**

*Heteroperdita* falls into a monophyletic group of *Perdita* that includes the subgenera *Epimacrotera* Timberlake, 1954 and *Hesperoperdita* Timberlake, 1954, along with *Perdita* (*Glossoperdita hurdi* Timberlake, 1956 (but not the rest of *Glossoperdita*) (Danforth 1996). Within this monophyletic group, Danforth (1996) found *Heteroperdita* to be sister to *P. hurdi*, which was in turn sister to subgenus *Epimacrotera*. The similarities in structure and genitalia among both *Heteroperdita* and *P. hurdi* to various members of *Epimacrotera* raise the possibility that *Heteroperdita* has arisen from within a paraphyletic *Epimacrotera*. The relationship between
Heteroperdita, Epimacrotera, and Glossoperdita Cockrell, 1916 remains poorly resolved and more work is needed to understand the phylogeny of this group (Neff 2003).

Danforth (1996) found support for the monophyly of Heteroperdita based on the following characters: (1) the hair basket on the venter of the gena, (2) yellow maculations on the male metanotum and/or propodeum, and (3) the presence of appressed hairs on the head and mesosoma. Characters one and three are supported by this revision, but character two is not supported since many male Heteroperdita lack these light maculations. Two additional characters that support the monophyly of Heteroperdita were revealed in the present study: a relatively sparse prepygidial fimbria of the female compared to related groups and the presence of distinctive (but minute) posteriorly-curved thick setae located apically on the outer face of the mid tibia. Many species of Epimacrotera (and Glossoperdita) contain a few similar curved or downward facing setae on the apex of the mid tibia, but none have any on the outer face.

It seems likely that P. scutellaris Timberlake and P. prodigiosa, sp. n., are basal within Heteroperdita. This is supported by the fine hairs on the metasoma (a character shared with P. hurdi, Epimacrotera, Glossoperdita, and Hesperoperdita) and the relative lack of a metallic sheen on the head and mesosoma. Perdita scutellaris is further supported as basal by the non-bifurcate spiculum on the eighth sternum.

**Floral preferences**

All Heteroperdita are strictly specialized (oligolectic) on the plant genus Tiquilia (Boraginaceae). They appear to rarely visit other plants for nectar, with Mojave species most commonly visiting Eriogonum (Polygonaceae) and Petalonyx (Loasaceae). Timberlake (1954) stated that Heteroperdita are specialized on Heliotropium (Boraginaceae), as well as Tiquilia. Other than the
initial series of *P. rhodogastra* on *Heliotropium* that Timberlake cites, there is no support for *Heteroperdita* using *Heliotropium* as a pollen source. It seems probable that the bees visited *Heliotropium* due to the unavailability of *Tiquilia* flowers. Rozen (1993) observed a similar pattern of *P. arenaria* visiting *Nama* (Hydrophyllaceae) (probably *N. hispidum* A. Gray) after the local *Tiquilia* blooms had ended. The most probable explanation for these records is that *Heteroperdita* are specialized on the pollen of *Tiquilia* but will occasionally use other related plants for pollen in its absence.

Additional confusion about the floral preferences of *Heteroperdita* can be traced to misidentification of floral hosts in museum specimens. Multiple collectors have probably misidentified *Tiquilia*, most commonly mistaking it for the unrelated, but often superficially similar genus *Nama*. Over 250 specimens of *Heteroperdita* in the BBSL database are listed as being collected off of *Nama* sp. (US NPID 2016); most of these are due to the misidentification of *Tiquilia* by a single collector who appears to have also passed along the mistaken identification to other collectors. As a rule of thumb, any *Heteroperdita* specimens recorded as being collected from “*Nama* sp.” should be considered suspect.

It is possible that some *Heteroperdita* are monolectic. While some species of *Heteroperdita* have been collected from multiple species of *Tiquilia*, others have been collected from only one species. This limitation often appears to be the result of restricted habitat preferences. For example, the dune specialist *Heteroperdita* only gather pollen from *T. plicata* (Torr.) A.T. Richardson, the only species of *Tiquilia* which grows directly on sand dunes in the Mojave Desert. In addition, *P. nuttalliae* sp. n. and *P. vesca* Timberlake are only known from *T. nuttallii* (Hook.) A.T. Richardson, the only species of *Tiquilia* present in the Great Basin where these bees occur. Most species of *Heteroperdita* appear to visit different species of *Tiquilia* indiscriminately where they co-occur. However, in areas where multiple species of *Tiquilia* are
present, some species of *Heteroperdita*, such as *P. maculosa* Timberlake, have only been collected on *T. plicata*. It is unclear whether this represents an innate preference on the part of the bees or collecting bias.

One of the defining features of *Heteroperdita* is the hair basket on the venter of the head in the female sex, which is made up of inward-facing hairs which are hooked or slightly crinkled apically (Fig. 2-2). The specialized hair basket is used to extract otherwise inaccessible pollen from the long, narrow corollas of the minute *Tiquilia* flowers. In addition to the modified hairs on the venter of the head, hooked hairs are also present on the fore-coxae and, in certain species, extend down onto the venter of the mesopleuron. Further hair modifications are found in *P. scutellaris*, which are unique in *Heteroperdita* in having spatulate mandibles with a distinct hair fringe along the ventral margin (Fig. 2-13F). Similar hair baskets made up of a mass of crinkled hairs have arisen in *Hesperapis* Cockerell, 1898 (Hymenoptera: Melittidae) species specialized on *Tiquilia* (Stage 1966). In addition, certain species of *Geodiscelis* Michener and Rozen, 1999 (Hymenoptera: Colletidae) associated with *Tiquilia* in Peru and Chile have bizarrely elongate faces and mouthparts (Packer 2005; Packer & Dumesh 2014).

**Behavior on flowers**

The period of activity of *Heteroperdita* matches the temporal pattern of *Tiquilia* bloom. The flowers don’t open until relatively late in the day, from 10am–12pm, depending on temperature and time of year. As a result, *Heteroperdita* are most active during the hottest part of the day. Activity on flowers generally slackens then disappears relatively early in the afternoon (2–4 pm), though some *Heteroperdita*, particularly males, can be active even later in the day. *Heteroperdita* are most likely to be caught nectaring on other species of flowers before the *Tiquilia* flowers
open. Individuals can often be found flying around and investigating *Tiquilia* flowers before they open. Observation of individual flowers of *Tiquilia* in both the Mojave/Sonoran and Chihuahuan Deserts indicate that they only bloom for a single day.

When female *Heteroperdita* visit flowers they gather pollen by sticking their head or most of their body (more or less, depending on the size of the bee and the flower) entirely into the narrow corolla. It is unclear whether the bees use their hair baskets directly uptake the pollen from the anthers or if they use their forelegs to temporarily load the pollen into the modified hairs of the head and fore-coxae. After visiting a flower, the female will fly to a new flower or transfer the pollen to the back legs, either while perched on the flower or after having flown to a leaf or the ground. Like most other *Perdita*, *Heteroperdita* moisten the pollen with nectar and transport it as an agglutinated mass on short, sparse, simple hairs on the anterior face of the hind tibia and basitarsus. *Heteroperdita*, despite their minute size, are likely to be effective pollinators of *Tiquilia* since they regularly contact both anthers and stigma during floral visits.

Depending on the locality and availability of flowers, there can be female-female interactions at flowers as new females usurp flowers from females which are currently gathering pollen. This behavior appears rare in most areas, but was prominent at the Ibex Dunes, where floral resources were sparse. During one observation of flowers, a single flower was usurped by other females six times in one minute.

**Phenology**

Many *Heteroperdita* can be found throughout the flowering season of *Tiquilia* whenever there is bloom, while others appear to be limited to the spring. There are no species that are only active in the fall. *Perdita hooki* has only been collected during summer and fall, from July to September,
but additional sampling may expand the known phenology of this poorly known species. In the species that can be active anytime throughout the overall blooming season of *Tiquilia*, they appear to be opportunistically active based on the amount of rainfall and *Tiquilia* bloom; it is unknown whether the apparently continuous activity represents multiple generations per year or staggered emergence.

**Distribution and diversity**

*Heteroperdita* are restricted to the arid regions of the western United States and adjacent Mexico (Fig. 2-1). The center of diversity for *Heteroperdita* is the hot deserts: Mojave/Sonoran Desert with 15 known species and the Chihuahuan Desert with four known species. Some *Heteroperdita* are also found in cold deserts: the Colorado Plateau (one species), and the Great Basin (two species). The high level of diversity in the Mojave Desert especially suggests that *Heteroperdita* may have originated there. It seems likely that additional species will be found in the Chihuahuan Desert and Colorado Plateau, as these areas are relatively sparsely collected. In addition, *Heteroperdita* is not documented for most of Baja California, presumably due to limited sampling, since *Tiquilia* occurs throughout the peninsula. Taken together, *Heteroperdita* generally tracks the range of its host genus, *Tiquilia*, in the United States and Mexico (with the exception of *T. canescens* (DC.) A.T. Richardson, which seems to be quite widespread in Mexico, going as far south as Puebla, Guanajuato, Queretaro and even Oaxaca). Interestingly, *Tiquilia* has high diversity in the Chihuahuan Desert and low diversity in the Mojave/Sonoran Deserts (Moore & Jansen 2006), the reverse of the pattern of biogeographic diversity seen in *Heteroperdita*.

**Nesting biology**
Nests of *Heteroperdita* are currently unknown. All other *Perdita* whose nesting biologies have been investigated nest in the ground in sandy soils (e.g. Rozen 1967; Danforth 1989), and *Heteroperdita* likely nest in sandy soils as well. However, many of the *Tiquilia* species are gypsophiles (associated with gypsum soils), so the associated *Heteroperdita* presumably nest in them as well — gypsum soil ranges in texture from the loose sand of White Sands to the firm soils found in many of the gypsum deposits of west Texas, though these *Perdita* could be nesting in sandy microsites. Some *Heteroperdita* species have only been found in sand dunes (e.g. *P. titania* sp. n. and *P. frontalis* Timberlake), and given their minute size and relatively weak flight, they likely nest somewhere within the dunes.

Other species of Perditini — the tribe containing *Perdita* and its sister genus *Macrotera* — have been documented to delay emergence and enter extended diapause for two or three years (e.g. Torchio 1975; Danforth 1999; Norden *et al.* 2003). Given their arid habitats, it seems probable that *Heteroperdita* practice extended diapause as well. This could help explain why certain rare species have not been found in areas where they have been previously collected and how so many species manage to coexist — they may remain in diapause in drier years, and only emerge when floral resources are abundant and competition with other species is minimal.

**Ant-like males**

Two species, *P. pilonotata* and *P. prodigiosa*, have males that are more or less uniformly brown-colored, have large heads, modified metasomas, and relatively small eyes (Fig. 2-13). Superficially they bear a striking resemblance to ants, as do the flightless dimorphic males of *Macrotera portalis* Timberlake, 1954 (Danforth 1991). While males of these two *Heteroperdita* are capable of flight, and can be found patrolling and nectaring on flowers, their form raises the
possibility that they spend much of their time in the nest. Alternatively, the ant-like males could be similar to the giant-headed males of *Macrotera texana* Cresson, 1878, which can fly and mate at flowers but often spend the night in nests where additional mating is likely (Danforth & Neff 1992). Since nests are unknown, one cannot rule out the possibility of a flightless form.

**Mating**

We have observed mating on flowers in multiple *Heteroperdita* species. Mating on flowers has been definitively observed for the species *P. bellula* and *P. rhodogastra*. While additional matings have been observed, either these specimens have not been collected or the presence of multiple *Heteroperdita* species made it impossible to determine which species were actually mating. Since nesting behavior is unknown, it remains possible that mating also takes place at the nest site.

Observation in the field has also shown that males actively patrol patches of flowers and pounce on females that are in flowers. Many attempts are unsuccessful. Males have been observed erroneously pouncing on other males, and potentially females of different species. When mating occurs, it is generally brief, often lasting for only a few seconds, but occasionally extending to nearly a minute in length. When collected separately into an aspirator, males and females will often mate inside the collection tube.

**Collecting**

Due to their minute size and inconspicuous host plants, *Heteroperdita* are generally net-collected only by experienced and skilled collectors. However, *Heteroperdita* are often collected in pan
traps, as long as the pan traps are relatively close to their host plants (Z. Portman, pers. obs.). In a study comparing the efficacy of net-collecting versus pan trapping in the same plots, Wilson et al. (2008) collected 557 specimens of *P. nuttalliae* [referred to as “*Perdita* n. sp. (nr. *arenaria* Timberlake)’]. Of those, 550 were collected in pan traps, while only seven were net-collected.

The most effective way to collect *Heteroperdita* is by locating their host plant, *Tiquilia*. There is such a strong association between the two that if *Tiquilia* is found in bloom, *Heteroperdita* will likely be present. *Tiquilia* is often abundant along sandy, graded roadsides. When collecting, it is often easier to see the shadows of the bees rather than the bees themselves. They are easiest to collect when visiting flowers, since they jam themselves so far down into the corollas that they cannot easily extricate themselves and fly away. Often, slapping a net down over the entire *Tiquilia* plant is the easiest way to trap the bees, though it can be difficult to then extricate the bees from the net since they rarely fly up to the top. They also can be collected simply by putting a collecting vial directly over a bee containing flower; eventually the bee will fly out. Aspirating bees directly from flowers is possible, depending on the reflexes of the collector and abundance of the bees. Sweeping can work as well, but is limited by the low, compact growth form (of all except *T. greggii* (Torr. & A. Gray) A.T. Richardson) and the stiffness of the plants.

**Coloration**

*Heteroperdita* contains numerous metasomal color patterns. Based on the morphology of male terminalia, none of the major color patterns appear to be monophyletic, with amber, dark striped, and light striped color patterns evolving independently at least twice. The spotted color group appears to have a single origin, but has undergone an apparent reversal in *P. exusta*. It is unclear
what purpose these different color patterns serve. They could potentially be used for camouflage or batesian mimicry, since *Heteroperdita*, and *Perdita* in general, lack a well-developed sting (Timberlake 1968).

There is also a high degree of color variation within species in both the face marks and metasoma. Many species, particularly *P. vesca, P. rhodogastra*, have polymorphic coloration, containing both light and dark forms. For example, most *P. rhodogastra* have the metasoma reddish-amber, but many specimens, particularly in northern populations, have the metasoma darkened to brown or black. In addition to normal color variation, melanized forms are also relatively common (Fig. 2-20B). The melanization takes the form of a triangular dark mark on the metasoma. This type of dark mark is also seen in other *Perdita*, but appears be more common in *Heteroperdita*.

While the different color patterns do not represent monophyletic groups, they are important for identification. The species can be roughly divided into groups based on their metasomal color patterns (Table 2-1) and these groups are reflected in the identification key. Males and females typically have similar metasomal color patterns, not only those with ant-like males (*P. prodigiosa* and *P. pilonotata*), but also others (e.g. *P. optiva* and *P. exusta*).

**Methods**

This study is based on the examination of over 5,100 specimens including the holotypes of all species (except the missing holotype of *P. pilonotata*). Material was examined from the following collections:
Material was also examined from the University of California Berkeley, University of California Davis, the Los Angeles County Museum, and Arizona State University, but data from those institutions was not included in the present study due to a lack of novel specimens in those collections. All paratypes are deposited at BBSL unless specified otherwise.
Specimens were examined using a Leica M125 stereomicroscope with a Techniquip ProLine 80 LED ring light. A Keyence VHX-500F digital microscope was used to take images and measure specimens. The length of the forewing was measured from the apical margin of the costal sclerite to the most apical margin of the wing. Total body length was calculated by adding up the length of each of the three body segments. Body length is underestimated in the males because the apex of the metasoma is generally strongly curled ventrally. Forewing length and body length are based on an average of three to five specimens (when available). Body and forewing length should be treated as the typical size; a size range would not be particularly useful since there is such a large variation in size, particularly in the males.

Historic location data was georeferenced using Google Earth. Maps of examined specimens were generated with ArcGIS software using the NAD 1983 projection on a basemap of elevation with lighter colors representing lower elevations.

Material examined sections follow the same format of STATE: County: Location, number of specimens per collection event, date, collector(s), floral record. In the case of multiple collection events at the same location, the number of specimens, date, collectors, and floral records are all repeated after a semicolon. For collections in Mexico, the format is the same but the location data does not report the municipality; instead they follow the format of COUNTRY: State: Location.

Morphological terminology follows Michener (2007). Terga are separated into a disc and marginal zone, divided by the premarginal line (illustrated in Michener 2007: Figs. 2-10–12). Terga and sterna are abbreviated as T1...T6 and S1...S8, respectively. OD = median ocellar diameter.

The following characters are important taxonomic characters for *Heteroperdita*:
Second medial cell. The second medial cell can be either present or absent. Absence of the second medial cell is defined by the absence or weakening of the Cu1 and 2m-cu veins. In many species, it is variable whether the second medial cell is completely absent or represented by substantially weakened veins; as a result weakened or absent veins are considered variations on the same character state. The presence or absence of the second medial cell only occurs in the females; it is always absent in males. Most species have the entire cell present or absent; the one exception is P. prodigiosa, where the 2m-cu vein is weakened or absent dorsally and the Cu1a and the ventral portion of the 2m-cu vein are still present.

Lateral extensions. Lateral extensions of the face refer to the area of the face that is below the lateral areas and connected to the clypeus. Lateral extensions should be viewed by looking at the face straight on, and they range from short and folded over under the face or long and extending to the base of the mandibles. In some species the lateral extensions extend apically below the apical margin of the clypeus (e.g. P. scutellaris, Fig. 2-12G).

Male head form. Male heads can be oval, quadrate, or subquadrate. Head form is generally consistent throughout a species, independent of overall head size (i.e. small males still have quadrate heads). The major exception is P. pilonotata, which has oval heads in the small males (Fig. 2-14A) and quadrate heads in the large males (Fig. 2-14B). There does not appear to be dimorphism in any males, whose head sizes range continuously from small to large.

Metasomal width. Many males have the metasoma broader than the mesosoma. This character refers to the maximum width of the metasoma and mesosoma as measured from the dorsal view (e.g. Fig. 2-5A). This character is strongly correlated with head form; males with quadrate heads generally have the metasoma broader than the mesosoma.

Propodeal macula. Many species have a white or yellow triangular maculation anteriorly
on the dorsal face of the propodeum (e.g. Figs. 2-5A, B). While the triangular maculation may be reduced or absent in some species, its presence and shape is important for the identification of some species.

*Lateral mesosomal macula.* Often associated with the propodeal triangle, many species have a white or yellow band on the side of the mesosoma, occurring on the “metapleuron and anterior propodeum,” following the terminology of Timberlake (1954). This side band is often reduced to a yellow mark directly below the wing base.

Other useful taxonomic characters include the coloration pattern on the metasoma, head length/width, the shape of the mandible in the male, the presence or absence of a subapical tooth on the mandible in the female, the shape of the pygidial plate, and the male terminalia, especially the shape of the male S8.

**Systematics**

**Genus *Perdita* Smith**

**Subgenus *Heteroperdita* Timberlake**

Type species: *Perdita rhodogastra* Timberlake, 1954, by original designation.

**Diagnosis**

*Heteroperdita* is unique within Perditini in having an inward-facing hair basket on the venter of the head of the females (Fig. 2-2). Both sexes of *Heteroperdita* can be further distinguished by the following characters: minute size (2–4 mm body length), lanceolate stigma, appressed white
pubescence and tesselate sculpturing on the head and mesosoma, and the presence of multiple posteriorly-curved thick setae apically on the outer face of the mid tibia (Fig. 2-3). Females typically have at least five such curved setae; they are also present in the males, but to a lesser degree, generally with two to three curved setae on the apex of the mid tibia.

**Description of shared characters**

*Females.* Head and mesosoma strongly tesselate, slightly shiny, impunctate or with obscure, sparse punctures, with short, moss-like white pubescence; head oval or round; clypeus and supraclypeal area nude or with sparse pubescence; two well-defined subantennal sutures, with outer suture longer than inner suture; malar space linear; mandibles simple or with small subapical tooth; antenna short and squat; flagellomeres much broader than long, becoming longer apically, apical flagellomeres slightly longer than broad; venter of head with inward-facing hair basket; forewing with stigma lanceolate, approximately 3X longer than broad, slightly lightened medially; marginal cell short and truncate, equal in length or slightly shorter than length of stigma; two submarginal cells; second submarginal cell more or less subtriangular; second medial cell either present or absent; mid tibiae with at least five posteriorly-curved thick setae apically on the outer face; basitibial plate absent; short and sparse scopal hairs on hind tibia and basitarsus; all tarsal claws bifurcate; metasoma tesselate, impunctate or with minute punctures; prepygidial fimbria reduced and sparse.

*Males.* Similar to females, except: head often quadrate; mandibles simple (except large-headed *P. pilonotata*); antennae slightly longer with second to last flagellomere generally with width and length equal; venter of head with short, branched pubescence; second medial cell always absent; basitibial plate present but generally poorly defined; mid tibia with only two or
three posteriorly-curved thick setae; hairs of hind tibia and basitarsus short and branched; metasoma generally strongly curled over ventrally; genitalia with gonobase and gonocoxite fused; gonostylus divided into dorsal and ventral branch; ventral branch of gonostylus with hairs on or near apex.

Separation of males and females

While the sexes can be separated based on the number of antennal segments (12 in females and 13 in males) or the number of tergal segments (6 in females and 7 in males), these characters can be difficult to discern given the minute size of *Heteroperdita*. The easiest way to separate the sexes is that female *Heteroperdita* have a pollen basket of inward-facing hairs on the venter of the head (Fig. 2-2), which is lacking in males. In addition, males generally have the metasoma curled ventrally while females generally do not.

Key to Males

1 Metasoma yellow or white with multiple well-defined black or brown spots (Fig. 2-6); facial maculations yellow or white … 2

- Metasoma various, including black with white stripes, orange, amber, dark brown, tan, or with vague brown spots, but without distinct spots; facial maculations various, can be yellow, white, or otherwise … 9

2 Lower half of face entirely yellow up to level of antennae (Figs. 2-8B, G) … 3

- Lower half of face with at least some dark markings below antennae … 4
3 Scutellum and propodeum entirely yellow (Fig. 2-5C); eyes strongly converging below (Fig. 2-8G) … *P. wasbaueri* Timberlake

- Scutellum and dorsal area of propodeum dark; eyes parallel or only slightly converging below (Fig. 2-8B) … *P. frontalis* Timberlake

4 Metapleuron and anterior propodeum with a yellow band, or band reduced to a yellow mark directly below the wing base; generally with a yellow triangle dorso-anteriorly on the propodeum (Fig. 2-5B); lateral face marks various, generally subtriangular to triangular … 5

- Metapleuron and anterior propodeum lacking light markings; lacking a yellow triangle dorso-anteriorly on the propodeum; lateral face marks narrowly transverse (Fig. 2-8C) … *P. maculosa* Timberlake

5 Head distinctly broader than long; pygidial plate either narrow and bluntly pointed (Fig. 2-23A, P, U) or broadly triangular (Fig. 2-23Q) … 6

- Head round or longer than broad (Fig. 2-8D); pygidial plate narrow and sharply pointed (Fig. 2-23I); Great Basin … *P. nuttalliae* Portman (Note: some *P. sycorax* may key out here, but they can be separated by their geographic range in the Colorado Plateau and more golden-yellow color of the light maculations)

6 Posterior face of propodeum yellow except for distinctive Y-shaped dark mark (Fig. 2-7F); pygidial plate broadly triangular (Fig. 2-23Q) … *P. titania* Portman & Griswold

- Posterior face of propodeum lacking distinctive Y-shaped mark; pygidial plate very narrow (Figs. 2-23A, P, U) … 7

7 Face marks and metasoma white or yellowish-white; Mojave/Sonoran Deserts … 8

- Face marks and metasoma golden yellow (Figs. 2-6E, 2-8E); Colorado Plateau … *P. sycorax*
Portman

8 Hind leg with dark marks; metapleuron completely covered by a yellow band (Fig. 2-25B) …

*P. arenaria* Timberlake

- Hind leg entirely yellow; yellow band on metapleuron reduced to a mark directly below the wing base (Fig. 2-55B) … *P. yanegai* Portman

9 (1) Metasoma with white stripes apically on the discs of the terga (Fig. 2-10) … 10

- Metasoma various, generally solid amber or brown, sometimes whitish or tan (Figs. 2-14C, F, 2-15, 2-19) … 15

10 Metasoma with base color black or dark brown (Figs. 2-10B, C) … 11

- Metasoma with base color amber or brownish (Figs. 2-10A, D–G) … 12

11 Metasoma dark with white stripes on T1–T6 (Fig. 2-10B); omaulus carinate; pygidial plate truncate (Fig. 2-23O) … *P. sexfasciata* Timberlake

- Metasoma dark with white stripes on only T1–T3 or occasionally T4 (Fig. 2-10C); omaulus normal, rounded; pygidial plate notched or slightly forked (Fig. 2-23R) … *P. trifasciata* Timberlake

12 Lateral face marks large, extending up to apex of eye (Fig. 2-12G); pygidial plate sharply pointed (Fig. 2-23N) … *P. scutellaris* Timberlake

- Lateral face marks small, not extending above level of antennal sockets; pygidial plate not pointed … 13

13 Propodeum with broad yellow triangle dorso-anteriorly (Fig. 2-5A) … *P. coldeniae* Timberlake
- Propodeum lacking yellow triangle … 14

14 Metasoma broader than mesosoma (e.g. 5A); head quadrate; lateral face marks very narrowly transverse; eyes parallel (Fig. 2-12A) … *P. optiva* Timberlake

- Metasoma equal in width or narrower than mesosoma; head oval; lateral face marks subtriangular to triangular; eyes converging below (Fig. 2-12D) … *P. bellula* Timberlake

15(9) Body entirely brown or blackish; metallic tints of head and mesosoma absent or limited to small area on mesosoma; metasoma peculiarly modified, either slender and tubular or broadly expanded (Fig. 2-14C, F) … 16

- Body with metallic tints on head and mesosoma (particularly frons and scutum); metasoma normal … 17

16 Pronotal collar deeply incised; metasoma narrow and tubular (Fig. 2-14C); Chihuahuan Desert … *P. pilonotata* Timberlake

- Pronotal collar not deeply incised; metasoma very broad and dorsoventrally flattened (Fig. 2-14F); Mojave … *P. prodigiosa* Portman & Griswold

17 (15) Metasomal coloration light, either orange-amber (Fig. 2-15) or tan (Figs. 2-19A, B, F) … 18

- Metasomal coloration dark, ranging from brown to black (Figs. 2-19C, E, G, H) … 22

18 Head quadrate (Figs. 2-17D, E); metasoma broader than mesosoma; legs with well-defined dark markings; Chihuahuan Desert … 19

- Head oval or subquadrate (e.g. Figs. 2-17A–C); metasoma equal in width or narrower than mesosoma; legs lacking well-defined dark markings; Mojave/Sonoran Deserts or Great Basin … 20

19 Mandible distinctly constricted right before tip (Fig. 2-17D); paraocular marks generally restricted to paraocular lobes; head and mesosoma with a metallic greenish-bronze luster;
pygidial plate narrow, about twice as long as broad (Fig. 2-23F) … *P. hippolyta* Portman & Griswold

- Mandible sharply bent medially, not narrowed before tip (Fig. 2-17E); paraocular marks transverse; head and mesosoma with a metallic bluish luster; pygidial plate broad, length and width equal (Fig. 2-23G) … *P. hooki* Portman & Neff

20 Pygidial plate triangular with bluntly pointed apex (Fig. 2-23B); eyes more strongly converging below (Figs. 2-21A–B); face marks white … *P. bellula* Portman

- Pygidial plate truncate (Figs. 2-22M or S); eyes less strongly converging below (Figs. 2-21C, E, F); face marks generally more yellowish or tan (Figs. 2-21C, E, F) … 23

22 (17) Pygidial plate narrow and pointed (Fig. 2-23D) … *P. exusta* Portman & Griswold

- Pygidial plate truncate (Figs. 2-23S or M) … 23

23 Pygidial plate relatively narrow (Fig. 2-23S); legs lacking well-defined dark marks; metasoma tan or brown, terga generally with nebulous lateral brown spots (Figs. 2-19F–H); Great Basin … *P. vesca* Timberlake

- Pygidial plate relatively broad (Fig. 2-23M); legs with well-defined dark marks; metasoma amber or brown, basal terga often with medial white bar (Figs. 2-15B, 2-19D–E); Mojave/Sonoran Deserts … *P. rhodogastra* Timberlake

**Key to females**

1 Metasoma black with white stripes apically on the discs of the terga (Figs. 2-11A–C) … 2

- Metasoma patterning various, lacking distinct white stripes … 4

2 Omaulus carinate; pygidial plate wide and broadly rounded (Fig. 2-24Q) … *P. sexfasciata* Timberlake

- Omaulus rounded, lacking a carina; pygidial plate either triangular or narrowly spatulate (Figs.
3 Pygidial plate narrowly spatulate (Fig. 2-24T); second medial cell weakened/absent (e.g. Fig. 2-4C); Chihuahuan Desert … *P. trifasciata* Timberlake

- Pygidial plate triangular (Fig. 2-24K); second medial cell present (e.g. Fig. 2-4A); Mojave/Sonoran Deserts … *P. optiva* Timberlake

4 (1) Metasoma yellow (rarely white) with well-defined dark spots (Fig. 2-7) and pygidial plate triangular (Figs. 2-23A, E, F, I, J, R, S V, W) … 5

- Metasoma various, if well-defined dark marks, then lacking yellow coloration; pygidial plate various, can be triangular or otherwise … 11

5 Scutellum dark; 2nd submedial cell present (Fig. 2-4A) … 6

- Scutellum yellow (Fig. 2-5C); 2nd submedial cell absent (Fig. 2-4D) … *P. wasbaueri* Timberlake

6 Metapleuron and the contiguous part of the anterior propodeum with whole or partial yellow band; propodeum generally with yellow triangle dorso-anteriorly (Fig. 2-5B); lateral face marks various, ranging from transverse to filling area below antenna … 7

- Metapleuron and the contiguous part of the anterior propodeum lacking a yellow band (Fig. 2-37A); propodeum always lacking yellow triangle dorso-anteriorly; lateral face marks transverse (Fig. 2-9D) … *P. maculosa* Timberlake

7 Face not entirely light below level of antennae; eyes not encircled by thin yellow line; apex of pygidial plate pointed … 8

- Face entirely yellow below level of antennae (Figs. 2-9B–C); eyes encircled by thin yellow line;
frons often (but not always) with yellow marks (Fig. 2-9B); apex of pygidial plate slightly truncate (Fig. 2-24F); dune habitat … *P. frontalis* Timberlake

8 Head broader than long … 9

- Head width and length equal or slightly longer than broad (Fig. 2-9E); head and mesosoma strongly metallic green; Great Basin … *P. nuttalliae* Portman

9 Posterior face of propodeum with distinctive Y-shape (Fig. 2-7F), pygidial plate very narrow (Fig. 2-24S); rare dune specialist … *P. titania* Portman & Griswold

- Lacking distinctive Y-shaped mark posteriorly on propodeum; pygidial plate broadly triangular … 10

10 Light markings of face and metasoma dull yellow (Fig. 2-7E); dark spots of metasoma reduced; Colorado Plateau … *P. sycorax* Portman (in part)

- Light marking whitish; dark spots of metasoma present on all or most terga (Figs. 2-7A and H); Mojave/Sonoran Deserts … *P. arenaria* Portman or *yanegai* Portman (refer to the diagnosis and remarks of *P. arenaria* for information on separating these two species)

11 (4) Metasoma amber with white stripes apically on discs (Figs. 2-11D–E); propodeum with dorso-anterior yellow triangle (e.g. Figs. 2-5A–B) … 12

- Metasoma various, lacking white stripes; propodeum lacking a dorso-anterior yellow triangle … 13

12Paraocular marks travelling up to apex of eye (Fig. 2-13E); scutellum yellow; pygidial plate very narrow and bifurcate (Fig. 2-24P) … *P. scutellaris* Timberlake

- Paraocular marks not going above level of antennal socket; scutellum dark; pygidial plate
triangular with rounded apex (Fig. 2-24C) … *P. coldeniae* Timberlake

13 (11) Pygidial plate triangular with apex truncate (Fig. 2-24M); second medial cell with 2m-cu vein weakened dorsally (Fig. 2-4B); metasoma tan with vestigial brown bands (Figs. 2-20E–F); Mojave Desert … *P. prodigiosa* Portman & Griswold

- Pygidial plate apex not truncate, shape can be triangular or otherwise; second medial cell either completely present or completely absent/weakened (Figs. 2-4A or C) … 14

14 Metasomal coloration amber, can be orange-amber, brownish-amber, or tannish-amber (Fig. 2-16) … 15

- Metasomal coloration various, potentially white, dark brown, tan, or yellow (Figs. 2-20A–D, G–I) … 18

15 Second medial cell weakened/absent (Fig. 2-4C); Mojave/Sonoran Deserts … *P. rhodogastra* Timberlake (in part)

- Second medial cell present (Fig. 2-4A); Chihuahuan Desert … 16

16 Head much broader than long (Fig. 2-18E); posterior face of T1 generally with very faint white bar medially … *P. hooki* Portman & Neff

- Head not much broader than long or slightly longer than broad (Figs. 2-18C–D, F) … 17

17 Lower margin of facial tubercles parallel to apical margin of clypeus; metasoma tannish-amber; face always dark brown (Fig. 2-18F) … *P. pilonotata* Timberlake

- Lower margin of facial tubercles angled down towards apical margin of clypeus; metasoma orange-amber; face marks ranging from tan to brown (Figs. 2-18C–D) … *P. hippolyta* Portman & Griswold
18 (14) Second medial cell weakened/absent (Fig. 2-4C); face marks and metasoma white (Figs. 2-22A and 2-20A); Mojave/Sonoran Deserts, very common … 19

- Second medial cell present (Fig. 2-4A); face marks and metasoma various … 20

19 Metasomal coloration white or tan (Fig. 2-20A); pygidial plate spatulate (Fig. 2-24B) … P. bellula Timberlake

- Metasomal coloration brown (Figs. 2-19D–E or 2-20G); pygidial plate generally more triangular, though sometimes approaching spatulate (Figs. 2-24N–O) … P. rhodogastra Timberlake (in part)

20 Pygidial plate with apex pointed (Figs. 2-24E, R); metasoma yellowish (Fig. 2-20D) … 21

- Pygidial plate with apex rounded (Figs. 2-24D, U); metasoma light or dark brown, rarely white (Figs. 2-20C, H–I) … 22

21 Metasoma lacking well-defined spots (Fig. 2-20D); pronotal collar yellow with brown along medial suture; pronotum almost always lacking yellow triangle; Mojave Desert … P. exusta Portman & Griswold

- Metasoma with well-defined lateral spots (Fig. 2-7E); pronotal collar brown with light marks limited to dorso-posterior marks; pronotum with yellow dorso-anterior triangle (e.g. Fig. 2-5B); Colorado Plateau … P. sycorax Portman (in part)

22 Metasoma dark brown (Fig. 2-20C); mesosoma with metallic bluish luster; legs with prominent and relatively well-defined dark marks; Mojave Desert … P. desdemona Portman

- Metasomal color ranging from white to brown (Figs. 2-20H–I), but never completely dark brown; mesosoma with greenish-bronze metallic luster; legs either lacking dark markings or with nebulous dark marks; Great Basin … P. vesca Timberlake
**Perdita arenaria** Timberlake


*Perdita (Heteroperdita) arenaria* Timberlake, 1954: 368, m#f#. Holotype m# (CAS type no. 14426), 4 miles east of Edom, Riverside Co., California, USA.

**Diagnosis.** Both sexes of *P. arenaria* have the metasoma white or yellow with dark spots (Figs. 2-6A, 2-7A). They can be separated from all similar species except *P. yanegai* by the following combination of characters: face distinctly broader than long, scutum and scutellum dark, face not entirely yellow below the level of the antenna, metapleuron and anterior propodeum yellow, and propodeum with yellow triangle dorso-anteriorly.

**Redescription of female.** Length: 3.4 mm. Forewing length: 2.0 mm.

*Coloration.* Head (Fig. 2-9A) and mesosoma base color black with greenish metallic luster except luster generally lacking on frons; clypeus white; supracylpeal mark white, large, transverse; paraocular mark white, transverse to subtriangular, extending to level of summit of clypeus, sometimes with thin line extending along eye to level of top of antennal socket; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; frons generally black, lacking metallic tints medially; scape white; antenna more or less brown dorsally, whitish ventrally; pronotal collar pale yellow, more or less marked with brown along medial suture; pronotal lobe white; metapleuron and anterior propodeum pale yellow (Fig. 2-25A); propodeum with narrow white or yellow triangle dorso-anteriorly (Fig. 2-5B); ventral surface of
mesepisternum pale yellow along posterior margin; legs pale yellow except more or less darkened to brown on distal hind tarsi; wing veins tan or light brown; metasoma white or yellowish-white with multiple lateral and medial dark brown spots; T1 with pair of sublateral splotches on anterior face (splotches often split into two distinct spots) and pair of sublateral spots on dorsal face; T2–T5 with five spots: one large basomedial triangle, two small baso-lateral spots, and two apico-sublateral spots, basal spots on T2 often merging into continuous basal line, T2 fovea dark brown, lateral spots on T4–T5 generally reduced or absent; pygidial plate transparent white.

*Structure and vestiture.* Head broader than long (Fig. 2-9A); face, except for clypeus, lower supraclypeal area, and frons covered by dense recumbent white pubescence; eyes subparallel, slightly converging ventrally; facial fovea diverging dorsally, narrowly oval, extending from top of antennal socket 2/3 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, wide basally, tapering apically, widest at T3; terga tessellate and impunctate; T2 fovea linear, slightly thickened, slightly more than 1/2 length of T2; pygidial plate triangular, apex generally rounded (Fig. 2-24A); hairs of prepygidial fimbria thin, sparse.

*Redescription of male.* Length: 2.7 mm. Forewing length: 1.8 mm.

*Coloration.* Head (Fig. 2-8A) and mesosoma base color metallic greenish-bronze; clypeus white, yellow on dorsal and lateral margins; supraclypeal mark yellowish-white, large,
transverse; paraocular mark white below, yellow above, more or less completely covering lateral
areas below level of facial fovea, continuing up and encircling eye in thin line; subantennal area
yellow along margin of antennal socket; mandible white, tip reddish; labrum white, sometimes
with basomedial dark spot; scape yellow; antenna yellow, brownish dorsally; pronotal collar
yellow; pronotal lobe yellow; metapleuron and anterior propodeum yellow; ventral surface of
mesepisternum yellow medially and posteriorly; propodeum with yellow triangle dorso-anteriorly
(Fig. 2-25B); legs yellow except brown on dorsoapical spot on hind femur, large mark medially
on hind tibia, and hind tarsi slightly darkened (Fig. 2-25B); wing veins transparent tan or light
brown; metasoma yellow or white with multiple brown spots (Fig. 2-7A); T1 with pair of
sublateral splotches on anterior and pair of sublateral spots on dorsal face; T2–T6 with five spots:
one medial irregular spot, two baso-lateral small spots (spot on T2 more transverse), and two
prominent apico-sublateral spots, medial spots and spots on apical terga often reduced or absent;
T2 fovea dark brown, merging with baso-lateral spots; pygidial plate transparent yellow.

**Structure and vestiture.** Head oval, width and length equal or slightly broader than long
(Fig. 2-8A); face, except for clypeus and lower supraclypeal area densely covered by recumbent
white pubescence; eyes subparallel, slightly converging ventrally; mandible simple, extending to
far side of labrum in repose; labrum quadrate, nearly 2X broader than long; disc of clypeus
broader than high, convex, apically protruding less than 1 OD from face; lateral extension
reaching 2/3 distance to base of mandible; head with dense long thickened pubescence ventrally;
mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed,
humeral angle weak; mesepisternum and scutum densely covered by combination of recumbent
and erect white pubescence; hind tibia with sparse, short, thickened hairs; metasoma equal in
width or very slightly wider than mesosoma, suboval, wide basally, tapering apically, widest at
T3 (Fig. 2-7A); terga tessellate and impunctate; T2 fovea narrowly oval, 1/4 length of T2;
pygidial plate narrowly triangular, apex rounded, approaching truncate (Fig. 2-23A); hairs of prepygidial fimbria slightly thickened, sparse.

Terminalia. S8 (Fig. 2-56A) with spiculum bifurcate, lateral apodemes not prominent, slightly flexed downwards; apical portion slightly convex, much longer than broad, sides subparallel, weakly converging to strongly truncate apex; apex strongly folded over dorsally, flattened on top, forming a rough C-shape (with lobes pointing dorsally); sparse short hairs ventrally, circle of cuticle thinned subapically. Genital capsule as in Figs. 2-58A–B. Gonostyli separated dorsally by relatively broad V-shape; lobes of gonostylus extending slightly beyond level of penis valve, ventral lobe of gonostylus slightly longer than dorsal lobe with few minute hairs on apex; volsella much shorter than gonostylus; cuspis with couple spicules on outer margin of apex; digitus shorter than cuspis with single spicule on inner margin of apex; penis valve narrow, subparallel, slightly bowed inward medially, narrowed slightly before expanded apex, apex turned slightly outward; endophallus weakly sclerotized basally, extending slightly beyond level of apex of penis valve.

**Floral records.** Boraginaceae (62 m# 9 f#): Cryptantha sp. 9 m#, Nama sp. 4 m#, Tiquilia palmeri 31 m# 3 f#, T. plicata 9 m# 6 f#, T. sp. 9 m#, Fabaceae (1 f#): Prosopis sp. 1 f#

**Phenology.** Primarily spring (April to May), except one male collected in September.

**Distribution.** Mojave and Sonoran Deserts (Fig. 2-26A), USA and Mexico.

**Type material examined.** Holotype data: m#, CALIFORNIA: Riverside Co.: 4 miles east of Edom, 17 April 1937, P.H. Timberlake, at flowers of Coldenia palmeri [=Tiquilia palmeri (A. Gray) A.T. Richardson] (CAS type no. 14426). Allotype data: f#, same data as holotype (CAS). Paratype data: CALIFORNIA: Imperial Co.: 2.5 mi N Plaster City (32.82777 - 115.85194): 7 m# 2 f#, 1 May 1952, P.H. Timberlake, Tiquilia palmeri; 1 m#, 1 May 1952, R.C.

**Additional material examined.** Total specimens: 57 m# 13 f#.

**MEXICO:** Baja


**Remarks.** What Timberlake considered *P. arenaria* is here split into three separate species: *P. arenaria*, *P. nuttalliae*, and *P. yanegai*. While *P. nuttalliae* is distinct and relatively easy to separate, females of *P. arenaria* and *P. yanegai* can be difficult. Despite the relatively distinct characters of the males, the females of these two are extremely similar and often impossible to separate with any level of confidence. These two species mirror the pattern seen in other bee species where the males are able to be separated but the females are largely indistinguishable (e.g. *Agapostemon texanus* Cresson, 1872 and *A. angelicus* Cockerell, 1924; *P. punctosignata sulphurea* Timberlake, 1964 and *P. punctosignata flava* Timberlake, 1964). As with these two examples, *P. arenaria* and *P. yanegai* often co-occur throughout much of their range and are often collected together, though there appear to be areas of their range where only one species is present. Additional specimens and/or molecular investigation may help better resolve the two species.

*Perdita arenaria* and *P. yanegai* are extremely similar species that co-occur over most of their ranges. The males can be easily separated but the females cannot be confidently separated in most cases. In the females, there appears to be a tendency for the apex of the pygidial plate to be rounded in *P. arenaria* (Fig. 2-24A) and pointed in *P. yanegai* (Fig. 2-24W). However, there are many specimens that fall between this dichotomy and defy attempts at identification. In addition to the pygidial plate, the frons of *P. arenaria* appears to be more extensively black and lacking metallic tints while the frons of *P. yanegai* generally lacks black areas and is metallic throughout. Association with males as a means of identification should be used with caution because the two species commonly co-occur.

Unlike the females, the male of *P. arenaria* and *P. yanegai* can be easily separated. The
most definitive character is the shape of S8: in *P. arenaria*, S8 is broader, the sides are more parallel, and has a smaller thinned area of the cuticle (Fig. 2-56A), whereas *P. yanegai* has S8 narrower, the sides slightly converging apically, and has a smaller thinned area of the cuticle (Fig. 2-56H). In addition, males can be separated from *P. yanegai* by the following characters: *P. arenaria* has a well-developed yellow band on the mesopleuron and anterior propodeum (Fig. 2-25B). This band is more or less reduced in *P. yanegai*, typically limited to a yellow spot dorsally on the metapleuron directly below the wing (Fig. 2-54B). *P. arenaria* also has the dark marks on the hind leg well-developed whereas *P. yanegai* lacks dark marks on the legs (though some specimens may have faint vestigial spots). The light face marks are typically more extensive in *P. arenaria*, which has a larger subantennal mark and larger paraocular marks which typically fill up the entire lateral area. The pygidial plate of *P. arenaria* is slightly narrower than *P. yanegai*, but this character is difficult to assess without direct comparison between species.

*Perdita bellula* Timberlake


*Perdita (Heteroperdita) bellula* Timberlake, 1954: 369, m#f#. Holotype m# (CAS type no. 14442), 4 miles north of Palm Springs, Riverside Co., California, USA.

**Diagnosis.** In the female, the metasoma is white or whitish-tan and dark lateral spots may be present or absent (Figs. 2-7I, 2-20A). In addition to the metasomal coloration, the female can
be distinguished from all similar species by the combination of the pygidial plate spatulate (Fig. 2-24B), the eyes converging ventrally, the propodeum lacking a yellow triangle, and the second medial cell absent (Fig. 2-4C).

In the male, the metasoma is generally a mix of white and amber, and rarely the amber can be darkened to brown. In the typical form (Figs. 2-10E, 2-19A–B), T1–T3 are mainly white with amber along the apical borders of the terga, then T4–T6 are mainly amber with white restricted to apical the margin of the disc. The terga often have dark brown sublateral spots on T1–T5 (Fig. 2-10D); these spots can either be small and well-defined or large and diffuse, and are generally reduced on the apical terga. The male also can be distinguished by the metasoma light, head non-quadrate, pygidial plate triangular with a narrow rounded apex that approaches truncate (Fig. 2-23B), the eyes converging ventrally, and lack of a yellow triangle on the propodeum. The male can be further recognized by having the head wider than long, coloration of face with bluish tint, and metasoma equal in width or narrower than the mesosoma.

**Redescription of female.** Length: 3.0 mm. Forewing length: 1.9 mm.

*Coloration.* Head (Fig. 2-22A) and mesosoma base color black with bluish metallic luster; clypeus ranging from dirty-white to whitish-tan; supraclypeal mark dirty white, large, transverse; paraocular mark white, transverse, not going above level of summit of clypeus; mandible white or tan, tip reddish-brown; labrum dirty white; scape tannish-white; antenna light brown dorsally, tannish-white ventrally; pronotal collar black or dark brown with slight metallic tints with pair of white transverse marks dorso-posteriorly, transverse marks often reduced or even absent; pronotal lobe white or tan, light marks often restricted to margins; legs entirely whitish-tan, except often with faint, nebulous brown marks basally on hind coxa, medially on all femora and medially on hind tibia; distal hind tarsi more or less brown; wing veins ranging from tan to brown; metasoma variable, base color ranging from white to tan (Figs. 2-20A–B), terga
generally with two faint baso-lateral and two apico-sublateral small brown spots, spots often reduced or poorly defined, especially on apical segments, terga often slightly darkened along apical margin; T2 fovea dark brown; pygidial plate tan.

Structure and vestiture. Head broader than long (Fig. 2-22A); face, except for clypeus, supraclypeal area, and frons covered by dense recumbent white pubescence; eyes converging ventrally; facial fovea diverging dorsally, narrowly oval, extending from top of antennal socket 2/3 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum densely covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell absent (Fig. 2-4C); metasoma suboval, wide basally, tapering apically, widest at T3 (Fig. 2-20A); terga tessellate and impunctate; T2 fovea linear, slightly thickened, half length of T2; pygidial plate spatulate, apex broadly and evenly rounded (Fig. 2-24B); hairs of prepygidial fimbria slightly thickened, dense.

Redescription of male. Length: 2.4 mm. Forewing length: 1.7 mm.

Coloration. Head (Figs. 2-21A–B) and mesosoma base color black with metallic bluish or greenish luster; clypeus yellowish-white, rarely tan; supraclypeal mark large, transverse, white, more or less yellowish; paraocular mark white, transverse, reaching level of summit of clypeus; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; scape tan; antenna light brown dorsally, tan ventrally; pronotal collar dark brown with slight metallic tints
with pair of white transverse marks dorso-posteriorly; pronotal lobe white or tan, light marks often restricted to margins; ventral surface of mesepisternum lightened to white next to bases of mid and hind coxae; legs whitish-tan, ranging from entirely whitish-tan to more or less brown basally on all coxae, medially on all femora, and medially on mid tibia; wing veins ranging from tan to brown; metasoma extremely variable, coloration ranging from mostly white (Fig. 2-19A) to mostly amber (Fig. 2-19B), amber marks rarely darkened to brown, typical form (Figs. 2-10E, 2-19A) with T1–T3 white with amber along borders of terga, T4–6 mainly amber with white restricted to apical margin of disc, T1–T5 rarely with pair of sublateral brown spots (Fig. 2-10D); T2 fovea dark brown; pygidial plate tan or amber.

**Structure and vestiture.** Head oval, rarely subquadrate, broader than long (Figs. 2-21A–B); face, except for clypeus, and supraclypeal area covered by dense recumbent white pubescence (often more or less worn off); eyes converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrate, 2X broader than long; disc of clypeus broader than high, moderately convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/2 distance to base of mandible; head with moderately dense pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and most of scutum densely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma generally equal in width to mesosoma or slightly narrower, suboval, wide basally, tapering apically, widest at T3 (Fig. 2-19A); terga tessellate and impunctate; T2 fovea linear, slightly thickened, generally 1/4 length of T2; pygidial plate broadly triangular, apex rounded, approaching truncate (Fig 2-23B); hairs of prepygidial fimbria slightly thickened, sparse.

**Terminalia.** S8 (Fig. 2-56B) with spiculum short, bifurcate, lateral apodemes not prominent, slightly flexed downwards; apical portion slightly convex, quadrate, sides roughly
parallel, slightly diverging before converging at truncate apex; short hairs ventrally; poorly-defined circle of thinned cuticle subapically. Genital capsule as in Figs. 2-58C–D. Gonostyli separated dorsally by narrow U-shape; dorsal lobe of gonostylus broadly turned inward at apex; ventral lobe longer than dorsal lobe, extending to level of penis valve with minute hairs on outer edge of apex; volsella much shorter than gonostylus; cuspis with two spicules on apex; digitus shorter than cuspis with single spicule on inner margin of apex; penis valve long, strongly undulating on inner margin, apex strongly turned outward; endophallus weakly sclerotized with two vague parallel arms, extending slightly beyond level of penis valve.

**Floral records.** *Boraginaceae* (185 m# 170 f#): *Nama* sp. 3 m# 3 f#, *Tiquilia latior* 69 m# 66 f#, *T. palmeri* 29 m# 20 f#, *T. plicata* 80 m# 73 f#, *T. sp.* 4 m# 8 f#, *Polygonaceae* (2 f#): *Eriogonum inflatum* 1 f#, *Erythranthe* sp. 1 f#.

**Phenology.** Active from April to October.

**Distribution.** Mojave and Sonoran Deserts (Fig. 2-28A) USA (and likely Mexico). Very common, particularly along roadsides.

**Type material examined.** Holotype data: m#, **CALIFORNIA**: Riverside Co.: 4 miles north of Palm Springs, 28 June 1941, P.H. Timberlake, at flowers of *Celenia plicata* [=*Tiquilia plicata* (Torr.) A.T. Richardson] (CAS type no. 14442). Allotype data: f#, same data as holotype (CAS). Paratype data: 2 m# 6 f#, same data as holotype (UCRC).

**Additional material examined.** Total specimens: 608 m# 1231 f#. **ARIZONA:**


**Remarks.** *Perdita bellula* is the most common *Heteroperdita* in the Mojave and Sonoran Deserts. It is also one of the most variable species in terms of coloration, making it difficult to differentiate from numerous similar-looking species. In addition to being naturally variable, the coloration of the metasoma can be quite altered by the collection method. For example, the white coloration is very susceptible to discoloration due to cyanide, and the resulting specimens can have a reddish or amber metasoma (Fig. 2-15E) that resemble *P. rhodogastra*. When pan-trapped or malaise-trapped, specimens can often be bleached, which reduces the dark maculations and can bring out the amber coloration, resulting in specimens that resemble *P. coldeniae*. Darker
specimens often have larger lateral spots (Fig. 2-10D), resulting in male specimens that resemble *P. optiva*.

*Perdita coldeniae* Timberlake


*Perdita (Heteroperdita) coldeniae* Timberlake, 1954: 368, m#f#. Holotype m# (CAS type no. 14462), near Westmoreland, Imperial Co., California, USA.

**Diagnosis.** Both sexes have the metasoma amber with white apical bands on the discs of the terga (Figs. 2-10F, 2-11D), and the propodeum with a broad (width much greater than length) yellow triangle dorso-anteriorly (Fig. 2-5A), a character unique in *Heteroperdita*, though it is rarely reduced or even absent in some specimens. Other species have yellow triangles in the same position, but the triangles are narrower, with the length of the triangle greater than or equal to the width (e.g. Fig. 2-5B).

The female can be further recognized by the head broader than long, pygidial plate triangular with the apex broadly rounded (Fig. 2-24C), and the second medial cell of the forewing present (e.g. Fig. 2-4A). The male can be further recognized by the head quadrate or subquadrate (Figs. 2-12E–F), paraocular area with subtriangular marks not reaching beyond the level of the tops of the antennal sockets, and relatively small size (2.3 mm).

**Redescription of female.** Length: 2.8 mm. Forewing length: 1.8 mm.
**Coloration.** Head (Fig. 2-13D) and mesosoma base color black with greenish-bronze luster; clypeus yellowish-white; supraclypeal mark white, transverse; paraocular mark white, transverse to subtriangular, not going above level of summit of clypeus except in thin line along eye reaching level of middle of antennal socket; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; scape yellow; antenna light brown dorsally, yellow ventrally, dark brown on anterobasal margin of F2–F4; pronotal collar dark brown with slight metallic tints with pair of yellow transverse marks dorso-posteriorly; pronotal lobe yellow; propodeum with yellow triangle dorso-anteriorly, triangle much broader than long (Fig. 2-5A); legs yellow except brown basally on all coxae, basal fore femur, basal 2/3 of mid femur, medially on hind femur; hind tibia with faint brown mark basomedially, distal hind tarsi more or less darkened to brown; wing veins ranging from tan to brown; metasoma amber (occasionally brownish) except T1–T5 with white bands along margins of discs and lateral margins of terga, white bands narrowed sublaterally (Fig. 2-11D); T1 with lateral brown splotches; T2 fovea black; pygidial plate amber.

**Structure and vestiture.** Head broader than long (Fig. 2-13D); face, except for clypeus, supraclypeal area, and frons, covered by dense recumbent white pubescence; eyes slightly converging ventrally; facial fovea parallel to eye but slightly diverging dorsally, linear, extending from top of antennal socket 2/3 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum densely covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly
hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma suboval, wide basally, tapering apically, widest at T3 (Fig. 2-11D); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/2 length of T2; pygidial plate triangular, apex broadly rounded (Fig. 2-24C); hairs of prepygidial fimbria slightly thickened, dense.

**Redescription of male.** Length: 2.3 mm. Forewing length: 1.6 mm.

**Coloration.** Head (Figs. 2-12E–F) and mesosoma base color black with greenish or bluish metallic luster; clypeus yellowish-white, sometimes with pair of brownish sublateral vertical bands; supraclypeal mark yellow, transverse; paraocular mark yellowish-white, transverse to subtriangular, not reaching above level of top of antennal socket; subantennal area generally dark, occasionally entirely yellow or with yellow mark along margin of antennal socket; mandible white, tip brownish or reddish; labrum white, sometimes with basomedial dark spot; scape yellow; antenna brownish dorsally, yellow ventrally; pronotal collar with pair of well-separated yellow transverse marks dorso-posteriorly; pronotal lobe yellow; propodeum with yellow triangle dorso-anteriorly, triangle much broader than long (Fig. 2-5A); legs yellow except brown on coxae, basally on femora, and basomedially on hind tibia, more or less brown on all trochanters and distal hind tarsi; wing veins ranging from tan to brown; metasoma amber (occasionally brownish), except T1–T6 with white bands along the margins of discs and lateral margins of terga, white bands narrowed sublaterally (Fig. 2-10F); T1 generally with pair or lateral brown splotches on anterior face; T2 fovea dark brown; pygidial plate amber.

**Structure and vestiture.** Head subquadrate or quadrate, broader than long (Figs. 2-12E–F); face, except clypeus, supraclypeal area, and frons covered by dense recumbent white pubescence; eyes slightly converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, slightly
convex, apically protruding less than 1 OD from face; lateral extension reaching 1/4 distance to base of mandible; head with sparse pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum mostly covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma generally broader than mesosoma, oval, wide basally, tapering apically, widest at T3 (Fig. 2-10F); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/3 length of T2; pygidial plate narrowly triangular to spatulate, apex strongly truncate (Fig. 2-23C); hairs of prepygidial fimbria slightly thickened, sparse.

**Terminalia.** S8 (Fig. 2-56C) with spiculum slightly bifurcate basally, lateral apodemes strongly angled downwards; apical portion convex, longer than broad, sides parallel, converging slightly towards truncate apex; dense short hairs ventrally; cuticle slightly thinned medially just below apex. Genital capsule as in Figs. 2-58E–F. Gonostylus separated dorsally by narrow U-shape; lobes of gonostylus equal in length, dorsal lobe curved medially, ventral lobe with multiple long hair on apex; volsella extending to slightly below level of apex of gonostylus; cuspis slightly curving dorsally with multiple spicules apically; digitus shorter and narrow than cuspis, lacking spicules; penis valve relatively close together, parallel, abruptly turned outward at apex; endophallus extending to level of apex of penis valve.

**Floral records.** *Asteraceae* (1 m#): *Palafoxia linearis* 1 m#, *Boraginaceae* (127 m# 230 f#): *Nama* sp. 3 m# 3 f#, *Tiquilia latior* 1 m#, *T. nuttallii* 4 f#, *T. palmeri* 12 m# 29 f#, *T. plicata* 107 m# 188 f#, *T. sp.* 4 m# 6 f#, *Zygophyllaceae* (1 m# 3 f#): *Larrea tridentata* 1 m# 3 f#.

**Phenology.** Active from April to October.
**Distribution.** Mojave and Sonoran Deserts (Fig. 2-28B), USA (and likely Mexico). Very common, particularly along roadsides.

**Type material examined.** Holotype data: m#, **CALIFORNIA**: Imperial Co.: near Westmoreland, 31 May 1930, on flowers of *Coldenia palmeri* [= *Tiquilia palmeri* (A. Gray) A.T. Richardson] (CAS type no. 14462). Allotype data: f#, same data as holotype (CAS). Paratype data: **CALIFORNIA**: Imperial Co.: 3.5 mi N Mount Signal Corner (32.72888 -115.63777): 1 m#, 28 Apr 1949, R.C. Dickson, *T. palmeri*; Seeley (33.71555 -115.67888): 3 m#, 4 May 1949, R.C. Dickson, *T. palmeri* (UCRC); Westmorland (33.0372 -115.6206): 1 m#, 31 May 1930, P.H. Timberlake, *T. palmeri* (UCRC).

**Remarks.** *Perdita coldeniae* is one of the most common *Heteroperdita* in the Sonoran Desert and it is often found along roadsides and in otherwise disturbed habitats. It’s defining character — the broad yellow triangle on the anterior propodeum — is rarely reduced or absent in some specimens, particularly smaller males.

*Perdita desdemona* Portman, sp. n.

Figs. 2-20C, 2-22B, 2-24D, 2-30, 2-31A

**Diagnosis.** Male unknown. Female with the metasoma uniformly dark brown (Fig. 2-20C). It can be distinguished by the following combination of characters: second submedial cell present, pygidial plate triangular with the apex strongly rounded (Fig. 2-24D), and facial markings reduced, limited to transverse paraocular marks (prominent on the paraocular lobes) and a narrow medial line on the clypeus (Fig. 2-22D). It is very similar to darker specimens of *P. rhodogastra*, but *P. rhodogastra* has the facial markings more extensive and the second submedial cell weakened or absent. *Perdita desdemona* is also similar to *P. vesca*, but *P. desdemona* has the mesosoma with a metallic bluish tint, the legs with well-defined dark marks, the metasoma darker, the head slightly broader, and the pygidial plate slightly broader, whereas *P. vesca* has the mesosoma with a greenish-bronze tint, legs with nebulous dark marks, the metasoma lighter (and often obscurely spotted), the head only slightly broader than long, and the pygidial plate slightly narrower.

**Description of female.** Length: 3.1 mm. Forewing length: 1.8 mm.

**Coloration.** Head (Fig. 2-22B) and mesosoma base color black with bluish metallic luster
(except slightly greenish metallic around frons); clypeus dark brown with narrow, vertical white stripe medially, stripe sometimes partially reduced; supraclypeal mark dark brown; paraocular mark white, narrowly transverse, more or less limited to paraocular lobe; subantennal mark dark brown; mandible white, tip reddish; labrum dark brown, except lightened to tan along basal margin; scape tan, more or less marked with brown anteriorly; antenna light brown dorsally, tan ventrally; pronotal collar dark brown with slight metallic tints; pronotal lobe light brown on margins; legs brown except tan on joints of fore and mid tibiae and femora, anterior face of fore and mid tibiae, fore and mid tarsi, slightly lightened on joint of hind tibia and hind femur, and distal tarsi; wing veins ranging from tan to brown; metasoma dark brown, except slightly lightened at borders of terga (Fig. 2-20C); T2 fovea black; pygidial plate brown.

**Structure and vestiture.** Head broader than long (Fig. 2-22B); lateral areas and circle around antennal socket sparsely covered in recumbent white pubescence, vertex with sparse erect pubescence; eyes subparallel, slightly converging ventrally; facial fovea parallel to eye but slightly diverging dorsally, linear, extending from level of middle of antennal socket 1/2 distance to apex of eye, generally more or less obscured by pubescence; mandible appearing simple (but mandibles largely obscured in existing specimens); labrum quadrate, 1.2X broader than long; disc of clypeus broader than high, strongly convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum very sparsely covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, narrow basally, tapering apically, widest at T3 (Fig. 2-20C); terga tessellate and impunctate; T2 fovea linear, slightly thickened, over 1/2 length
of T2; pygidial plate triangular, apex strongly and evenly rounded (Fig. 2-24D); hairs of prepygidial fimbria thin, sparse.

Male. Unknown.

Floral records. None.

Phenology. Only collected in May and June.

Distribution. Mojave Desert, USA.


Etymology. The name comes from the character in Shakespeare's Othello. Treat as a noun in apposition.

Remarks. This species is known from only three female specimens. This is surprising since it occurs in the Mojave Desert, and occurs in relatively well-collected areas. One of the females was at UCRC in material determined by Timberlake as P. rhodogastra. Perdita desdemona shares many similarities with P. vesca, but is considered distinct based on its darker coloration, wider head, broader pygidial plate, and larger size. While no floral records are known for this species, two of the females have what appears to be Tiquilia pollen in their scopa and ventral head basket.

Perdita exusta Portman & Griswold, sp. n.
Diagnosis. The female of *P. exusta* has the metasoma yellowish-tan, often with vestigial dark spots laterally (Fig. 2-20D). It can be recognized from similar species by the combination of the second medial cell present (e.g. Fig 2-4A), and the pygidial plate narrowly triangular and bluntly pointed (Fig. 2-24E).

Unlike the female, the metasoma of the male is dark brown with the terga more or less lightened to light brown or tan on the apical margins (Fig. 2-19C). It can be distinguished from all similar species by the shape of the pygidial plate, which is quite narrow with the apex slightly truncate (Fig. 2-23D). It can be further recognized by the face marks yellowish-tan, and the head broader than long and oval in shape, approaching subquadrate in some specimens (Fig. 2-21D).

Description of female. Length: 3.4 mm. Forewing length: 2.1 mm.

Coloration. Head (Fig. 2-22C) and mesosoma base color black with greenish-bronze or bluish metallic luster; clypeus whitish-tan, occasionally with pair of submedial faint dark vertical bars; supraclypeal mark whitish-tan, large, transverse; paraocular mark tannish-white, transverse, reaching level of summit of clypeus except in thin line along the eye not going above top of antennal socket; mandible whitish-tan, tip reddish; labrum whitish-tan, sometimes with small medial dark spot; scape tan; antenna light brown dorsally, tan ventrally; pronotal collar brown with pair of large, narrowly separated yellowish-tan transverse marks dorso-posteriorly; pronotal lobe tan; metapleuron and anterior propodeum ranging from entirely brown to entirely yellowish-tan (Fig. 2-32A); propodeum generally dark, rarely with pair of reduced yellow marks dorso-anteriorly; legs yellowish tan except occasionally with poorly-defined vestigial brown marks basally on fore femur, dorsoapical spot on hind femur, medially on hind tibia, and distal hind
tarsi; wing veins ranging from tan to brown; metasoma yellowish-tan, except T1 with pair of C-shaped brown marks on anterior face, T1–T5 often with pair of small apico-sublateral brown spots and even smaller baso-lateral spots, spots often reduced or absent on apical terga, joints of terga often slightly darkened Fig. 2-20D); T2 fovea dark brown; pygidial plate tan.

*Structure and vestiture.* Head broader than long (Fig. 2-22C); lateral areas and circle around antennal socket densely covered in recumbent white pubescence, vertex with combination of recumbent and erect pubescence; eyes subparallel, slightly converging ventrally; facial fovea diverging dorsally, oval, extending from top of antennal socket 2/3 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma suboval, wide basally, tapering apically, widest at T3 (Fig. 2-20D); terga tessellate and impunctate; T2 fovea linear, 2/3 length of T2; pygidial plate narrow, triangular, apex bluntly pointed (Fig. 2-24E); hairs of prepygidial fimbria thin, sparse.

*Description of male.* Length: 2.8 mm. Forewing length: 1.9 mm.

*Coloration.* Head (Fig. 2-21D) and mesosoma base color black with greenish-bronze or bluish metallic luster; clypeus yellowish-tan; supraclypeal mark yellowish-tan, large, transverse; paraocular mark yellowish-tan, transverse to subtriangular, reaching level of summit of clypeus, except continuing in thin line along eye to level of top of antennal socket; mandible whitish-tan,
tip reddish; labrum whitish-tan, sometimes with basomedial dark spot; scape yellowish tan, anterior face more or less brown medially; antenna light brown dorsally, tan ventrally; pronotal collar brown with pair of large, narrowly separated yellowish-tan transverse marks dorso-posteriorly; pronotal lobe yellowish-tan; legs tan except more or less marked with brown on coxae, dorsobasally on all femora, medially on hind tibia, and distal hind tarsi; wing veins dark brown; metasoma dark brown except T1–T6 more or less lightened to tan on apical margin (Fig. 2-19C); T2 fovea black; pygidial plate tan or brown.

Structure and vestiture. Head oval or subquadrate, broader than long (Fig. 2-21D); lateral areas and circle around antennal socket densely covered in recumbent white pubescence, vertex with combination of recumbent and erect pubescence; eyes slightly converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, moderately convex, apically protruding 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; head with sparse pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum mostly covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma narrower or equal in width to mesosoma, narrowly oval, wide basally, tapering apically, widest at T3 (Fig. 2-19C); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/3 length of T2; pygidial plate narrowly triangular, apex thin, slightly truncate (Fig. 2-23D); hairs of prepygidial fimbria thin, sparse.

Terminalia. S8 (Fig. 2-56D) with spiculum bifurcate basally, lateral apodemes not prominent, apical portion convex, longer than broad, sides expanding medially before converging slightly towards truncate apex; a short hairs ventrally; lacking an obviously thinned area. Genital capsule as in Figs. 2-58G–H. Gonostyli separated dorsally by narrow V-shape; lobes of
gonostylus nearly equal in length, extending slightly beyond level of penis valve; ventral lobe slightly longer than dorsal lobe with few sparse hairs along outer margin of apex; volsella much shorter than gonostylus; cuspis with multiple spicules on apex; digitus shorter and thicker than cuspis, lacking spicules; penis valve relatively close together, slightly converging above, slightly turned outward at apex; endophallus extending slightly beyond level of penis valve.

**Floral records.** **Boraginaceae** (54 m# 59 f#): *Heliotropium* sp. 1 f#, *Nama* sp. 30 m# 30 f#, *Tiquilia latior* 20 m# 24 f#, *T. sp.* 4 m# 4 f#, **Loasaceae** (1 f#): *Eucnide* sp. 1 f#.

**Phenology.** Spring (April and May).

**Distribution.** Mojave Desert (Fig. 2-31B), USA. Known only from the northeastern part of Clark County, Nevada, USA.

**Type material.** Holotype data: f#, **NEVADA: Clark Co.:** Blue Point Spr. (36.3912 - 114.4295): 30 Apr 2004, S.M. Higbee, *Tiquilia* sp. (BBSL, accession no. BBSL578253).

Additional material examined. Total specimens: 71 m# 49 f#. NEVADA: Clark Co.:


Etymology. From Latin *exustus* meaning “burned” or “burned out” in reference both to the color of the metasoma and the Valley of Fire where it was found.

Remarks. *Perdita exusta* was originally reported by Griswold et al. (1999) and again in Griswold et al. (2006) in reports to the Nature Conservancy and Clark County, NV. However, the species has not been described until now.

The structure of the male terminalia indicates that *P. exusta* is a close relative of *P. arenaria* and the other species with a yellow metasoma with dark spots. Apparently *P. exusta* has
largely lost the distinctive spotted pattern.

 perdita frontalis Timberlake

Figs. 2-6B, 2-7B, 2-8B, 2-9B–C, 2-23E, 2-24F, 2-31B, 2-33, 2-56E, 2-58I–J

perdita (Heteroperdita) frontalis Timberlake, 1968: 12, f#. Holotype f# (CAS type no. 14701), sand dunes, 5.7 miles west of Glamis, Imperial Co., California, USA.

Diagnosis. Both sexes of P. frontalis have the metasoma yellow with dark spots (Figs. 2-6B, 2-7B). They can be distinguished from similar species by the face completely yellow below the level of the antennae (Fig. 2-8B), the scutum and scutellum entirely dark, and the lack of a dorso-anterior yellow triangle on the propodeum. The female is unique in having lollipop-shaped yellow maculations on the face behind the antennal scape (Fig. 2-9B). However, these maculations are reduced or even absent in many specimens (Fig. 2-9C).

The female can be further distinguished by the head only slightly broader than long and the pygidial plate triangular with the apex narrowly truncate (Fig. 2-24F). The male can be further distinguished by the pygidial plate narrowly triangular (Fig. 2-23E) and the eyes only slightly converging ventrally.

Redescription of female. Length: 3.2 mm. Forewing length: 2.2 mm.

Coloration. Head (Figs. 2-9B–C) and mesosoma base color black with metallic greenish-bronze luster; clypeus white with two faint lateral yellow bands; supraclypeal mark yellowish-
white, large, transverse; paraocular mark white below, yellow above, completely covering lateral areas below level of facial fovea, continuing up and encircling eye in thin line; subantennal mark yellowish-white; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; frons generally with yellow lollipop-shaped mark behind antennal scape (Fig. 2-9B), though these marks may be reduced or entirely absent (Fig. 2-9C); scape yellow; antenna yellow, brownish ventrally; pronotal collar and pronotal lobe yellow; metapleuron and anterior propodeum yellow (Fig. 2-33A); propodeum yellow laterally and basally on posterior face; ventral surface of mesepisternum yellow medially and posteriorly; legs yellow except brownish on dorsoapical spot on hind femur and basally on anterior face of hind tibia, distal hind tarsi more or less darkened; wing veins tan or light brown; metasoma yellow with multiple lateral and medial dark brown spots and with faint white bands apically on the terga (Fig. 2-7B); T1 with pair of sublateral splotches on anterior face and pair of sublateral spots on dorsal face, T2–T5 with five more or less round spots: one small medial spot, two small baso-lateral spots, and two small apico-sublateral spots, medial spot often reduced or absent on basal and apical terga, T2 fovea dark brown, merging with baso-lateral spots; pygidial plate transparent yellow.

Structure and vestiture. Head slightly broader than long (Figs. 2-9B–C); face except for clypeus and lower supraclavicular area densely covered by recumbent white pubescence; eyes subparallel, slightly converging ventrally; facial fovea diverging dorsally, oval, extending from slightly above level of antennal socket 2/3 distance to apex of eye, generally obscured by pubescence; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum mostly covered by combination of recumbent
and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia
with some short, thick, curved setae; forewing with second medial cell present; metasoma oval,
wide basally, tapering apically, widest at T3 (Fig. 2-7B); terga tessellate and impunctate; T2
fovea linear, slightly thickened, 1/2 length of T2; pygidial plate triangular, apex slightly truncate
(Fig. 2-24F); hairs of prepygidial fimbria slightly thickened, dense.

**Description of male.** Length: 3.0 mm. Forewing length: 2.1 mm.

**Coloration.** Head (Fig. 2-8B) and mesosoma base color metallic greenish-bronze; clypeus
white, yellow on dorsal and lateral margins; supraclypeal mark yellowish-white, large, transverse;
paraocular mark white below, yellow above, completely covering lateral areas below level of
facial fovea, continuing up and encircling eye in thin line; subantennal area yellow; mandible
white, tip reddish; labrum white, sometimes with basomedial dark spot; scape yellow; antenna
yellow except brownish dorsally; pronotal collar and pronotal lobe yellow; metapleuron and
anterior propodeum yellow (Fig. 2-33B); ventral surface of mesepisternum yellow medially and
posteriorly; legs yellow except slightly darkened on distal hind tarsi; wing veins transparent tan or
light brown; metasoma yellow or white with multiple brown spots (Fig. 2-6B); T1 with pair of
sublateral splotches on anterior and pair of sublateral spots on dorsal face, T2–T6 with five spots:
one medial irregular spot, two baso-lateral small spots (spot on T2 more transverse), and two
prominent apico-sublateral spots, medial spots and spots on apical terga often reduced or absent,
T2 fovea dark brown, merging with baso-lateral spots; pygidial plate transparent yellow.

**Structure and vestiture.** Head subquadrate, width and length equal or slightly broader
than long (Fig. 2-8B); face except for clypeus and lower supraclypeal area densely covered by
recumbent white pubescence; eyes subparallel, slightly converging ventrally; mandible simple,
extending to far side of labrum in repose; labrum quadrate, nearly 2X broader than long; disc of
clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension
reaching 2/3 distance to base of mandible; head with dense long thickened pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum densely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, thickened hairs; metasoma equal in width or very slightly wider than mesosoma, suboval, wide basally, tapering apically, widest at T3 (Fig. 2-6B); terga tessellate and impunctate; T2 fovea narrowly oval, 1/4 length of T2; pygidial plate narrowly triangular, apex rounded, approaching truncate (Fig. 2-23E); hairs of prepygidial fimbria slightly thickened, sparse.

_Terminalia_. S8 (Fig. 2-56E) with spiculum short, bifurcate into two thick arms, lateral apodemes not prominent; apical portion slightly convex, quadrate, sides parallel, converging sharply just before apex; dense short hairs ventrally; large circle of thinned cuticle apically. Genital capsule as in Figs. 2-58I–J. Gonostyli separated dorsally by shallow U-shape; dorsal lobe of gonostylius reduced, short and broad; ventral lobe of gonostylus short and broad, extending from apex of reduced dorsal lobe with long minute hairs on apical margin; volsella reduced, extending less than half length of penis valve; cuspis short and broad, approaching transverse, lacking spicules; digitus slightly larger than cuspis, broad, evenly rounded on inner margin, lacking spicules; penis valve greatly expanded, broad, fused basally, minutely and evenly spotted dorsally, extending beyond other parts of genitalia, turned sharply outwards at apex; endophallus also expanded with minute spots, extending to level of penis valve, combining with them to form broad, truncate apex.

_Floral records_. **Boraginaceae** (12 m# 41 f#): _Tiquilia plicata_ 12 m# 41 f#, **Polygonaceae** (1 f#): _Eriogonum deserticola_ 1 f#.

_Phenology_. Collected in May, July, and September.
**Distribution.** Mojave and Sonoran Deserts (Fig. 2-31B), USA (and likely Mexico). Dune specialist, currently known only from the Ibex and Algodones Dunes.

**Type material examined.** Holotype data: f#, **CALIFORNIA**: Imperial Co.: sand dunes, 5.7 miles west of Glamis, 25 July 1960, Dickson, on flowers of *Eriogonum deserticola* (CAS type no. 14701). Paratype data: (2 f#) **CALIFORNIA**: Imperial Co.: west of Glamis, 22 June 1960, Dickson, 1 f# on *Eriogonum deserticola*, 1 f# on *Coldenia plicata [=Tiquilia plicata]* (UCRC).


**Remarks.** While most specimens are from the Algodones Dunes, there is a single female specimen from the Ibex Dunes in Death Valley National Park. Despite relatively intensive collecting at that locality, no other specimens have been collected. The lone female has a relatively dark face, lacking the lollipop-shaped yellow facial markings. It is tentatively assigned to *P. frontalis* pending additional material, especially males. Nevertheless, the absence of *P. frontalis* specimens anywhere other than at the Ibex and Algodones dunes, combined with the distance between the dune systems, suggests that at the very least these two populations are genetically isolated.
**Perdita hippolyta** Portman & Griswold, sp. n.


*Perdita (Macroterella) pilonotata* Timberlake, 1980: 6, m# only (not f# holotype).

*Perdita (Heteroperdita) pilonotata* (m# only); Danforth 1996: 691 (change of subgenus).

**Diagnosis.** Both sexes of *P. hippolyta* have the metasoma orange-amber (Figs. 2-15C, 2-16C). Females generally have prominent tan face marks (Fig. 2-18C), but these can be entirely darkened in some specimens (Fig. 2-18D). The female can be recognized by the following combination of characters: face longer than broad, second medial cell present, and paraocular lobe generally lightened. The female is quite similar to *P. pilonotata*; see diagnosis of *P. pilonotata* for additional information. The male of *P. hippolyta* can be recognized by the following combination of characters: head quadrate (Fig. 2-17D), metasoma broader than mesosoma, face metallic greenish-bronze with tan face marks on clypeus and especially on paraocular lobes, and mandibles distinctly narrowed subapically.

**Description of female.** Length: 3.2 mm. Forewing length: 1.8 mm.

**Coloration.** Head (Figs. 2-18C–D) and mesosoma base color black with greenish-bronze metallic luster; clypeus ranging from entirely dark brown (Fig. 2-18D) to entirely tan (Fig. 2-18C); supraclypeal mark tan, transverse, often absent; paraocular area generally dark except for tan spot on paraocular lobe; mandible tan, tip reddish; labrum ranging from dark brown to tan; scape tan, often marked with brown medially; antenna brown dorsally, tan ventrally; pronotal
collar dark brown, generally with metallic tints; pronotal lobe with small tan spot, sometimes entirely dark; propodeum sometimes lightened to tan or brown laterally on anterior margin; legs dark brown except more or less lightened to tan on anterior face of fore tibia, joints, and all distal tarsi; wing veins dark brown; metasoma orange-amber (Fig. 2-16C), sometimes darkened on apical segments; T2 fovea dark brown; pygidial plate brown, margins dark.

Structure and vestiture. Head slightly longer than broad (Figs. 2-18C–D); lateral areas covered in dense recumbent white pubescence, sparse pubescence encircling eyes, vertex with sparse erect pubescence; eyes parallel; facial fovea parallel to eye, linear, extending from level of top of antennal socket halfway to apex of eye, lower parts generally obscured by pubescence; mandible with very small sharp preapical tooth (often worn); labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding 1 OD from face; lateral extension completely folded over; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely covered with combination of recumbent and erect white pubescence; fore coxa and anterior margin of venter of mesepisternum with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma suboval, narrow basally, tapering apically, widest at T3 (Fig. 2-16C); terga tessellate and impunctate; T2 fovea short, linear, slightly thickened, 1/3 length of T2; pygidial plate narrowly triangular, apex bluntly pointed (Fig. 2-24F); hairs of prepygidial fimbria thickened, sparse.

Description of male. Length: 2.4 mm. Forewing length: 1.6 mm.

Coloration. Head (Fig. 2-17D) and mesosoma base color black with greenish metallic luster; clypeus brownish-tan; supraclypeal mark tan, transverse, small; paraocular area brown, transverse, lightened to yellow-tan only on paraocular lobe; subantennal area often lightened to
tan; mandible tan, tip reddish; labrum tan; scape tan except dark brown medially; antenna dark brown, tan ventrally; pronotal collar brown with slight metallic tints generally with very faint and small tan transverse marks on dorso-posterior margin; pronotal lobe tan or light brown; propodeum lightened to tan or brown laterally on anterior margin; legs dark brown except tan on anterior fore tibia, joints of tibiae and femora, distal tarsi; wing veins dark brown; metasoma uniformly orange-amber (Fig. 2-15C); T2 fovea dark brown; pygidial plate amber.

Structure and vestiture. Head quadrate, broader than long (Fig. 2-17D); face with appressed white pubescence encircling antennal base; eyes parallel or slightly diverging below; mandible simple, expanded medially, constricted and bent subapically (Fig. 2-17D), extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, moderately convex, apically protruding less than 1 OD from face; lateral extension completely folded over; head with fine, sparse, pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely covered with combination of recumbent and erect white pubescence; hind tibia with sparse, very short thickened hairs; metasoma broader than mesosoma, oval, wide basally, tapering apically, widest at T3 (Fig. 2-15C); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/4 length of T2; pygidial plate broadly triangular, apex broadly rounded (Fig. 2-23F); hairs of prepygidial fimbria slightly thickened, sparse.

Terminalia. S8 (Fig. 2-56G) with spiculum triangular, lateral apodemes prominent, slightly curved towards; apical portion slightly convex, longer than broad, sides roughly parallel below, diverging slightly before strongly converging towards apex; apex narrow, strongly folded over dorsally, folded over portion broadly emarginate medially with two lateral points; short hairs ventrally; cuticle apparently lacking thinned area. Genital capsule as in Figs. 2-58K–L. Gonostyli
separated dorsally by broad V-shape; dorsal lobe of gonostylus not differentiated; ventral lobe of gonostylus small with few minute hairs on apex, extending below cuspis and well below level of penis valve; volsella short, not reaching level of apex of penis valve; cuspis relatively large, gradually curving dorsally with spicules on dorsal margin of apex; digitus short, near gonostylus, lacking spicules; penis valve long, extending well beyond rest of genitalia, gradually diverging apically and curving ventrally, apex slightly expanded, approaching club-shaped; endophallus not reaching level of apex of penis valve.

**Floral records.** Boraginaceae (35 m# 62 f#): *Tiquilia canescens* 6 m# 24 f#, *T. hispidissima* 17 m# 7 f#, *T.* sp. 12 m# 31 f#.

**Phenology.** Active from May to September.

**Distribution.** Chihuahuan Desert (Fig. 2-36A), USA (and likely Mexico).

**Type material.** Holotype data: m#, TEXAS: Culberson Co.: Linda Lake Salt Basin, Along Rd to dune area (31.81346 -105.08996): 22 Aug 2010, T.L. Griswold, *Tiquilia* sp. (BBSL, accession no. BBSL844675). Paratype data: (35 m# 27 f#) NEW MEXICO: Eddy Co.: Longview Spring, 0.7km E (32.1007 -104.6137): 1 f#, 9 Jun 2010, J.D. Herndon, A. Druk; Main Cave Entrance, 1.9km SSW (32.16147 -104.4494): 1 m# 1 f#, 27 May 2010, J.D. Herndon, A. Druk; Rattlesnake Springs (32.10953 -104.47161): 1 m#, 19 Jul 2010, J.D. Herndon, H. Ikerd; Seven Rivers, 3 km S (32.5791 -104.4331): 4 m# 8 f#, 16 May 1989, T.L. Griswold, *Tiquilia canescens*; Upper Lowe Springs (32.1669 -104.50281): 1 m#, 18 May 2010, A. Druk, J.D. Herndon, T.L. Griswold; 1 m#, 27 Jul 2010, J.D. Herndon; Otero Co.: White Sands National Monument; Site E2; ~0.18 km SW of Dunes Dr; gypsum dunes; interdune flats (32.7921 -106.2405): 1 m#, 2–7 Aug 2010, K. Wright (MSBA). TEXAS: Culberson Co.: Linda Lake Salt Basin, Along Rd to dune area (31.81346 -105.08996): 9 m# 10 f#, 22 Aug
2010, T.L. Griswold, T. sp. (1 m# 1 f# at UCRC); Pine Spring, 11 mi NW (31.935 -104.723): 1 m#, 12 Jun 2004, J.L. Neff, T. hispidissima (CTMI); Hudspeth Co.: Salt Flat, 1.5 mi E (31.748 -105.051): 13 m# 7 f#, 14 Jun 2005, J.L. Neff, A. Hook, T. hispidissima (1 m# 1 f# at each of AMNH, CAS, SEMC, TAMU, USNM; 8 m# 2 f# at CTMI); Winkler Co.: Kermit, 13 mi S (31.665 -103.016): 3 m#, 15 Jun 2005, J.L. Neff, A. Hook, T. hispidissima (CTMI).


Etymology. The name comes from the character in Shakespeare’s A Midsummer Night’s Dream. Treat as a noun in apposition.

Remarks. In his original description of P. pilonotata, Timberlake incorrectly associated the sexes. The name of P. pilonotata is retained by the female, while what was incorrectly ascribed as the male is here described as P. hippolyta.
Perdita hooki Portman & Neff, sp. n.


**Diagnosis.** Both sexes of *P. hooki* have an amber metasoma (Figs. 2-15D, 2-16D). The female can be recognized by the following combination of characters: head very broad (Fig. 2-18E), T1 with a very faint white bar medially on the posterior face, and the second medial cell present (e.g. Fig. 2-4A). The male can be distinguished by: head large and quadrate (Fig. 2-17E), clypeus and transverse paraocular marks white or yellowish-white, mandibles bent and lacking a modified tip, and pygidial plate broadly truncate (Fig. 2-23G).

**Description of female.** Length: 3.4 mm. Forewing length: 1.9 mm.

**Coloration.** Head (Fig. 2-18E) and mesosoma base color black with bluish metallic luster; clypeus brown with medial white stripe which may be more or less reduced; supraclypeal mark brown; paraocular mark white, transverse, not reaching level of summit of clypeus; mandible amber, tip reddish; labrum brown; scape dark brown, more or less lightened on apex; antenna brown dorsally, tan ventrally; pronotal collar and pronotal lobe dark brown; legs dark brown except tan on anterior leg with joint of femur and tibia, anterior face of tibia, and all distal tarsi; wing veins dark brown; metasoma amber (Fig. 2-16D), sometimes darkened to black on apical segments; T1 generally with obscure basomedial white bar; T2 fovea dark brown; pygidial plate brown.

**Structure and vestiture.** Head much broader than long (Fig. 2-18E); lateral areas and circle around antennal socket covered in dense recumbent white pubescence, vertex with sparse
erect pubescence; eyes parallel; facial fovea straight, parallel to eye, linear, extending from level of middle of antennal socket halfway to apex of eye; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely covered with combination of recumbent and erect white pubescence; fore coxa and venter of mesepisternum with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma suboval, wide basally, tapering apically, widest at T3 (Fig. 2-16CD; terga tessellate and impunctate, dullish on discs; T2 fovea short, linear, slightly thickened, 1/3 length of T2; pygidial plate triangular, apex bluntly pointed (Fig. 2-24G); hairs of prepygidial fimbria thickened, dense.

**Description of male.** Length: 2.8 mm. Forewing length: 1.8 mm.

**Coloration.** Head (Fig. 2-17E) and mesosoma base color black with bluish or greenish metallic luster; clypeus white, sometimes with pair of vertical sublateral brown stripes; supraclypeal mark white, transverse, often reduced or absent; paraocular mark white, transverse, reaching level of summit of clypeus; mandible tan or amber, tip reddish; labrum tan or amber; scape dark brown, lightened on apical tip; antenna light brown dorsally, tan ventrally; pronotal collar brown laterally; pronotal lobe brown, slightly lightened to tan dorsally; legs dark brown except tan on anterior fore tibia, joints of tibiae and femora, and distal tarsi; wing veins dark brown; metasoma uniformly amber (Fig. 2-15D); T2 fovea dark brown; pygidial plate amber or brown.

**Structure and vestiture.** Head quadrate, much broader than long (Fig. 2-17E); face with appressed white pubescence encircling antennal base; eyes parallel; mandible simple, strongly
bent medially, bend approaching 90 degree angle (Fig. 2-17E), mandible length extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, slightly convex, apically protruding less than 1 OD from face; lateral extension reaching 1/4 distance to base of mandible; head with fine, sparse, pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely covered with combination of recumbent and erect white pubescence; hind tibia with sparse, very short thickened hairs; metasoma broader than mesosoma, oval, wide basally, tapering apically, widest at T2/T3 (Fig. 2-16D); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/3 length of T2; pygidial plate broadly triangular, apex very broadly truncate (Fig. 2-23G); hairs of prepygidial fimbria sparse and slightly thickened laterally.

*Terminalia.* S8 (Fig. 2-56G) with spiculum triangular, lateral apodemes prominent, flexed upwards; apical portion moderately convex, longer than broad, sides diverging slightly before converging at apex, apex strongly folded over at a right angle dorsally with slight carina at location of fold, folded-over area with prominent rounded medial emargination apically; sparse short hairs ventrally; circle of thinned cuticle medially. Genital capsule as in Figs. 2-58M–N. Gonostyli separated dorsally by broad U-shape; lobes of gonostylus nearly equal in length, extending well below level of penis valve; dorsal lobe constricted basally, expanding apically into large, broad, rounded club, ventral lobe relatively narrow with few minute hairs on apex; volsella extending slightly beyond level of gonostylus; cuspis with multiple spicules on outer margin of apex; digitus short, narrow with single spicule apically; penis valve large and long, extending well beyond level of rest of genitalia, fused basally before splitting at level of gonostylus, apices sharply diverging and ending in relatively narrow point; endophallus with wavy internal structures, extending just beyond level of splitting of penis valve.
Floral records. 

**Boraginaceae** (11 m# 18 f#): *Tiquilia hispidissima* 1 m# 1 f#, *T. mexicana* 10 m# 17 f#.

**Phenology.** July to September. The limited phenology may be an artifact of the few collection events.

**Distribution.** Chihuahuan Desert (Fig. 2-36B), USA and Mexico.


**Additional material examined.** Total specimens: 4 f#. **TEXAS:** Terrell Co.: Dryden, 16 mi N (30.25 -102.017): 1 f#, 9 Sep 2012, J.L. Neff, *Tiquilia mexicana*; Dryden, 24 mi E (29.9008 -101.7844): 5 m# 2 f#, 15 Aug 2008, J.L. Neff, A. Hook, *T. Mexicana* (1 m# 1 f# at each of AMNH, TAMU; 1 m# at each of CAS, SEMC, USNM); 3 m# 7 f#, 22 Aug 2008, J.L. Neff, *T. mexicana* (1 f# at each of CAS, SEMC, USNM; 3 m# 4 f# at CTMI); Dryden, 8 mi SE (29.9732 -102.0173): 2 m# 22 f#, 28 Aug 1974, G.E. Bohart, W.J. Hanson (1 f# UCRC).
**Etymology.** The species is named for Dr. Allan Hook, an avid student of aculeate Hymenoptera, who has collected many interesting species of Texas bees, including part of the type series of this species.

**Remarks.** *Perdita hooki* is the southernmost occurring *Heteroperdita*, with a single male collected in San Luis Potosi.

*Perdita maculosa* Timberlake

Figs. 2-6C, 2-7D, 2-8C, 2-9D, 2-23H, 2-24I, 2-37, 2-39, 2-56H, 2-59A–B

*Perdita (Heteroperdita) maculosa* Timberlake, 1958: 378, m#f#. Holotype f# (CAS type no. 14594), Oasis, Riverside Co., California, USA.

**Diagnosis.** Both sexes have the metasoma yellow with brown spots (Figs. 2-6C, 2-7D). They can be distinguished from similar species by the lack of a yellow band on the metapleuron and contiguous area of the anterior propodeum (Fig. 2-37), though rarely with metapleuron partly yellow. Some related species often have a reduced yellow band; in these cases the metapleural area is generally brown and lacks the metallic sheen that is present in *P. maculosa* in this area. Both sexes of *P. maculosa* also lack a yellow triangle dorso-anteriorly on the propodeum, the scutum and scutellum are dark, and the lateral face marks are generally transverse.

The male can be further distinguished by the face with dark marks below the level of the antennae, head wider than long (Fig. 2-8C), facial markings creamy white, and fore and mid tibiae with prominent dark marks. The female can be further distinguished by the head broader
than long (Fig. 2-9D) and pygidial plate with apex pointed (Fig. 2-24I).

**Redescription of female.** Length: 3.2 mm. Forewing length: 1.9 mm.

**Coloration.** Head (Fig. 2-9D) and mesosoma base color black with bluish or greenish metallic luster; clypeus white; supraclypeal mark white, large, transverse; paraocular mark white, transverse, not going above level of summit of clypeus except in thin line along margin of eye to level of top of antennal socket; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; scape tan; antenna light brown dorsally, tan ventrally; pronotal collar black or brown with pair of large, narrowly separated yellow transverse marks dorso-anteriorly; pronotal lobe yellowish-white; metapleuron and anterior propodeum metallic, matching coloration of rest of mesosoma (Fig. 2-37A); propodeum lacking yellow triangle dorso-anteriorly; legs yellow except more or less marked with brown dorsally on all femora, medially on hind femur, and distal hind tarsi; wing veins ranging from tan to brown; metasoma yellowish-white with multiple lateral and medial brown spots; T1 marked with brown on anterior face, posterior face with two large apico-sublateral spots (Fig. 2-7C); T2–T5 with five spots: one medial large triangular mark, two small baso-lateral spots (spots on T2 more transverse with basal spots often merging into continuous band), and two relatively large, prominent apico-sublateral spots; T2 fovea dark brown; pygidial plate tan.

**Structure and vestiture.** Head broader than long (Fig. 2-9D); face except for clypeus, lower supraclypeal area, and frons covered by dense recumbent white pubescence; eyes subparallel, slightly converging ventrally; facial fovea diverging dorsally, oval, extending from top of antennal socket 2/3 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 2/3 distance to base of mandible; venter of head with abundant inward-facing broadly
hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, wide basally, tapering apically, widest at T3 (Fig. 2-7C); terga tessellate and impunctate; T2 fovea linear, moderately thickened, 2/3 length of T2; pygidial plate narrowly triangular, apex sharply pointed (Fig. 2-24I); hairs of prepygidial fimbria thin, sparse.

Redescription of male. Length: 2.5 mm. Forewing length: 1.7 mm.

Coloration. Head (Fig. 2-8C) and mesosoma base color black with greenish or bluish metallic luster; clypeus yellowish-white; supraclypeal mark white or yellowish white, large, slightly broader than long; paraocular mark white, transverse to subtriangular, often continuing in thin line along eye to level of top of antennal socket; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; scape yellow anteriorly, more or less brown posteriorly; antenna light brown dorsally, tan ventrally; pronotal collar with pair of prominent, narrowly-separated white or yellowish-white transverse marks dorso-posteriorly; pronotal lobe white or yellowish-white; metapleuron and anterior propodeum metallic, matching coloration of rest of mesosoma (Fig. 2-37B); propodeum lacking yellow triangle dorso-anteriorly; legs yellow except dark brown basally on all coxae, all femora except for joints and ventral margin, medioanteriorly on mid and hind tibiae, and distal hind tarsi; wing veins light brown; metasoma yellowish-white with multiple large dark brown spots (Fig. 2-6C); T1 with pair of spots laterally on anterior face and pair of spots sublaterally on posterior face, posterior spots sometimes merged together medially; T2–T6 with five spots: one large triangular medial spot, two small baso-lateral spots (spots on T2 more transverse), and two prominent apico-sublateral spots, medial spots and spots on apical terga often reduced or absent; T2 fovea dark brown, merging with baso-lateral spots;
pygidial plate transparent yellow.

*Structure and vestiture.* Head oval, broader than long (Fig. 2-8C); face except for clypeus and lower supraclypeal area covered by dense recumbent white pubescence; eyes converging ventrally; mandible simple, not quite extending to opposite side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching 1/2 distance to base of mandible; head with moderately dense pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum mostly covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma narrower or equal in width to mesosoma, oval, wide basally, tapering apically, widest at T3 (Fig. 2-6C); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/3 length of T2; pygidial plate narrowly triangular, apex bluntly pointed (Fig. 2-23H); hairs of prepygidial fimbria slightly thickened, sparse.

*Terminalia.* S8 (Fig. 2-56H) with spiculum bifurcate, lateral apodemes not prominent; apical portion slightly convex, longer than broad, sides parallel, apex strongly truncate; sparse short hairs ventrally; cuticle very slightly thinned in subapical circle. Genital capsule as in Figs. 2-59A–B. Gonostyli separated dorsally by narrow V-shape; ventral lobe longer than dorsal lobe, extending beyond level of rest of genitalia with few short hairs on apex; dorsal lobe shorter and wider, extending slightly beyond level of penis valve; volsella extending below level of penis valve; cuspis with multiple spicules on apex; digitus shorter and slightly thicker than cuspis, lacking spicules; penis valve parallel, slightly turned outward at apex; endophallus extending slightly below level of penis valve.

*Floral records.* **Boraginaceae** (25 m# 19 f#): *Tiquilia plicata* 25 m# 18 f#, *T*. sp. 1 f#, **Zygophyllaceae** (1 m#): *Larrea tridentata* 1 m#.
Phenology. Active in the spring (March to May).

Distribution. Mojave and Sonoran Deserts (Fig. 2-39), USA (and likely Mexico).

Type material examined. Holotype data: f#, CALIFORNIA: Riverside Co.: Oasis, 29 March 1957, E.J. Schlinger, on Coldenia plicata [=Tiquilia plicata] (CAS type no. 14594).

Allotype data: m#, same data as holotype (CAS). Paratype data: 3 m# 1 f#, same data as holotype.

Additional material examined. Total specimens: 27 m# 26 f#. ARIZONA: Maricopa Co.: Mesa, 8 km NE; Gilbert Bridge (33.48595 -111.7863): 1 m#, 10 Apr 2014, Z.M. Portman, T. plicata; Yuma Co.: Yuma, 15 mi NE (32.8637 -114.4773): 1 m#, 12 Apr 1961, R.&E. Painter.


Remarks. There is one female specimen from Clark County, Nevada which is abnormally...
light and has a light triangle on the propodeum and a light band on the metapleuron and contiguous propodeum, as well as a male and female from Anza-Borrego State Park that have a reduced light triangle and light marks on the metapleuron below the wing bases. However, all of these specimens match *P. maculosa* in morphological characters.

*Perdita nuttalliae* Portman, sp. n.

Figs. 2-6D, 2-7D, 2-8D, 2-9E, 2-23I, 2-24J, 2-38, 2-39, 2-56I, 2-59C–D

**Diagnosis.** Both sexes have the metasoma yellow with dark spots (Figs. 2-6D, 2-7D). The extent of the light maculations are variable on the face, side, and metasoma. The spots on the metasoma range in size from small to large and overlapping, the side marks can be complete or reduced to the area under the tegula, and the face marks range from transverse to large and triangular. Generally the basal spots on T2–T3 unite, forming a line along the terga basally.

The female can be recognized by the combination of the head and mesosoma with green or greenish-bronze metallic luster, head width and length equal (Fig. 2-9E), and the presence of a whole or partial yellow band on the metapleuron and contiguous sides of the propodeum (Fig. 2-38). The male can be distinguished by having the head round or longer than broad (Fig. 2-8D), the face partly dark below the level of the antennae, and face with transverse or subtriangular white or yellowish-white maculations.

**Description of female.** Length: 2.8 mm. Forewing length: 1.9 mm.

**Coloration.** Head (Fig. 2-9E) and mesosoma base color black with metallic greenish or greenish-bronze luster; clypeus yellowish-white; supraclypeal mark yellowish-white, large,
transverse; paraocular mark white or yellowish-white, transverse to triangular, reaching between level of summit of clypeus and level of antennal socket; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; scape yellowish-white; antenna tan or brown dorsally, yellowish-tan ventrally; pronotal collar yellow anteriorly and posteriorly, marked with brown in and around pronotal suture; pronotal lobe yellowish-white; metapleuron and anterior propodeum yellow (Fig. 2-38A); propodeum with narrow yellow triangle dorso-anteriorly, triangle occasionally reduced or absent; ventral surface of mesepisternum with small yellow border around base of mid coxae; legs yellow except more or less brown basally on fore coxa, dorsobasally on fore and mid femora, dorsoapical spot on hind femur, and hind tibia and distal hind tarsi; wing veins ranging from light to dark brown; metasoma yellowish-white with multiple lateral and medial brown spots, spot size extremely variable, ranging from reduced to covering majority of metasoma (Fig. 2-7D); T1 mostly brown on anterior face, posterior face with two large apico-sublateral spots; T2–T5 with five spots: one medial large triangular mark, two small baso-lateral spots (spots on T2–T3 more transverse with basal spots generally merging into continuous band), and two relatively large, prominent apico-sublateral spots; T2 fovea dark brown; pygidial plate clearish-tan.

*Structure and vestiture.* Head length and width equal (Fig. 2-9E); face except for clypeus, lower supraclypeal area, and frons covered by sparse recumbent white pubescence; eyes slightly converging ventrally; facial fovea diverging dorsally, broadly oval, extending from top of antennal socket 2/3 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/2 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly
impressed, humeral angle weak; mesepisternum and margins of scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, wide basally, tapering apically, widest at T3 (Fig. 2-7D); terga tessellate and impunctate; T2 fovea linear, slightly thickened, slightly over 1/2 length of T2; pygidial plate triangular, apex slightly blunted (Fig. 2-24J); hairs of prepygidial fimbria thin, sparse.

**Description of male.** Length: 2.4 mm. Forewing length: 1.7 mm.

**Coloration.** Head (Fig. 2-8D) and mesosoma base color black with metallic greenish or greenish-bronze luster; clypeus yellowish-white; supraclypeal mark yellowish-white, large, transverse; paraocular mark yellowish-white, subtriangular, reaching level of summit of clypeus, generally extending in thin line along eye above level of antennal socket; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; scape yellowish-tan; antenna tan or brown dorsally, yellowish-tan ventrally; pronotal collar variably marked, ranging from yellow with traces of brown medially to entirely brown with pair of dorso-posterior transverse yellow marks; pronotal lobe yellow; metapleuron and anterior propodeum variable, ranging from entirely yellow to mostly brown with yellow limited to area directly below wing base (Fig. 2-38B); propodeum with narrow yellow triangle dorso-anteriorly, triangle often reduced or absent; legs yellow, except more or less brown (brown marks ranging from large and distinct to nearly absent) basally on all coxae, posterior face of fore tibia, dorsoapical spot on mid and hind femora, basally on mid tibia, medioanteriorly on mid tibia, and distal hind tarsi; wing veins ranging from light to dark brown; metasoma yellowish-white with multiple large dark brown spots (Fig. 2-6D); T1 mostly brown on anterior face, posterior face with two large apico-sublateral spots; T2–T6 with five spots: one medial large triangular mark, two small baso-lateral spots (spots on T2–T3 more transverse with basal spots often merging into continuous band), and two relatively large,
prominent apico-sublateral spots; T2 fovea dark brown; pygidial plate transparent yellow.

**Structure and vestiture.** Head oval, width and length equal or slightly longer than broad (Fig. 2-8D); face except for clypeus, lower supraclypeal area, and frons covered by sparse recumbent white pubescence; eyes slightly converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; head with sparse pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum sparsely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma narrower or equal in width to mesosoma, suboval, wide basally, tapering apically, widest at T3 (Fig. 2-6D); terga tessellate and impunctate; T2 fovea typically linear, slightly thickened, 1/3 length of T2; pygidial plate narrowly triangular, apex narrow, point slightly rounded (Fig. 2-23I); hairs of prepygidial fimbria slightly thickened, sparse.

**Terminalia.** S8 (Fig. 2-56I) with spiculum narrow, bifurcate, lateral apodemes not prominent; apical portion slightly convex, longer than broad, sides weakly converging above, apex truncate, strongly folded over dorsally, flattened on top, flattened area slightly and evenly emarginate dorsally; sparse short hairs ventrally; large circle of cuticle thinned subapically. Genital capsule as in Figs. 2-59C–D. Gonostyli separated dorsally by narrow V-shape; ventral lobe slightly longer than dorsal lobe, extending to level of apex of penis valve with few minute hairs on apex; volsella much shorter than gonostylus; cuspis with two spicules subapically on outer margin; digitus shorter than cuspis with one spicule subapically on inner margin; penis valve parallel, narrowed slightly before expanded apex, apex turned slightly outward; endophallus extending slightly beyond level of apex of penis valve.
**Floral records.** *Asteraceae* (2 m#): *Tetradymia comosa* 1 m#, *Te.* sp. 1 m#.

*Boraginaceae* (47 m# 51 f#): *Nama* sp. 14 m# 31 f#, *Tiquilia nuttallii* 32 m# 19 f#, *T.* sp. 1 m# 1 f#.

*Fabaceae* (1 m#): *Astragalus* sp. 1 m#.

*Tamaricaceae* (2 f#): *Tamarix* sp. 2 f#.

**Phenology.** Active from April to September.

**Distribution.** Great Basin (Fig. 2-39), USA.

**Type material.** Holotype data: f#, OREGON: Harney Co.: Road to Mickey Hot Springs; BM 4125 0.9 km E (42.66242 -118.42136): 17 Jun 2012, Z.M. Portman, *Tiquilia nuttallii* (BBSL, accession no. BBSL816147). Paratype data: (30 m# 22 f#) NEVADA:


**Additional material examined.** Total specimens: 228 m# 564 f#.

1997, T. Toler; Dugway Proving Grounds; Ditto HQ, 2 km S (site 34B, W) (40.1639 -112.9297):
1 m#, 2 Jun 1998, T. Toler; Dugway Proving Grounds; Ditto HQ, 2.5 km N (site 33B, Y)
(40.2014 -112.92): 1 f#, 2 Jun 1998, T. Toler; Dugway Proving Grounds; Dog Area (Ditto), 1 km
W (site 19B) (40.1741 -112.9191): 3 m# 1 f#, 27 May 1997, T. Toler; 2 f#, 3 Jun 1997, T. Toler;
4 f#, 1 Jul 1997, T. Toler; 1 m# 3 f#, 10 Jul 1997, T. Toler; Dugway Proving Grounds; Dog Area
(Ditto), 9 km N (site 21B) (40.2668 -112.9478): 1 m# 1 f#, 3 Jun 1997, T. Toler; Dugway
Proving Grounds; Wig Flats, S (site 18) (40.17113 -112.94218): 1 f#, 12 Jun 1997, T. Toler;
Dugway Proving Grounds; Wig Mt., 5.5 km E (site5) (40.1937 -112.8586): 1 f#, 3 Jun 1997, T.
Toler; 1 m#, 10 Jun 1997, T. Toler.

**Etymology.** The specific epithet refers to the host plant of *P. nuttalliae, Tiquilia nuttallii*
(Hook.) A. Richardson.

**Remarks.** Numerous specimens of *P. nuttalliae* were examined by Timberlake and
identified as *P. arenaria*.

*Perdita optiva* Timberlake


*Perdita (Heteroperdita) optiva* Timberlake, 1954: 371, m# (not f#). Holotype m# (CAS
type no. 14645), 2.5 miles north of Plaster City, Imperial Co., California, USA.

**Diagnosis.** The male and female have different metasomal color patterns. The female can
be distinguished by the combination of the metasoma with a black and white striped pattern (Fig
2-11A) and the triangular pygidial plate (24K). The male has a variable color pattern on the metasoma which can potentially be confused with numerous different species. In the typical form (Fig. 2-10A), the terga are amber with white bands on the apices of the discs. The shade of amber on the terga ranges from a light orange amber to a dark brown amber. The terga generally (but not always) have large, poorly defined dark marks laterally — these are more prominent on the basal terga. The male of *P. optiva* can be distinguished from similar species by the following combination of characters: head quadrate (Fig. 2-12A), metasoma broader than mesosoma, propodeum lacking a yellow triangle dorsally, and pygidial plate with the apex squared-off (Fig. 2-23J).

**Description of female.** Length: 3.3 mm. Forewing length: 2.0 mm.

**Coloration.** Head (Fig. 2-13A) and mesosoma base color black with metallic greenish luster; clypeus variably marked, ranging from entirely white to brown with white limited to broad medial stripe; supraclypeal mark typically brown, sometimes with small white transverse mark; paraocular mark white, narrowly transverse, not reaching above level of summit of clypeus; mandible white, tip brown; labrum ranging from white to brown; scape white, more or less brown posteriorly; antenna brown dorsally, whitish ventrally; pronotal collar dark brown with metallic tints, occasionally with pair of reduced white transverse marks dorso-posteriorly; pronotal lobe generally dark, sometimes white in whole or part; legs dark brown basally, transitioning to white at apex of femora, brownish posteriorly on distal fore tarsi, often marked with brown medially on hind tibia, more or less brown on hind basitarsus; wing veins light brown; metasoma black, T1–T5 with white bands along apical margins of discs, bands thicker laterally and medially (Fig. 2-11A); T2 fovea black; pygidial plate brown.

**Structure and vestiture.** Head broader than long (Fig. 2-13A); face with appressed white pubescence encircling antennal base and on vertex; eyes subparallel, slightly converging
ventrally; facial fovea extremely faint, typically obscured by pubescence, linear, slightly broadened basally, extending from level of tops of antennal sockets half distance to apex of eye; mandible with small blunt subapical tooth; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension strongly folded over, not extending towards base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely covered with combination of recumbent and erect white pubescence; fore coxa and anterior venter of mesepisternum with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, slightly wide basally, tapering apically, widest at T3 (Fig. 2-11A); terga tessellate and impunctate; T2 fovea long, linear-ovoid, 2/3 length of T2; pygidial plate triangular, apex bluntly rounded (Fig. 2-24K); hairs of prepygidial fimbria slightly thickened, dense.

**Redescription of male.** Length: 2.8 mm. Forewing length: 2.0 mm.

**Coloration.** Head (Fig. 2-12A) and mesosoma base color black with bluish or greenish metallic luster; clypeus yellowish-white; supraclypeal mark yellowish-white, broad, narrowly transverse; paraocular mark yellowish-white, transverse, reaching level of summit of clypeus; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; scape white except more or less brown posteriorly; antenna tan, brownish dorsally and basally on F2–F4; pronotal collar with pair of narrowly-separated, white transverse marks dorso-posteriorly; pronotal lobe white; legs dark brown basally, transitioning to white at apex of femora, often marked with brown medially on hind tibia and distal hind tarsi; wing veins brown; metasoma amber or brown, brown coloration often more prominent on basal terga and laterally on apical terga, T1–T6 with white bands along apical margins of discs, white bands thicker laterally and
medially (Fig. 2-10A); T2 fovea dark brown; pygidial plate amber.

Structure and vestiture. Head quadrate, much broader than long (Fig. 2-12A); face with appressed white pubescence on vertex and encircling antennal base; eyes parallel or slightly diverging below; mandible simple, thickened medially, distinctly and abruptly narrowed apically, extending to far side of labrum in repose; labrum quadrate, 2X broader than long; disc of clypeus broader than high, slightly convex, apically protruding less than 1 OD from face; lateral extension reaching 1/4 distance to base of mandible; head with sparse pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely covered with combination of recumbent and erect white pubescence; hind tibia with sparse, short, thickened hairs; metasoma broader than mesosoma, oval, wide basally, tapering apically, widest at T3 (Fig. 2-10A); T2 slightly depressed apically; terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/2 length of T2; pygidial plate broadly triangular, apex broadly truncate (Fig. 2-23J); hairs of prepygidial fimbria slightly thickened, sparse.

Terminalia. S8 (Fig. 2-56J) with spiculum triangular, lateral apodemes prominent, pointing straight out; apical portion moderately convex, longer than broad, sides moderately diverging before converging subapically; apex strongly folded over dorsally, apex of folded-over portion strongly emarginate medially with two prominent lateral prongs; dense short hairs ventrally; cuticle thinned in a small circle medially. Genital capsule as in Figs. 2-59E–F. Gonostyli separated dorsally by narrow, deep U-shape; lobes of gonostylus equal in length, extending well below level of apex of penis valve; dorsal lobe large and broad; ventral lobe narrow with minute hairs on margin of apex; volsella extending slightly beyond gonostylus but still well below level of apex of penis valve; cuspis relatively large, slightly curving dorsally with six spicules on dorsal margin of apex; digitus short and narrow with single spicule on inner
margin of apex; penis valve large and long, fused basally before splitting above level of volsella, extending well beyond rest of genitalia, apices narrow, diverging laterally; endophallus extending slightly beyond level of splitting of penis valve.

**Floral records.** **Boraginaceae** (43 m# 11 f#): *Nama* sp. 9 m# 3 f#, *Tiquilia latior* 2 m#, *T. palmeri* 30 m# 8 f#, *T. plicata* 1 m#, *T. sp.* 1 m#, **Fabaceae** (1 f#): *Prosopis* sp. 1 f#.

**Phenology.** Active in the spring (April and May).

**Distribution.** Mojave and Sonoran Deserts (Fig. 2-41A) USA (and likely Mexico).

**Type material examined.** Holotype data: m#, **CALIFORNIA: Imperial Co.:** 2.5 miles north of Plaster City, 1 May 1952, P.H. Timberlake and P.D. Hurd, at flowers of *Coldenia palmeri [= Tiquilia palmeri]* (CAS type no. 14645).


**Remarks.** When it was originally described by Timberlake (1954), the male of *P. optiva* was incorrectly associated with the female of *P. sexfasciata*. That mistake was corrected by Timberlake (1968). Here, the true female of *P. optiva* is described for the first time.

*Perdita pilonotata* timberlake


*Perdita* (*Macroterella*) *pilonotata* Timberlake, 1980: 6, f#, (not m#), 35 miles northeast of Las Cruces, Otero Co., New Mexico, USA. Neotype f# (UCRC 182770). **Designation of neotype.**

*Perdita* (*Heteroperdita*) *pilonotata*; Danforth, 1996: 691 (change of subgenus).

**Diagnosis.** The female of *Perdita pilonotata* has the metasoma tan with a faint amber cast (Fig. 2-16E). It is very similar to *P. hippolyta* from which is can be definitively separated by the position of the paraocular lobes: in *P. pilonotata* they extend parallel to the apical margin of the clypeus (Fig. 2-18E), whereas in *P. hippolyta* the paraocular lobes are angled down towards the apical margin of the clypeus (Fig. 2-18F). Additionally, *P. pilonotata* has the face always dark and the metasoma more tan-colored, whereas *P. hippolyta* can have the face either light or dark (Figs. 2-18D–E) and the metasoma is more orange-colored (Fig. 2-16D). *Perdita hippolyta* is also similar to *P. hooki*, but *P. hooki* has the head much wider head, the white facial markings more
well-defined, and the metasoma tesselate and orange.

The male of *Perdita pilonotata* can be recognized by its brown or black coloration (Fig. 2-42B) and the deeply impressed pronotal collar which is unique among *Heteroperdita*. The face lacks a metallic luster, but one is sometimes present on the mesosoma. The head size is variable (Figs. 2-14A–B), but it typically has a quadrate head with small compound eyes, giving it an ant-like appearance. It can be distinguished from *P. prodigiosa* — the only similar species — by distribution (Chihuahuan Desert, not Mojave Desert), as well as by the shape of the metasoma, which is extremely narrow, almost tubular (Fig. 2-14C), the pygidial plate narrow and squared-off apically (Fig. 2-23K), and in larger males by the distinct, squarish tooth medially on the inner margin of the mandible.

**Redescription of female.** Length: 2.9 mm. Forewing length: 1.6 mm.

**Coloration.** Head (Fig. 2-18F) and mesosoma base color black with faint bluish or greenish metallic luster; clypeus, triangular paraocular mark, subantennal mark, and supraclypeal area dark brown, lacking any light maculations; mandible tan, tip reddish; labrum tan or brown; scape brown; antenna brown, more or less lightened ventrally; pronotal collar brown with slight metallic tints dorsally, lacking transverse marks; pronotal lobe brown; metapleuron and anterior propodeum brown, lacking metallic sheen; legs dark brown except lightened to tan on distal tarsi; wing veins dark brown; metasoma base color tan, often with amber cast, T1 with pair of lateral brown splotches, apical terga sometimes darkened apically (Fig. 2-16E); T2 fovea black; pygidial plate brown.

**Structure and vestiture.** Head broader than long; lateral areas of face covered in dense recumbent white pubescence extending over antennal socket up to top of facial fovea (Fig. 2-18F); eyes subparallel, slightly converging ventrally; facial fovea parallel to eye, narrowly oval,
extending from level of tops of antennal socket half distance to apex of eye, generally obscured
by pubescence; mandible with small blunt subapical tooth; labrum quadrate, slightly less than 2X
broader than long; disc of clypeus broader than high, convex, apically protruding 1 OD from face;
lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-
facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal
collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely
covered with combination of recumbent and erect white pubescence; fore coxa and anterior
margin of venter of mesepisternum with abundant, broadly hooked hairs; apex of mid tibia with
some short, thick, curved setae; forewing with second medial cell present; metasoma oval, narrow
basally, tapering apically, widest at T3 (Fig. 2-16E); terga tessellate and impunctate; T2 fovea
short, linear, slightly thickened, 1/2 to 1/3 length of T2; pygidial plate triangular, apex narrow,
bluntly pointed (Fig. 2-24L); hairs of prepygidial fimbria thickened, sparse.

**Description of male.** Length: 2.5 mm. Forewing length: 1.6 mm.

**Coloration.** Head (Figs. 2-14A–B) and mesosoma base color ranging from light to dark
brown, occasionally blackish; metallic luster absent or faint; face lightened to tan below level of
antenna, light coloration sometimes extending up to level of medial ocellus in large-headed
specimens; mandible tan, tip reddish or brown; labrum tan; scape and antenna uniformly light or
dark brown; pronotal collar generally slightly lightened laterally; pronotal lobe tan; scutum,
mesepisternum, and propodeum sometimes with metallic tints; legs brown or dark brown,
generally somewhat lighter apically; wing veins dark brown; metasoma uniformly light or dark
brown, terga somewhat lightened basally (Fig. 2-14C); T2 fovea black; pygidial plate ranging
from tan to dark brown.

**Structure and vestiture.** Head quadrate to subquadrate, slightly broader than long, antenna
relatively low on face, vertex prominent (Figs. 2-14A–B); face nearly nude, pubescence well-
spaced, minute; frons with scattered minute punctures, tessellation reduced or absent in large-headed specimens; eyes parallel, relatively reduced in size; mandible with broad medial tooth on the inner margin, only prominent in large-headed specimens; mandible length variable, ranging from reaching slightly beyond labrum to nearly base of mandible in large-headed specimens; labrum quadrate, 2X broader than long; disc of clypeus short, broader than high, slightly convex, only slighting protruding apically from face; lateral extension completely folded over in large-headed specimens, extending up to 1/3 distance to base of mandible in small-headed specimens; head with fine, sparse pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar more or less strongly impressed, humeral angle pointed and prominent; mesepisternum and anterior scutum with very sparse, erect pubescence; hind tibia with sparse, short, thickened hairs; metasoma extremely narrow, almost tubular, narrow at both apices, widest at T3 (Fig. 2-14C); terga faintly tessellate, impunctate, shiny; T2 fovea oval, length two times width, 1/5 length of T2; pygidial plate small, narrow, squared off apically, sometimes shallowly emarginate medially (Fig. 2-23K); hairs of prepygidial fimbria thickened, sparse.

**Terminalia.** S8 (Fig. 2-56K) with spiculum rounded triangular, lateral apodemes large and blunt, barely protruding; apical portion relatively small with internal medial carina which splits apically forming inflated sphere apically; cuticle noticeably thinned on either side of internal median carina; sides of apical portion strongly convex, appearing short and parallel, ending in acute corners apically; ring of minute hairs ventrally lining apical sphere. Genital capsule as in Figs. 2-59G–H. Gonostyli separated dorsally by very deep, narrow U-shape; dorsal lobe of gonostylus large and broad, extending slightly beyond level of rest of genitalia; ventral lobe small, narrow with extremely minute hairs apically; volsella extending to level of ventral lobe of gonostylus; cuspis with multiple spicules on outer margin; digitus slightly shorter than cuspis with single spicule on inner margin of apex; penis valve short, thick, gradually diverging
and narrowing apically before sharply diverging at apex; endophallus extending to level of apex of penis valve with pair of slightly sclerotized vertical areas basally.

**Floral records.** Boraginaceae (6 m# 8 f#): *Tiquilia canescens* 1 m#, *T. gossypina* 2 m# 2 f#, *T. hispidissima* 1 m# 1 f#, *T. mexicana* 2 m# 5 f#.

**Phenology.** June, August, and September.

**Distribution.** Chihuahuan Desert (Fig. 2-43A), USA and Mexico.


**Remarks.** *Perdita pilonotata* was originally described in the subgenus *Macroterella* Timberlake (at that time a subgenus of *Perdita*, but now a subgenus of *Macrotera*). Danforth (1996) correctly placed *P. pilonotata* in the subgenus *Heteroperdita*. The female and male of *P.
pilonotata, as originally described by Timberlake (1980) are not conspecific. There female is retained as *P. pilonotata* while the incorrectly associated male is described in this paper as *P. hippolyta*, sp. n.

Unfortunately the types of this species are plagued with multiple issues. Timberlake (1980) described *P. pilonotata* from four specimens: a female holotype, male allotype, male paratype, and female paratype. The holotype female and male allotype have been lost — the holotype has been missing since at least 1996 (Danforth 1996). The two remaining paratypes are deposited at UCRC; the other museums designated as type repositories for this species (CAS, Michigan State University, and Oregon State University) do not have any specimens. It appears that the missing types issue is not limited to *P. pilonotata*; all the types from Timberlake (1980) that were designated to be deposited at CAS were likely lost as well. This includes the following species: *P. (Epimacrotera) albomarginata* Timberlake, 1980, *P. (E.) pauxilla* Timberlake, 1980, *P. (Perdita) brevicornis* Timberlake, 1980, and *P. (P.) janzeni* Timberlake, 1980.

The two available paratypes of *P. pilonotata* — a female and a male — are different species, necessitating the designation of a neotype. The male and female paratypes, while both from New Mexico, were collected at different dates and localities. The female paratype was chosen for the neotype because it was collected at the same collection event as the missing female holotype.

*Perdita prodigiosa* Portman & Griswold, sp. n.

**Diagnosis.** The female of *P. prodigiosa* is distinctive due to the lack of a metallic luster on the head and mesosoma. In the typical form, the metasoma is tan with a slight amber cast and dark brown markings on the borders of the terga (20F), however the dark marks can be reduced to nebulous lateral spots (20E). The male is entirely dark brown in the typical form (Fig. 2-22F), but the clypeus and paraocular marks especially can be more or less lightened to tan (Fig. 2-22G). The female is relatively distinct among *Heteroperdita* in having the pygidial plate triangular with a distinctly truncate apex (Fig. 2-24M, *P. frontalis* has a similar pygidial plate), as well as having the 2m-cu vein of the second medial cell weakened dorsally (Fig. 2-4B).

The male of *P. prodigiosa* is distinctive and bizarre. Along with *P. pilonotata*, it lacks the metallic sheen of most other *Heteroperdita*, and instead the body coloration ranges from tan to brown or black; the coloration is generally not uniform, and is instead splotchy and uneven (Fig. 2-44B). It is also unique in that the metasoma is broad and dorsoventrally flattened (Fig. 2-14F) and the pygidial plate lacks lateral definition and is expanded, resembling the other terga (Fig. 2-23L). There is significant variation in the head size (Figs. 2-14D–E), but the typical form is large and quadrate with small eyes, giving it an ant-like appearance. In general, the upper portion of the head is darker in small-headed specimens and lighter in large-headed specimens, and the mesosoma can be lightened to tan on the sides. *Perdita prodigiosa* can be further distinguished from the similar *P. pilonotata* male by the weakly impressed pronotal collar and layer of relatively dense, minute pubescence on the metasoma.

**Description of female.** Length: 2.9 mm. Forewing length: 1.7 mm.

**Coloration.** Head and mesosoma base color black or dark brown, lacking a distinct metallic sheen; clypeus ranging from dark brown to tan; supraclypeal mark generally dark brown, sometimes with tan transverse mark; paraocular mark generally dark brown, sometimes with tan transverse or subtriangular mark; subantennal mark generally dark brown, sometimes tan;
mandible tan, tip reddish; labrum generally dark brown, sometimes tan; scape brown; antenna brown dorsally, tan ventrally; pronotal collar lacking transverse marks dorso-posteriorly; pronotal lobe white or tan; metapleuron and anterior propodeum occasionally slightly lightened to tan; legs dark brown except more or less tan on joints, anterior face of fore tibia, and all distal tarsi; wing veins dark brown; metasoma base color tan, often with amber cast, terga light medially and more or less bordered by poorly-defined dark brown marks on lateral, basal, and apical margins, T5 generally uniformly dark brown (Figs. 2-20E–F); T2 fovea black; pygidial plate tan, slightly darkened basally.

*Structure and vestiture.* Head broader than long; lateral areas of face sparsely covered in recumbent white pubescence extending up to bottom of facial fovea, vertex with sparse erect pubescence; eyes subparallel, slightly converging ventrally; facial fovea obscure, linear, parallel to eye, extending from above top of antennal socket halfway to apex of eye; mandible with extremely minute subapical tooth; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, flat, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum with very sparse, thin erect white pubescence; scutum with scattered sparse erect hairs, hairs becoming thickened, denser, and recumbent along posterior margin; propodeum with posterior face relatively smooth and shiny except for distinctly tessellate dorso-anterior triangle; fore coxa and anterior margin of venter of mesepisternum with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present but 2m-cu vein distinctly weakened dorsally (Fig. 2-4B); metasoma oval, narrow basally, tapering apically, widest at T3 (Fig. 2-20E); terga tessellate and impunctate; T2 fovea short, linear, slightly thickened, about half length of T2;
pygidial plate triangular, apex strongly truncate (Fig. 2-24M); hairs of prepygidial fimbria thickened, sparse.

**Description of male.** Length: 2.3 mm. Forewing length: 1.5 mm.

**Coloration.** Head (Figs. 2-14D–E) and mesosoma base color dark brown; face lightened to tan below level of antenna; mandible tan, tip brown; labrum tan, sometimes with basomedial dark spot; scape dark brown; antenna brown, more or less lightened to tan apically and ventrally; pronotal collar light brown or tan; pronotal lobe tan (Fig. 2-44B); mesepisternum often lighter brown than scutum; metapleuron and anterior propodeum often lightened to tan; legs dark brown except generally lightened to tan apically and at joints; wing veins dark brown; metasoma uniformly dark brown (Fig. 2-14F); T2 fovea black.

**Structure and vestiture.** Head quadrate, broader than long, antenna relatively low on face, vertex prominent (Figs. 2-14D–E); face nearly devoid of pubescence with well-spaced, minute hairs; eyes relatively reduced in size, parallel or slightly diverging dorsally; mandible simple, slender, extending to far side of labrum in repose; labrum quadrate, 2X broader than long; disc of clypeus short, broader than high, slightly convex, apically protruding less than 1 OD from face; lateral extension completely folded over; head with fine, dense pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle indistinct; mesepisternum and scutum with very sparse, long, erect, fine pubescence; hind tibia with sparse, short, thickened hairs; metasoma broader than mesosoma, strongly oval, narrow basally, widest at margin of T2/T3 (Fig. 2-14F), strongly dorsoventrally flattened; terga tessellate, slightly shiny with minute, close punctures; terga covered in short, fine, obscure pubescence, particularly laterally and on apical terga; T2 fovea obscurely placed on lateral margin of terga, linear, 1/2 length of T2; pygidial plate lacking lateral definition, appearing similar to other terga, tessellate and obscurely punctate, apical rim smooth and slightly flexed outward, medial tuft of
hairs apically on ventral surface (Fig. 2-23L); hairs of prepygidial fimbria with few thickened hairs laterally.

Terminalia. S8 (Fig. 2-56L) with spiculum lacking, reduced to short ventrally-folded segment, apex with two poorly-defined sublateral points; lateral apodemes protruding straight out; apical portion slightly convex, longer than broad, sides converging slightly; apex strongly truncate; sparse hairs ventrally; oval of thinned cuticle basally. Genital capsule as in Figs. 2-59I–K. Gonobase/gonocoxite enlarged and broad; gonostyli separated dorsally by broad, shallow U-shape; dorsal lobe of gonostylus with narrow base, apex large and bulbous, expanded dorsoventrally (resembling balancing rock formation); ventral lobe of gonostylus long, narrow, abruptly bent ventrally before gradually curving along margin of dorsal lobe of gonostylus until pointing upwards again, apex with few minute hairs; volsella exceeding rest of genitalia; cuspis exceptionally enlarged and elongate with apex expanded, slightly bifurcate, ornamented with multiple spicules, particularly along lateral margins; digitus reduced to small flap at inner base of cuspis; penis valve long and narrow, close together basally, slightly diverging dorsally, strongly curving ventrally, course paralleling lobes of gonostylus; endophallus reduced, not extending beyond gonobase.

Floral records. Boraginaceae (24 m# 78 f#): Nama sp. 18 m# 66 f#, Tiquilia latior 6 m# 11 f#, T. sp. 1 f#, Malvaceae (4 f#): Sphaeralcea sp. 4 f#. Note: as discussed in the introduction, the Nama sp. records almost certainly represent misidentified Tiquilia.

Phenology. Active from April to August.

Distribution. Mojave Desert (Fig. 2-41A), USA. Currently known only from the northeastern portion of Clark County, Nevada, USA.

**Etymology.** The specific epithet refers to the Latin *prodigiosus*, meaning “unnatural,” “wonderful,” or “prodigious” due to the bizarre features of the male.

**Remarks.** The male of *P. prodigiosa* is unique among *Perdita* in having the metasoma dorsoventrally flattened. That character, along with the quadrate head and brown coloration suggest that the male may spend a lot of time in the nest. This hypothesis is tentatively supported by the relatively few males that have been collected compared to females (28 males versus 127 females). However, the largest specimens do not show a reduced wing size found in the nestbound dimorphic males of *Macrotera portalis* (Danforth 1991). The female is variable in the extent of dark markings on the face and metasoma. The metasoma can range from almost entirely tan to tan heavily marked with brown. Especially in specimens that have been lightened from pan-trapping or storage in alcohol, the area of the face below the antennae can take on a very light tan color.

*Perdita rhodogastra* Timberlake


*Perdita (Heteroperdita) rhodogastra* Timberlake, 1954: 367, m#f#. Holotype f# (CAS type no. 14686), near Westmoreland, Imperial Co., California, USA.

**Diagnosis.** Both sexes of *P. rhodogastra* have the metasoma orange-amber (Figs. 2-15A–B, 16A–B), though the coloration often ranges to light or dark brown in whole or part (Figs. 2-
19D–E). The female can be distinguished from species with similar-colored metasomas by the combination of the second medial cell weakened/absent (e.g. Figs. 2-4C–D), clypeal marks white (which can cover the clypeus or be reduced to an abbreviated medial white mark and white on the lateral margins) and the pygidial plate triangular or subtriangular (Figs. 2-24N–O). The male can be further recognized by the head oval and broader than long (Figs. 2-17A–C), the head and mesosoma with bluish metallic luster, and the pygidial plate truncate apically (Fig. 2-23M). The male can have medial white bars on the margin of the discs of T1, T2, and/or T3 (Fig. 2-15B), but these are often reduced or absent. *Perdita rhodogastra* can be extremely variable in terms of coloration; see remarks below.

**Redescription of female.** Length: 3.1 mm. Forewing length: 1.9 mm.

*Coloration.* Head (Figs. 2-18A–B) and mesosoma base color black with bluish or greenish metallic luster; clypeus dark except for basomedial white stripe and white on lateral margins of clypeus, dark markings generally forming U-shape, occasionally reduced to pair of bands; supraclypeal mark white, large, transverse, sometimes absent; paraocular mark white, transverse to subtriangular, extending to level of summit of clypeus, occasionally traveling up in thin line along eye; mandible white, tip reddish; labrum brown; scape brown, more or less white posteriorly and at apex; antenna brown dorsally, tan ventrally; pronotal collar dark brown with strong metallic tints with pair of small, well-separated transverse marks dorso-posteriorly; pronotal lobe white; legs dark brown except white on joints of femora and tibiae, anterior fore tibia, and distal fore tarsi, distal mid tarsi more or less lightened; wing veins dark brown; metasoma orange-amber, T1 generally darkened basally (Figs. 2-16A–B); T1 sometimes with medial white bar on apical margin of disc; T2 fovea dark brown; pygidial plate orange-amber.

*Structure and vestiture.* Head broader than long (Figs. 2-18A–B); lateral areas and circle around antennal socket covered in dense recumbent white pubescence, vertex with sparse erect
pubescence; eyes slightly converging ventrally; facial fovea parallel to eye, slightly diverging
dorsally, linear, extending from level of top of antennal socket 2/3 of distance to apex of eye,
generally obscured by pubescence; mandible simple; labrum quadrate, slightly less than 2X
broader than long; disc of clypeus broader than high, convex, apically protruding slightly less
than 1 OD from face; lateral extension reaching 2/3 distance to base of mandible; venter of head
with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate,
slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and
margins of scutum sparsely covered with combination of recumbent and erect white pubescence;
fore coxa and anterior margin of venter of mesepisternum with abundant, broadly hooked hairs;
apex of mid tibia with some short, thick, curved setae; forewing with second medial cell
weakened/absent; metasoma suboval, wide basally, tapering apically, widest at T3 (Figs. 2-16A–
B); terga tessellate and impunctate; T2 fovea linear, slightly thickened, over 1/2 length of T2;
pygidial plate triangular, edges slightly curved rather than straight, apex typically pointed (Fig. 2-
24N), though often more or less rounded Fig. 2-24O); hairs of prepygidial fimbria slightly
thickened, dense.

Redescription of male. Length: 2.6 mm. Forewing length: 1.8 mm.

Coloration. Head (Figs. 2-17A–C) and mesosoma base color black with bluish metallic
luster; clypeus white or yellowish-white, sometimes with narrow medial U-shaped dark mark;
supraclypeal mark white, large, broader than long; paraocular mark white or yellowish-white,
subtriangular to triangular, extending to level of antennal socket, sometimes continuing up along
eye in thin line; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot;
scape tan except more or less brown anteromedially; antenna dark brown dorsally, tan ventrally;
pronotal collar with pair of large white transverse marks dorso-posteriorly; pronotal lobe white;
legs dark brown except white on joints of femora and tibiae, fore tibia, distal fore tarsi, anterior
mid tibia, distal mid tarsi, and basally on hind basitarsus; wing veins dark brown; metasoma uniformly amber (Fig. 2-15A), T1–T3 often with medial white bar apically on disc (Fig. 2-15B), though bars often absent in whole or in part; T2 fovea dark brown; pygidial plate amber.

Structure and vestiture. Head broader than long, oval (Figs. 2-17A–C); face with dense appressed white pubescence encircling antennal base, sparse appressed pubescence on vertex; eyes converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, slightly convex, apically protruding less than 1 OD from face; lateral extension reaching 1/2 distance to base of mandible; head with dense pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely covered with combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma equal in width or narrower than mesosoma, wide basally, tapering apically, widest at T3 (Figs. 2-15A–B); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/3 length of T2; pygidial plate very broadly triangular, almost spatulate, apex broadly rounded (Fig. 2-23M); hairs of prepygidial fimbria slightly thickened, sparse.

Terminalia. S8 (Fig. 2-57A) with spiculum bifurcate, lateral apodemes slightly prominent, pointing straight out; apical portion convex, quadrate, sides roughly parallel, diverging slightly before converging at truncate apex; apex curved over ventrally, apical margin of curved over area evenly rounded; sparse hairs ventrally; cuticle thinned in poorly defined oval medially. Genital capsule as in Figs. 2-59L–M. Gonostyli separated dorsally by deep, narrow U-shape; dorsal lobe of gonostylus short and broad; ventral lobe extending slightly beyond level of penis valve with minute hairs on ventral edge of apex; volsella short and compact, cuspis narrow with two spicules on dorsal margin; digitus shorter and narrower than cuspis with single spicule
on inner margin of apex; penis valve long, strongly undulating on inner margin, slightly converging above until strongly turned out at apex; endophallus extending slightly beyond level of penis valve, weakly sclerotized in medial line.

**Floral records.** Asteraceae (1 m# 3 f#): *Helianthus* sp. 1 m# 2 f#, *Pectis papposa* 1 f#,

Boraginaceae (103 m# 119 f#): *Heliotropium curassavicum* 2 m# 19 f#, *Nama* sp. 7 m# 4 f#,

*Tiquilia latior* 67 m# 83 f#, *T. palmeri* 4 m# 1 f#, *T. plicata* 22 m# 9 f#, *T. sp.* 1 m# 3 f#.

**Phenology.** Active from April to October.

**Distribution.** Mojave and Sonoran Deserts (Fig. 2-41B), USA and Mexico.


Remarks. *Perdita rhodogastra* is one of the more variable *Heteroperdita*, showing large differences in coloration and minor variation in structure (see description of variation below). The species can be divided into relatively disjunct Mojave and Sonoran populations, each of which tend to have their own unique characters. It was initially thought that these two disjunct
populations could represent separate species, but no consistent morphological distinctions could be found. In terms of coloration, the northern populations have more extensive, dirty-white face marks in the female and the males tend to have a much darker metasoma. Structurally, in northern specimens the head is typically less broad and females generally have the pygidial plate slightly more rounded than in southern populations. However, in all of the preceding characters, intergrading forms are common both within and between populations. Particular attention was paid to the male terminalia, which showed considerable variation in S8, but again, no consistent differences. The picture was further muddied by the few specimens from south-central Arizona, which show intermediate characters between the Mojave and Sonoran populations. As a result, *P. rhodogastra* is here treated as a single species, but the discovery of additional material could potentially change this calculus. Variation seen in northern females: *Coloration*. Face marks generally dirty-white in color; clypeus typically entirely dirty-white; labrum white in whole or part; transverse marks on pronotal collar reduced or absent; tubercles ranging from white to dark; mid tarsi and anterior face of mid tibia white; metasoma terga often brown on apical margins. *Structure and vestiture*. Face only slightly broader than long; pygidial plate rounded triangle, often approaching spatulate, apex generally lacking a well-defined point.

Variation seen in northern males: *Coloration*. Face marks generally dirty-white in color; transverse marks on pronotal collar reduced or absent; tubercles ranging from white to dark; metasoma coloration variable, ranging from amber to entirely dark brown; basal terga generally lacking medial white bars, except some specimens with medial white bar on T1. *Structure and vestiture*. Head generally only slightly broader than long; eyes often slightly misaligned with one eye slightly more converging ventrally.

*Perdita scutellaris* Timberlake
Perdita (Heteroperdita) scutellaris Timberlake, 1962: 89, m#f#. Holotype f# (CAS type no. 14701), Hopkins Well, Riverside Co., California, USA.

**Diagnosis.** Both sexes of *P. scutellaris* have the metasoma amber or brownish with white stripes apically on the discs of the terga (Figs. 2-10G, 2-11E), propodeum with a yellow triangle (sometimes reduced), scutellum yellow (also sometimes reduced), and lateral face marks that travel up to the apex of the eye (Figs. 2-12G, 2-13E). The only other *Heteroperdita* with a yellow scutellum is *P. wasbaueri*, which has the metasoma yellow with black spots. Both sexes of *P. scutellaris* have a layer of copious, minute hairs on the terga, unique among females of *Heteroperdita* and in males otherwise present only in *P. prodigiosa*. The female is unique in having the pygidial plate slender and forked apically (Fig. 2-24P) — though the tines of the fork are often broken off, as well as the mandibles spatulate with a distinct ventral hair fringes (Fig. 2-13F), and the female can be further recognized by the second medial cell weakened/absent. Males can be further recognized by the head quadrate, pygidial plate triangular, and clypeus not extending apically from the face.

**Redescription of female.** Length: 3.7 mm. Forewing length: 2.3 mm.

**Coloration.** Head (Fig. 2-13F) and mesosoma base color black, metallic tints reduced or absent; clypeus yellowish-white; supraclypeal mark white, sometimes yellowish, large, transverse; paraocular mark white, narrowly following margin of eye up to apex, coloration increasingly yellow apically; subantennal mark generally dark, sometimes yellowish-white; mandible white, tip reddish; labrum white; scape yellow; antenna yellow except brownish
dorsally and on anterobasal margin of F2–F4; pronotal collar dark brown with large yellow transverse mark dorso-posteriorly, transverse mark may be narrowly interrupted medially; pronotal lobe yellow; scutum yellow along lateral margins; axilla yellow; scutellum yellow, sometimes slightly darkened; metanotum occasionally yellow along posterior margin; propodeum with medial yellow triangle, often reduced or poorly-defined; legs dark brown except yellowish-white on apical half of fore femur, anterior face of fore and mid tibiae, distal fore and mid tarsi, joint of mid and hind femora and tibiae, and posterior margin of hind tibia, distal hind tarsi ranging from brown to white; wing veins tan or light brown; metasoma amber or brownish except T1–T5 with white bands along margins of discs and lateral margins of terga, bands thicker laterally and medially (Fig. 2-11E); T2 fovea black; pygidial plate amber or brownish.

Structure and vestiture. Head slightly broader than long (Fig. 2-13F); face with appressed white pubescence encircling antennal base and on vertex; frons with handful of obscure punctures; eyes subparallel, slightly converging ventrally; facial fovea parallel to eye, oval, length 3X width, extending from top of antennal socket 1/3 distance to apex of eye, generally obscured by pubescence; mandible simple, wide and slightly spatulate with fringe of incurved hairs along ventral margin (Fig. 2-13F); labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, clypeus not protruding apically from face; lateral extension protruding below apical margin of clypeus, extending to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with many short, thick, curved setae; forewing with second medial cell absent/weakened; metasoma oval, narrow basally, tapering apically, widest at T3 (Fig. 2-11E); terga tessellate, slightly shiny with minute, close punctures; terga
covered in short, fine, obscure pubescence, particularly laterally and on apical terga, T1 with patches of short, thick pubescence laterally; T2 fovea short, oval, 1/3 length of T2; pygidial plate very narrow, apex forked with pair of small lateral spines (Fig. 2-24P); hairs of prepygidial fimbria slightly thickened, dense.

**Redescription of male.** Length: 3.5 mm. Forewing length: 2.2 mm.

*Coloration.* Head (Fig. 2-12G) and mesosoma base color black with slight metallic blue or green luster; clypeus, large transverse supracylpeal mark, subantennal mark, and lateral areas yellowish-white; facial sutures may be light or dark; paraocular mark extending up to top of eye, becoming more yellow above; mandible white, tip brown; labrum white; scape yellow; antenna yellow except brownish ventrally and F2–F4 brown dorsobasally; pronotal collar brown with large transverse yellow mark dorso-posteriorly, transverse mark may be slightly interrupted medially; pronotal lobe yellow; scutum lined with yellow along lateral margins; axilla yellow; scutellum yellow, sometimes slightly darkened; metapleuron and anterior propodeum dark brown, sometimes obscurily lightened to tan; metanotum yellow along posterior margin; propodeum black with poorly defined narrow yellow triangle dorso-anteriorly, yellow triangle often reduced or absent; ventral surface of mesepisternum dark brown, lightened to tan on posterior margin; legs yellow except generally marked with brown basally on coxae and basally on femora, hind tibia with faint brown mark medioposteriorly; wing veins tan or light brown; metasoma amber or brownish except T1–T6 with white bands along margins of discs and lateral margins of terga, bands thicker laterally and medially (Fig. 2-10G); T2 fovea dark brown; pygidial plate white basally, transparent amber apically.

*Structure and vestiture.* Head subquadrate or quadract, broader than long (Fig. 2-12G); face, except for clypeus and supracylpeal area, sparsely covered by recumbent white pubescence; eyes parallel or slightly diverging below; mandible simple, thick, slightly curved ventrally,
extending to far side of labrum in repose; labrum quadrate, 2X broader than long; disc of clypeus broader than high, slightly convex, not protruding from face apically; lateral extension protruding below apical margin of clypeus, extending to base of mandible; head with dense pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum completely covered by combination of recumbent and erect white pubescence; scutum mostly covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma equal in width or slightly wider than mesosoma, oval, narrow basally, tapering apically, widest at T3 (Fig. 2-10G); terga tessellate, slightly shiny with minute, close punctures; terga covered in extremely fine, obscure pubescence particularly on apical terga; T1 with patches of short, thick pubescence laterally; T2 fovea oval, 3X longer than broad, 1/4 length of T2; pygidial plate broadly triangular, apex narrowly constricted into dull point (Fig. 2-23N); hairs of prepygidial fimbria slightly thickened, sparse.

*Terminalia.* S8 (Fig. 2-57B) with spiculum narrow, club-shaped apically, apical edge semicircular; apodemes weakly prominent, very slightly flexed downwards; apical portion moderately convex, quadrate, sides roughly parallel, apex truncate; sparse short hairs ventrally, cuticle apparently lacking weakly sclerotized area. Genital capsule as in Figs. 2-59N–O. Gonostyli separated dorsally by broad V-shape; dorsal lobe of gonostylus long and broad, extending to level of penis valve; ventral lobe slightly shorter, narrow with multiple long hairs apically; volsella relatively short and compact; cuspis short, strongly curving dorsally with multiple spicules on outer margin of apex; digitus bizarre with basal flange with few hairs apically, then constricting to tubular shape, evenly curving down and under digitus until pointing upwards again with single spicule apically; penis valve parallel, very close together, apex slightly club-shaped and turned out laterally; endophallus extending to level of apex of penis valve.
**Floral records.** **Boraginaceae** (1 m# 66 f#): *Tiquilia plicata* 1 m# 63 f#, *T*. sp. 3 f#, **Euphorbiaceae** (1 m#): *Chamaesyce parryi* 1 m#, **Loasaceae** (8 m# 15 f#): *Petalonyx thurberi* 8 m# 15 f#, **Polygonaceae** (4 m# 2 f#): *Eriogonum deserticola* 4 m# 2 f#, **Zygophyllaceae** (2 m# 1 f#): *Larrea tridentata* 2 m# 1 f#.

**Phenology.** Active from April to October.

**Distribution.** Mojave and Sonoran Deserts (Fig. 2-47A), USA (and likely Mexico).

Shows a strong preference for dune habitats.


**Remarks.** Specimens from the southern localities tend to have the frons slightly shinier and the face with more extensive yellow coloration. For example, the northern specimens (Ibex Dunes) tend to have the subantennal areas dark, while the southern specimens (Algodones Dunes) have the subantennal areas yellow. These differences appear to be minor variation that do not indicate separate species.

*Perdita sexfasciata* Timberlake

**Perdita (Heteroperdita) sexfasciata** Timberlake, 1954: 368, m#. Holotype m# (CAS type no. 14706), 4 miles east of Edom, Riverside Co., California, USA.

**Perdita (Heteroperdita) optiva** Timberlake, 1954: 371, f# (not type m#).

**Perdita (Heteroperdita) fasciatella** Timberlake, 1980: 7, f#. Holotype f# (CAS type no. 14520), Bouse, Mojave Co., Arizona, USA. **Syn. n.**

**Diagnosis.** Both sexes of *P. sexfasciata* have the metasoma black with white stripes apically on the discs of the terga (Figs. 2-10B, 2-11B). Both sexes also share a slightly carinate omaulus, which is unique in *Heteroperdita*. The female is similar in coloration to *P. trifasciata* and *P. optiva*. It can be distinguished by the pygidial plate, which is large and broadly rounded (Fig. 2-24Q), whereas in *P. trifasciata* the pygidial plate is narrowly spatulate and in *P. optiva* it is triangular. The male can be further recognized by having the head oval and non-square (Fig. 2-12B), pygidial plate with apex evenly rounded (Fig. 2-23O), and five white bands on the terga.

**Redescription of female.** Length: 3.5 mm. Forewing length: 2.2 mm.

**Coloration.** Head (Fig. 2-13B) and mesosoma base color black with metallic greenish or bluish luster; clypeus black with medial abbreviated white stripe; supraclypeal mark dark brown; paraocular mark white, triangular, extending along eye up to level of top of antennal socket; mandible white, tip brownish-orange; labrum dark brown; scape dark brown, more or less lightened apically; antenna brown dorsally, tan ventrally and apically; pronotal collar dark brown with metallic tints with pair of white transverse marks dorso-posteriorly; pronotal lobe white; legs dark brown except more or less white on apex of femur, anterior fore and mid tibiae, joint of hind
femur and hind tibia, all basitarsi; wing veins brown; metasoma black except T1–T5 with white bands along margins of discs, bands thicker laterally and medially (Fig. 2-11B); T2 fovea black; pygidial plate brown.

**Structure and vestiture.** Head broader than long (Fig. 2-13B); lateral area covered by recumbent white pubescence up to level of fovea; eyes subparallel, slightly converging ventrally; facial fovea teardrop-shaped, angled medially towards antennal socket, extending from level of tops of antennal sockets half distance to apex of eye; mandible with small blunt subapical tooth; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; omaulus with distinct but weak carina; mesepisternum sparsely covered with combination of recumbent and erect white pubescence; scutum with exceptionally sparse and fine pubescence; fore coxa and anterior venter of mesepisternum with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, slightly wide basally, tapering apically, widest at T3 (Fig. 2-11B); terga tessellate and impunctate; T2 fovea long, linear, 3/4 length of T2; pygidial plate wide, apex broadly rounded, margin flexed dorsally (Fig. 2-24Q); hairs of prepygidial fimbria slightly thickened, sparse.

**Redescription of male.** Length: 3.1 mm. Forewing length: 1.9 mm.

**Coloration.** Head (Fig. 2-12B) and mesosoma base color black with metallic bluish luster; clypeus yellowish-white, sometimes invaded by brown basally; supraclypeal mark yellowish-white, small, often reduced or absent; paraocular mark yellowish-white, triangular, reaching level of top of antennal socket; mandible white, tip reddish; labrum ranging from dull white to dark brown; scape dark brown, more or less yellowish-white anteriorly; antenna dark
brown, lightened to tan ventrally; pronotal collar brown with slight metallic blue tints with pair of well-separated transverse yellowish-white marks dorso-posteriorly; pronotal lobe dull white; legs dark brown except yellowish-white on anterior fore and mid tibiae, basally on fore and mid basitarsi, joint of hind tibia and hind femur, and hind basitarsi; wing veins brown; metasoma dark brown except T1–T6 with white bands along margins of discs, bands thicker laterally and medially (Fig. 2-10B); T2 fovea black, obscure; pygidial plate dark brown.

_Structure and vestiture._ Head oval, broader than long (Fig. 2-12B); face, except for clypeus and frons, sparsely covered by recumbent white pubescence, pubescence thicker in lateral areas; eyes slightly converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrato, 1.5X broader than long; disc of clypeus broader than high, slightly convex, apically protruding 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; head with short thickened pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; omaulus with distinct but weak carina; mesepisternum and margins of scutum sparsely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, thickened hairs; metasoma more or less equal in width to mesosoma, oval, slightly wide basally, tapering apically, widest at T3 (Fig. 2-10B); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/3 length of T2; pygidial plate short, spatulate, apex broadly truncate, margins flexed upwards (Fig. 2-23O); hairs of prepygidial fimbria slightly thickened, sparse.

_Terminalia._ S8 (Fig. 2-57C) with spiculum bifurcate; lateral apodemes prominent, strongly curving downwards; apical portion broader than long, moderately convex, sides very slightly converging up to small subapical points, then converging more strongly to truncate apex, apex shallowly and broadly emarginate; short hairs ventrally; lacking thinned cuticular area. Genital capsule as in Figs. 2-60A–B. Gonostyli separated dorsally by relatively narrow V-shape;
dorsal lobe of gonostylus large, broad, rounded; ventral lobe equal in length to dorsal lobe, relatively narrow with few minute hairs on apex; volsella large, extending beyond gonostylus; cuspis slightly curved dorsally with spicules dorsally on apex; digitus short and slender with single spicule on inner margin of apex; penis valve large with minute spots basoventrally, extending beyond rest of genitalia, fused nearly to apex, apex broad and flat with acute lateral angles diverging outwards; endophallus not apparent.

**Floral records.** **Boraginaceae** (34 m# 9 f#): *Nama* sp. 19 m#, *Tiquilia latior* 2 m#, *T. palmeri* 8 m# 4 f#, *T. plicata* 5 m# 5 f#.

**Phenology.** Active in spring (April to June).

**Distribution.** Mojave and Sonoran Deserts (Fig. 2-47B), USA (and likely Mexico).

**Type Material examined.** *Perdita sexfasciata* Holotype data: m#, **CALIFORNIA:** Riverside Co.: 4 miles east of Edom, 17 April 1937, P.H. Timberlake, at flowers of *Coldenia palmeri* [=*Tiquilia palmeri* (A. Gray) A.T. Richardson] (CAS type no. 14706). *Perdita fasciatella* Holotype data: f#, **CALIFORNIA:** San Bernardino Co.: Bouse [since Bouse is not in California, the true state and county data is Arizona, Mojave Co.], 19 May 1970, P.F. Torchio, on flowers of *Nama* (P.F. Torchio often incorrectly identified *Tiquilia* as *Nama* (T. Griswold, pers. comm.)) (CAS type no. 14520). *Perdita fasciatella* Paratype data: 2 f#, same data as *P. fasciatella* holotype.

**Additional material examined.** Total specimens: 36 m# 9 f#. **ARIZONA:** La Paz Co.: Parker, 6 mi E; Shea Rd. (34.1322 -114.2288): 1 m# 2 f#, 17 Apr 2010, G.R. Ballmer, *Tiquilia palmeri*; **Mohave Co.:** Topock, 2 mi N (34.74 -114.48): 16 m#, 1 May 1983, P.F. Torchio, *Nama* sp.; Topock (34.71 -114.48): 3 m#, 13 May 1983, P.F. Torchio, *N. sp.*. **CALIFORNIA:** Imperial Co.: nr Mount Signal (32.67843 -115.64033): 1 m#, 15 Apr 1973, J.D. Pinto; **Riverside Co.:**
Remarks. *Perdita sexfasciata* was described from the male sex by Timberlake (1954). In the same publication, the female of *P. sexfasciata* was erroneously described as the female of *P. optiva*; this mismatch was rectified by Timberlake (1968).

Examination of the holotype and both paratypes of *P. fasciatella* reveal them to be specimens of *P. sexfasciata*. Timberlake (1980) cited differences in the facial maculations and the shape of the pygidial plate to split it from *P. sexfasciata*. The differences in the pygidial plate are not apparent and the facial maculations are within the natural level of variation seen in *P. sexfasciata*.

*Perdita sycorax* Portman, sp. n.

Figs. 2-6E, 2-7E, 2-8E, 2-9F, 2-23P, 2-24R, 2-39, 2-49, 2-57D, 2-60C–D

**Diagnosis.** Both sexes of *P. sycorax* have the metasoma yellow with dark spots, though the dark spots are reduced and sometimes absent in the females (Figs. 2-6E, 2-7E). They can be
recognized by their unique shade of golden or dull yellow coloration, a darker shade than similar species such as \textit{P. arenaria}, \textit{P. maculosa}, \textit{P. nuttalliae}, and \textit{P. yanegai}. Both sexes also have a yellow band on the metapleura and contiguous sides of the propodeum (Fig. 2-49) as well as a well-defined yellow triangular dorso-anteriorly on the propodeum (e.g. Fig. 2-5B).

The female can be further recognized by having the second medial cell present, head and mesosoma with greenish-bronze metallic tints, and the metasoma with reduced dark spots (Fig. 2-7E). The male can be further recognized by the head and mesosoma with strongly metallic greenish-bronze coloration, the larger yellow markings that fill the entire lateral area and extend slightly above the antennal sockets (Fig. 2-8A), and the pygidial plate narrowly triangular with the apex narrowly and bluntly pointed (Fig. 2-23P).

\textit{Description of female.} Length: 3.0 mm. Forewing length: 1.9 mm.

\textit{Coloration.} Head (Fig. 2-9F) and mesosoma base color black with metallic greenish-bronze luster; clypeus dull yellow; supraclypeal mark dull yellow, large, transverse; paraocular mark dull yellow, triangular or subtriangular, extending narrowly up along eyes to above level of antennal socket; subantennal mark typically yellow along margin of antennal socket; mandible yellowish-white, tip reddish; labrum yellowish-white, sometimes with basomedial dark spot; scape dull yellow; antenna light brown dorsally, yellowish-tan ventrally; pronotal collar yellow, more or less marked with brown along medial suture; pronotal lobe yellow; metapleuron and anterior propodeum yellow (Fig. 2-49A), often more or less invaded by brown ventrally; propodeum with large narrow yellow triangle dorso-anteriorly; ventral surface of mesepisternum yellow along posterior margin; legs dull yellow except more or less brown on distal hind tarsi; wing veins transparent tan; metasoma dull yellow, terga more or less lightened to white apically with multiple brown spots, though spots often reduced (Fig. 2-7E); T1 with pair of small sublateral spots on anterior and posterior face; T2–T5 with two to four spots: pair of small baso-
lateral transverse marks and pair of small apico-sublateral spots present on T2–T5, small basomedial spot often on T3–T4; T2 fovea brown; pygidial plate transparent yellow.

*Structure and vestiture.* Head broader than long (Fig. 2-9F); face, except for clypeus, lower supraclypeal area, and frons covered by sparse recumbent white pubescence; eyes subparallel, slightly converging ventrally; facial fovea diverging dorsally, oval, extending from top of antennal socket 2/3 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, wide basally, tapering apically, widest at T3 (Fig. 2-7E); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/2 length of T2; pygidial plate narrowly triangular, apex sharply pointed (Fig. 2-24R); hairs of prepygidial fimbria thin, sparse.

*Description of male.* Length: 2.4 mm. Forewing length: 1.7 mm.

*Coloration.* Head (Fig. 2-8E) and mesosoma base color metallic greenish bronze; clypeus dull yellow; supraclypeal mark dull yellow, large, transverse; paraocular mark dull yellow, triangular, extending slightly above level of top of antennal socket; subantennal area generally dark, sometimes with yellow mark along margin of antennal socket; mandible yellowish-white, tip reddish; labrum yellowish-white; scape dull yellow; antenna brown dorsally, yellowish-tan ventrally; pronotal collar yellow, more or less marked with brown along medial suture; pronotal lobe yellow; metapleuron and anterior propodeum yellow, often more or less invaded by brown
ventrally (Fig. 2-49B); propodeum with narrow yellow triangle dorso-anteriorly, triangle often reduced or absent; ventral surface of mesepisternum lightened to yellow along bases of mid and hind coxae; legs yellow except brown basally on fore and mid coxae, dorsoapical spot on hind femur, and anteromedially on hind femur, more or less darkened on distal hind tarsi; wing veins light brown; metasoma dull yellow or yellowish-white with multiple brown spots (Fig. 2-7E); T1 with pair of sublateral splotches on anterior and pair of sublateral spots on dorsal face; T2–T6 with two to four spots: prominent apico-sublateral spots present on T2–T6, small baso-lateral spots present on T2–T4 (spots more transverse on T2), and small basomedial spot present on T3–T5; T2 fovea brown; pygidial plate transparent yellow.

**Structure and vestiture.** Head oval, broader than long (Fig. 2-8E); face, except for clypeus, lower supraclypeal area, and frons covered by sparse recumbent white pubescence; eyes converging ventrally; mandible simple, not quite extending to opposite side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; head with sparse pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum sparsely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma equal in width to mesosoma, suboval, wide basally, tapering apically, widest at T3 (Fig. 2-7E); terga tessellate and impunctate; T2 fovea linear, thickened, generally approaching half length of T2; pygidial plate narrowly triangular, apex narrowly and bluntly pointed (Fig. 2-23P); hairs of prepygidial fimbria slightly thickened, sparse.

**Terminalia.** S8 (Fig. 2-57D) with spiculum relatively broad basally, bifurcate apically; lateral apodemes slightly prominent, weakly flexed downwards; apical portion slightly convex, much longer than broad, sides weakly converging above; apex strongly truncate; sparse short
hairs ventrally; cuticle thinned in small circle subapically. Genital capsule as in Figs. 2-60C–D. Gonostyli separated dorsally by narrow V-shape; dorsal lobe of gonostylus relatively narrow; ventral lobe slightly longer than dorsal lobe with minute hairs apically, extending slightly beyond level of penis valve; volsella relatively small; cuspis narrow with few spicules apically; digitus minute and unornamented; penis valve narrow, parallel, turned outwards at apex; endophallus extending to level of penis valve.

**Floral records.** *Apocynaceae* (1 m#): *Cycladenia humilis* 1 m#, *Boraginaceae* (6 m# 6 f#): *Tiquilia latior* 6 m# 6 f#.

**Phenology.** Active May to August.

**Distribution.** Colorado Plateau (Fig. 2-39), USA.


Etymology. The name comes from the unseen character in Shakespeare's *The Tempest*. Treat as a noun in apposition.

Remarks. *Perdita sycorax* is currently the only *Heteroperdita* known from the Colorado Plateau. However, given the relative dearth of collection on *Tiquilia* in the area, it seems likely that additional species occur there.

*Perdita titania* Portman & Griswold, sp. n.
Diagnosis. Both sexes of *P. titania* have the metasoma yellow with dark spots (Figs. 2-6F, 7F). They can be recognized by the unique color pattern on the propodeum, which is mostly yellow with the dark maculations limited to a distinctive V- or Y-shape (Fig. 2-7F). In addition, both sexes have the scutellum dark. The female can be further recognized by the scutum with margins yellow and the pygidial plate narrowly triangular with the apex sharply pointed (Fig. 2-24S). The male can be further recognized by having the head broader than long (Fig. 2-8F), eyes slightly enlarged, and the terga with relatively large, round dark spots.

**Description of female.** Length: 3.5 mm. Forewing length: 2.2 mm.

Coloration. Head (Fig. 2-9G) and mesosoma base color black with metallic greenish-bronze luster; clypeus white, faintly yellowish sublaterally; supraclypeal mark white, large, broadly transverse; paraocular mark white, transverse to triangular, not reaching above level of summit of clypeus except a thin line reaching 1/2 to 3/4 up eye; mandible white, tip reddish; labrum white with basomedial dark spot; scape yellowish-white; antenna yellowish-white, more or less marked with brown dorsally; pronotal collar and pronotal lobe yellow; scutum with thin yellow margin laterally; axilla yellow posteriorly; metapleuron and anterior propodeum yellow (Fig. 2-50A); propodeum yellow except greenish-bronze V- or Y-shaped mark on posterior face; ventral surface of mesepisternum yellowish-white along posterior margin; legs yellow except more or less brown on small apicodorsal spot on hind femur, medial hind tibia, and distal hind tarsi; wing veins transparent tan; metasoma white or yellowish-white with multiple dark brown spots (Fig. 2-7F); T1 with pair of sublateral spots on anterior and posterior face; T2–T5 with five spots: one more or less triangular medial mark, two small baso-lateral spots (spots on T2 more
transverse), and two large, prominent apico-sublateral spots; T2 fovea dark brown; pygidial plate transparent white with reddish tip.

**Structure and vestiture.** Head slightly broader than long (Fig. 2-9G; face, except for clypeus, lower supraclepeal area, and frons covered by dense recumbent white pubescence; eyes subparallel, slightly converging ventrally; facial fovea diverging dorsally, narrowly oval, extending from top of antennal socket 3/4 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, barely protruding apically from face; lateral extension reaching base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, slightly widened basally, tapering apically, widest at T3 (Fig. 2-7F); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/2 length of T2; pygidial plate very narrowly triangular, apex sharply pointed (Fig. 2-24S); hairs of prepygidial fimbria thin, sparse.

**Description of male.** Length: 2.8 mm. Forewing length: 1.9 mm.

Note: the lone male specimen has been reddened by cyanide. As a result, the exact color of the light maculations are inferred.

**Coloration.** Head (Fig. 2-8F) and mesosoma base color black with metallic greenish luster; clypeus yellowish-white; supraclepeal mark yellow, large, slightly broader than long; paraocular mark yellow, subtriangular, reaching level of summit of clypeus, extending up along eye in thin line to level of antennal socket; mandible white, tip reddish; labrum white; scape
yellow, brownish anteriorly; antenna yellow, slightly brownish dorsally and apically; pronotal collar and pronotal lobe yellow; metapleuron and anterior propodeum yellow (Fig. 2-50B); propodeum yellow except metallic green Y-mark on posterior face (Fig. 2-7F); legs yellow; wing veins transparent tan; metasoma yellowish-white with multiple large dark brown spots (Fig. 2-6F); T1 with pair of sublateral spots on anterior and posterior face; T2–T6 with four or five spots: T2–T6 with small basomedial spot and two prominent apico-sublateral spots, T2–T4 with pair of small baso-lateral spots (spots on T2 more transverse); T2 fovea dark brown, merging with baso-lateral spots; pygidial plate transparent yellow.

Structure and vestiture. Head oval, broader than long (Fig. 2-8F); face, except for clypeus, lower supraclypeal area, and frons covered by dense recumbent white pubescence; eyes slightly converging ventrally, relatively large; mandible simple, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching base of mandible; head with moderately dense pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum densely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma equal in width to mesosoma, suboval, wide basally, tapering apically, widest at T3 (Fig. 2-7F); terga tessellate and impunctate; T2 fovea narrowly oval, 1/3 length of T2; pygidial plate large, broadly triangular, apex slightly extended into narrow point (Fig. 2-23Q); hairs of prepygidial fimbria slightly thickened, sparse.

Terminalia. Not available.

Floral records. Boraginaceae (1 m#): Tiquilia sp. 1 m#, Loasaceae (1 f#): Petalonyx thurberi 1 f#.
**Phenology.** Known activity from March to May.

**Distribution.** Mojave and Sonoran Deserts (Fig. 2-51A) USA (and likely Mexico). Dune specialist, currently known only from the Ibex and Algodones Dunes.


**Etymology.** The name comes from the fairy queen Titania in Shakespeare’s play *A Midsummer Night’s Dream.* The name was chosen due to the beauty and rarity of this species. Treat as a noun in apposition.

**Remarks.** *Perdita titania* is one of the rarest *Heteroperdita,* known from only four specimens and likely limited to dune habitats. Of the four known specimens, two are from the Ibex Dunes and two from the Algodones Dunes, including the single male. The strongly disjunct range is unusual, and may be the result of rarity or incomplete sampling. If this is the true distribution, it seems likely that these are genetically isolated populations. However, there are no apparent morphological differences between the females from the two locations. Additional material, particularly males from the Ibex Dunes, could be informative. Dissection of the male terminalia proved not to be feasible.

*Perdita trifasciata* Timberlake
Perdita trifasciata Timberlake, 1953: 969, m#; Timberlake, 1954: 370, f#. Holotype m# (SEMC, accession no. SEMC1111156), White Sands, New Mexico, USA.

Perdita (Heteroperdita) trifasciata; Timberlake, 1954: 370.

**Diagnosis.** Both sexes of *P. trifasciata* have the metasoma dark brown or black with white bands apically on the discs of the terga (Figs. 2-10C, 2-11C). Particularly in the males, the white bands can be interrupted and split into two or four separate marks. The female is similar in coloration to *P. sexfasciata* and *P. optiva*, and be separated from those species by the metasoma with fewer bands (four vs. five), the second medial cell weakened/absent (e.g. Fig. 2-4C), mandibles simple, and the pygidial plate narrowly spatulate (24T). The male is distinctive in having only the first three terga with light bands (rarely extending to the fourth terga). It can be further recognized by the pygidial plate with the apex shallowly and broadly notched (Fig. 2-23R), clypeus strongly dentate, and omaulus lacking a weak carina.

**Redescription of female.** Length: 3.2 mm. Forewing length: 2.0 mm.

*Coloration.* Head (Fig. 2-13C) and mesosoma base color black with metallic bluish luster; clypeus variably marked, ranging from completely white to black with white limited to lateral margins and medial vertical band; supraclypeal mark ranging from completely dark to small white spot; paraocular mark white, transverse to subtriangular, extending to level of bottom of antennal socket; mandible white, tip brown; labrum variably marked, ranging from all white to dark with white around edges; scape light brown anteriorly, lightened to more or less white
posteriorly; antenna brown, more or less white ventrally; pronotal collar with pair of transverse white lateral marks dorso-posteriorly; pronotal lobe more or less white; legs dark brown except white on joints of femora and tibiae, anterior fore tibia, mid basitarsus, and distal fore tarsi; wing veins ranging from light to dark brown; metasoma dark brown except T1–T4 with white bands along margins of discs, bands more or less interrupted by sublateral dark spots (Fig. 2-11C); T2 fovea black; pygidial plate brown.

Structure and vestiture. Head broader than long (Fig. 2-13C); face, except for clypeus and lower supraclavicular area, covered by recumbent white pubescence, pubescence thinner on vertex; eyes subparallel, slightly converging ventrally; facial fovea linear, parallel to eye, extending from level of tops of antennal sockets half distance to apex of eye; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding slightly less than 1 OD from face; lateral extension strongly folded over, not extending towards base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle distinct; mesepisternum and scutum sparsely covered with combination of recumbent and erect white pubescence; fore coxa and anterior venter of mesepisternum with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell weakened/absent; metasoma suboval, wide basally, sides more or less parallel, widest at T3 (Fig. 2-11C); terga tessellate and impunctate; T2 fovea short, linear, generally less than 1/3 length of T2; pygidial plate narrowly spatulate, apex evenly rounded (Fig. 2-24T); hairs of prepygidial fimbria slightly thickened, dense.

Redescription of male. Length: 3.1 mm. Forewing length: 1.9 mm.

Coloration. Head (Fig. 2-12C) and mesosoma base color black with metallic bluish luster; clypeus white, sometimes brown with white restricted to lateral margins and medial
vertical band; supraclypeal mark generally absent, sometimes with small white mark; paraocular mark white, transverse or subtriangular, sometimes extending in thin line along eye to level of top of antennal socket; mandible white, tip brownish or reddish; labrum white, sometimes with basomedial dark spot; scape tan except more or less brown anteriorly; antenna brown, tan ventrally; pronotal collar brown, pair of well-separated transverse white marks dorso-posteriorly; pronotal lobe ranging from brown to white; legs dark brown except more or less yellowish-white on anterior fore and mid tibiae and distal fore and mid tarsi, hind legs white at joint of femur and tibia, hind tarsi more or less lightened; wing veins dark brown; metasoma dark brown except T1–T3 with white bands along margins of discs, bands thicker laterally and medially (Fig. 2-10C), bands often interrupted, T4 occasionally with vestigial white band; T2 fovea black, obscure; pygidial plate dark brown.

*Structure and vestiture.* Head oval or subquadrate, broader than long (Fig. 2-12C); face, except for clypeus and lower supraclypeal area, sparsely covered by recumbent white pubescence; eyes ranging from slightly converging to slightly diverging below; mandible simple, curved inwards, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, strongly convex, apically protruding 1 OD from face; lateral dentation relatively prominent, lateral extension reaching 1/3 distance to base of mandible; head with short thickened pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum sparsely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, thickened hairs; metasoma equal in width to mesosoma, oval, wide basally, tapering apically, widest at margin of T2/T3 (Fig. 2-10C); terga tessellate and impunctate; T2 fovea linear, 1/4 length of T2; pygidial plate short, sides slightly converging, apex broadly truncate, bifid with broad, shallow triangular emargination, lateral tips of apex well-defined (Fig. 2-23R); hairs of
prepygidal fimbria slightly thickened, sparse.

*Terminalia.* S8 (Fig. 2-57E) with spiculum bifurcate; lateral apodemes not prominent, slightly flexed downwards; apical portion strongly convex, slightly longer than broad, sides constricted basally, then bulging out before moderately converging at apex; apex flattened with weak carina medially; short sparse hairs ventrally; cuticle thinned in circle apically. Genital capsule as in Figs. 2-60E–F. Gonostyles separated dorsally by narrow U-shape; gonostylus with triangular ventral lobe stacked directly on top of short, squat, dorsal lobe, ventral lobe with few hairs on outer margins of apex; volsella small; cuspid long, narrow with two spicules apically; digitus extremely minute, unornamented; penis valve long, undulating, broadly turned out apically, extending beyond rest of genitalia; endophallus sclerotized with four distinct parallel vertical bands.

**Floral records.** *Asteraceae* (1 f#): *Psilostrophe tagetina* 1 f#, *Boraginaceae* (80 m# 78 f#): *Heliotropium* sp. 1 f#, *Nama havardii* 1 m#, *N. sp.* 1 m#, *Tiquilia canescens* 3 m# 1 f#, *T. gossypina* 9 m# 7 f#, *T. greggii* 1 m# 2 f#, *T. hispidissima* 42 m# 43 f#, *T. mexicana* 19 m# 23 f#, *T. sp.* 4 m# 1 f#, *Euphorbiaceae* (1 f#): *Chamaesyce* sp. 1 f#.

**Phenology.** April to December.

**Distribution.** Chihuahuan Desert (Fig. 2-43B), USA and Mexico.

**Type material examined.** Holotype data: m#, **NEW MEXICO:** White Sands, 27 Jun 1940, R.H. Beamer (SEMC, accession no. SEMC1111156).

**Additional material examined.** Total specimens: 93 m# 125 f#. **MEXICO:** Chihuahua:
Griswold, *T. gossypina*. **Coahuila:** Cuatro-Cienegas Prot. Area; Site E3; ~13 km SE
Cuatrociénegas; gypsum flat with sinkholes (26.87167 -102.01813): 1 m#, 22 Jul 2010, K.
Wright, *T. hispidissima*; Cuatro-Cienegas Prot. Area; Site F4; ~18 km E Cuatrociénegas; gypsum flat (26.87167 -102.01813): 1 f#, 14 May 2010, K. Wright, *T. hispidissima*. **NEW MEXICO:**

**Remarks.** The male typically has three white bands on the metasoma, but specimens from the more southern localities tend to have four bands.

*Perdita vesca Timberlake*

*Perdita (Heteroperdita) vesca* Timberlake, 1968: 11, m#f#. Holotype f# (CAS type no. 14749), Wadsworth, Washoe Co., Nevada, USA.

**Diagnosis.** Both sexes have an exceptionally variable coloration on the metasoma. In the typical form, the metasoma is tan with obscure, poorly defined dark spots (Figs. 2-19G, 2-20H), however the coloration can range from entirely whitish-tan (Figs. 2-19F, 2-20I) to solidly brown (Fig. 2-19H). The female can be further recognized by having the second medial cell present (Fig. 2-4A), the pygidial plate triangular with the apex broadly and evenly rounded (Fig. 2-24U), the head and mesosoma with greenish-bronze tint, and the head only slightly broader than long (Figs. 2-22D–E). The male can be further recognized by the head and mesosoma greenish-bronze, the pygidial plate broadly truncate (Fig. 2-23S), the tan legs that lack well-defined dark markings, and the metasoma equal in width or broader than the mesosoma.

**Redescription of female.** Length: 2.6 mm. Forewing length: 1.7 mm.

**Coloration.** Head (Figs. 2-22D–E) and mesosoma base color black with greenish-bronze luster; clypeus variably marked, ranging from dark brown to tan; supraclypeal mark generally dark, sometimes with narrowly transverse tan mark; paraocular mark tan, narrowly transverse, often reduced or absent; mandible tan, tip reddish; labrum tan, often brownish on apical half; scape tan; antenna brown dorsally, tan ventrally; pronotal collar brown or black with slight metallic tints; pronotal lobe tan, sometimes darkened; legs tan except brown on all coxae and often with blotchy, nebulous brown markings medially on fore and mid femora, posterior face of mid tibia, medially on hind femur, and distal hind tarsi; wing veins ranging from light to dark brown; metasoma exceptionally variable, base color generally tan, T1–T4 generally with five nebulous brown spots: two baso-lateral, two apico-sublateral, and one basomedial (Fig. 2-20H),
coloration sometimes ranging from entirely whitish-tan (Fig. 2-20I) to entirely brown; T2 fovea black; pygidial plate tan.

Structure and vestiture. Head slightly broader than long (Figs. 2-22D–E); lateral areas and circle around antennal socket covered in dense recumbent white pubescence, vertex with sparse erect pubescence; eyes subparallel, slightly converging ventrally; facial fovea obscure, parallel to eye, extending from top of antennal socket 1/2 distance to apex of eye, generally more or less obscured by pubescence; mandible with small preapical tooth; labrum quadrate, 1.2X broader than long; disc of clypeus broader than high, convex, apically protruding slightly less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum very sparsely covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, slightly narrowed basally, tapering apically, widest at T3 (Figs. 2-20H–I); terga tessellate and impunctate; T2 fovea linear, slightly over 1/2 length of T2; pygidial plate triangular, apex strongly and evenly rounded (Fig. 2-24U); hairs of prepygidial fimbria thin, sparse.

Redescription of male. Length: 2.4 mm. Forewing length: 1.8 mm.

Coloration. Head (Figs. 2-21E–F) and mesosoma base color metallic greenish-bronze; clypeus tan; supraclavateal mark variable, ranging from a large transverse tan mark to entirely absent; paraocular mark tan, subtriangular to triangular, generally reaching level of antennal socket; subantennal area generally dark, often lightened to tan along margin of antennal socket or even entirely light; mandible tan, tip reddish; labrum tan, sometimes with basomedial dark spot; scape tan, more or less marked with brown apically on anterior face; antenna light brown
dorsally, tan ventrally; pronotal collar generally lacking light markings, sometimes with pair of well-separated transverse marks on dorso-posterior margin; pronotal lobe tan; legs entirely tan except often with faint, nebulous brown marks medially on all femora and medially on mid and hind tibiae, hind tarsi often slightly darkened; wing veins dark brown; metasoma extremely variable, ranging from tan to dark brown, T1–T5 generally darkened along basal margin with poorly defined dark triangles basomedially and poorly defined large dark sublateral spots (Fig. 2-19G), coloration often entirely dark brown (Fig. 2-19H) or rarely entirely tan (Fig. 2-19F); T2 fovea dark brown; pygidial plate tan or brown.

Structure and vestiture. Head subquadrate or quadrate, broader than long or width and length equal (Figs. 2-21E–F); face, except for clypeus, lower supraclypeal area, and frons covered by sparse recumbent white pubescence; eyes slightly converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, moderately convex, apically protruding less than 1 OD from face; lateral extension reaching 1/4 distance to base of mandible; head with sparse pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins of scutum sparsely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma broader or equal in width to mesosoma, broadly oval, wide basally, tapering apically, widest at T3 (Figs. 2-19F–H); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/3 length of T2; pygidial plate broadly triangular, apex broadly truncate and evenly rounded (Fig. 2-23S); hairs of prepygidial fimbria thin, sparse.

Terminalia. S8 (Fig. 2-57F) with spiculum triangular, bottom edge approaching slightly emarginate; lateral apodemes prominent, strongly curving downwards; apical portion moderately convex, quadrate, sides roughly parallel below, slightly converging above to truncate and slightly
inflated apex; short hairs ventrally; lacking thinned cuticular area. Genital capsule as in Figs. 2-60G–H. Gonostyli separated dorsally by narrow V-shape; dorsal lobe of gonostylus broad and squat; ventral lobe narrow with few hairs apically; volsella small, strongly curved dorsally; cuspis with multiple spicules on outer face; digitus smaller than cuspis with single spicule apically; penis valve narrow, parallel, slightly turned outwards at apex, extending well beyond rest of genitalia; endophallus extending slightly beyond level of penis valve.

**Floral records.** *Asteraceae* (2 m#): *Tetradymia* sp. 2 m#, *Boraginaceae* (18 m# 26 f#): *Nama* sp. 2 m#, *Tiquilia nuttallii* 16 m# 26 f#, *Fabaceae* (5 m# 1 f#): *Astragalus* sp. 5 m#, *Dalea* sp. 1 f#, *Tamaricaceae* (1 f#): *Tamarix* sp. 1 f#.

**Phenology.** Active from April to August.

**Distribution.** Great Basin (Fig. 2-31A), USA.

**Type material examined.** Holotype data: f#, **NEVADA**: Washoe Co.: Wadsworth, 23 June 1962, G.I. Stage, on *Coldenia nuttallii* [=*Tiquilia nuttallii* (Hook.) A.T. Richardson] (CAS type no. 14749). Allotype data: m#, same data as holotype (CAS). Paratype data: 1 f#, same data as holotype (UCRC).


Remarks. Perdita vesca is widespread throughout the Great Basin and into the northern edge of the Mojave Desert. In general, the northern populations tend to be darker in color while the southern populations tend to be lighter. However, there is significant color variation within populations as well. In the southwestern portion of the range, the specimens are distinctly lighter (metasoma whitish and male faces light below the antennae) and the males appear to have slightly broader heads. However, no additional morphological differences could be found, even in the male terminalia. While there is the potential that P. vesca could represent a species complex, the variation in color, the lack of morphological characters, and the relative dearth of collection events through much of the likely range make it impossible to even speculate.
Perdita wasbaueri Timberlake


Perdita (Heteroperdita) wasbaueri Timberlake, 1960: 126, m#f#. Holotype f# (CAS type no. 14753), Mecca, Riverside Co., California, USA.

Diagnosis. Both sexes of P. wasbaueri have the metasoma yellow with dark spots (Figs. 2-6G, 2-7G), the face completely light below the level of the antennae (Figs. 2-8G, 2-9H), and the scutellum yellow (Fig. 2-5C). This combination of characters separates it from all other species of Heteroperdita. The female can be further distinguished by having the head much broader than long and the second medial cell absent (e.g. Fig. 2-4D). The male can be further distinguished by the very broad head with the eyes strongly convergent below, the propodeum entirely yellow, and the pygidial plate broadly triangular (Fig. 2-23T).

Redescription of female. Length: 2.7 mm. Forewing length: 1.7 mm.

Coloration. Head (Fig. 2-9H) and mesosoma base color black with metallic greenish-bronze luster; clypeus white, yellow on dorsal and lateral margins; supraclypeal mark yellow, large, transverse, filling area between antennal sockets; paraocular mark white below, yellow above, filling lateral area and reaching above antennal socket, extending above and completely encircling eye in thin line (sometimes slightly interrupted at apex); subantennal mark yellow; mandible yellow, tip reddish; labrum white; scape yellow; antenna yellow, more or less brownish dorsally; pronotal collar and pronotal lobe yellow; scutum lined with yellow on lateral margins (Fig. 2-5C); axilla yellow; scutellum yellow (Fig. 2-5C); mesepisternum more or less yellow on
dorsal, anterior, and basal margins; metapleuron yellow (Fig. 2-54A); propodeum yellow; ventral surface of mesepisternum entirely yellow; legs yellow except hind distal tarsi sometimes slightly darkened; wing veins transparent tan; metasoma pale yellow with multiple large black spots (Fig. 2-7G); T1 with pair of sublateral spots on anterior and posterior face; T2–T5 with five round spots: one medial spot, two small baso-lateral spots (spots on T2 more transverse), and two apico-sublateral spots; T2 fovea dark brown; pygidial plate transparent, slightly darkened apically.

Structure and vestiture. Head broader than long (Fig. 2-9H); face, except for clypeus, supraclypeal area, and frons, covered in dense white pubescence; eyes strongly converging ventrally; facial fovea diverging dorsally, parallel to eye, narrowly oval, extending from 1 OD above level of top of antennal socket 1/2 distance to apex of eye, relatively deeply scored, generally obscured by pubescence; mandible simple; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, barely protruding apically from face; lateral extension reaching base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa and anterior margin of venter of mesepisternum with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell absent; second submarginal cell approaching triangular shape; metasoma suboval, wide basally, tapering apically, widest at T3 (Fig. 2-7G); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/2 length of T2; pygidial plate very broadly triangular, apex bluntly pointed (Fig. 2-24V); hairs of prepygidial fimbria slightly thickened, dense.

Redescription of male. Length: 2.4 mm. Forewing length: 1.5 mm.

Coloration. Head (Fig. 2-8G) and mesosoma base color black with metallic greenish or greenish-bronze luster; clypeus white, yellow on dorsal and lateral margins; supraclypeal mark
yellow, large, transverse, filling area between antennal sockets; paraocular mark white below, yellow above, filling lateral area and reaching above antennal socket, extending above and completely encircling eye in thin line; subantennal area yellow; mandible white, tip slightly reddish; labrum white; scape yellow; antenna yellow, more or less brownish dorsally and apically; pronotal collar and pronotal lobe yellow; scutum lined with yellow on lateral margins; axilla yellow; scutellum yellow; mesepisternum more or less yellow dorsally, anteriorly, and basally; metapleuron yellow (Fig. 2-54B); propodeum entirely yellow; ventral surface of mesepisternum yellow; legs yellow except distal hind tarsi sometimes slightly darkened; wing veins transparent tan; metasoma yellowish-white with multiple large black spots (Fig. 2-6G); T1 with pair of sublateral spots on anterior and posterior face; T2–T6 with five spots: two large, prominent apico-sublateral spots, small apicolateral spots that are reduced or absent on apical terga, and small medial spot that is often reduced on basal terga; T2 fovea black; pygidial plate transparent yellow.

Structure and vestiture. Head oval, broader than long (Fig. 2-8G); face, except for clypeus and lower supraclypeal area covered by dense recumbent white pubescence; eyes strongly converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching base of mandible; head with moderately dense pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum mostly covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; forewing with second submarginal cell nearly triangular; metastoma narrower or equal in width to mesosoma, narrowly oval, slightly wide basally, tapering apically, widest at T3 (Fig. 2-6G); terga tessellate and impunctate; T2 fovea narrowly oval, 1/3 length of T2; pygidial
plate very broadly triangular, apex obtuse, slightly blunted (Fig. 2-23T); hairs of prepygidial fimbria slightly thickened, sparse.

Terminalia. S8 (Fig. 2-57G) transparent; spiculum very short, bifurcate; lateral apodemes not prominent; apical portion slightly convex; quadrate, sides converging medially before expanding at apex; apex broadly and shallowly emarginate; short hairs ventrally; cuticle not noticeably thinned. Genital capsule as in Figs. 2-60I–J. Gonostyli separated dorsally by very narrow V-shape; dorsal lobe reduced, short and squat; ventral lobe diverging slightly with hairs on outer margin; volsella relatively long, extending nearly to level of penis valve; cuspis long, narrow, with pair of subapical spicules, digitus short and broad with single spicule apically; penis valve long, narrow, curving ventrally, bent sharply laterally at apex; endophallus extending slightly beyond penis valve, slightly sclerotized basally.

Floral records. Boraginaceae (28 m# 19 f#): Tiquilia palmeri 1 f#, T. plicata 28 m# 17 f#, T. sp. 1 f#, Polygonaceae (9 m# 6 f#): Eriogonum deserticola 9 m# 6 f#.

Phenology. Active from May to October.

Distribution. Sonoran Desert (Fig. 2-51B), USA and likely Mexico. Prefers dune habitats.

Type material examined. Holotype data: f#, CALIFORNIA: Riverside Co.: Mecca, 25 August 1956, M. Wasbaueri, on Coldenia plicata [=Tiquilia plicata] (CAS type no. 14753). Allotype data: m#, same data as holotype, except: 20 August 1956 (UCRC). Paratype data: 2 m# 3 f#, same data as holotype (1 m# 2 f# UCRC, 1 m# 1 f# BBSL); 1 m# 1 f#, same data as holotype, except 20 August 1956 (1 m# BBSL, 1 f# UCRC).

Additional material examined. Total specimens: 34 m# 24 f#. CALIFORNIA: Imperial Co.: 2 mi W Glamis, Algodones Dunes (32.99388 -115.10388): 4 m# 6 f#, 25 Jul 1960, R.C.

**Remarks.** *Perdita wasbaueri* is unique in being one of the more minute *Heteroperdita*, though one female specimen is almost 4 mm long. It also holds the distinction of being the most extensively yellow-colored *Heteroperdita*. Wing veins are the most reduced in the subgenus; the female is the only one of similar-colored species that has the second medial cell absent, suggesting that this reduction may have arisen independently in this species. The wing is further reduced in the second submarginal cell, which is practically triangular in some specimens.
**Perdita yanegai** Portman, sp. n.

Figs. 2-6H, 2-7H, 2-8H, 2-9I, 2-32U, 2-24W, 2-26B, 2-55, 2-57H, 2-60K–L

**Diagnosis.** Both sexes of *P. yanegai* have the metasoma white or yellow with dark spots (Figs. 2-6H, 2-7H). They can be separated from similar species by the following combination of characters: face distinctly broader than long, scutum and scutellum dark, face not entirely yellow below the level of the antenna, metapleuron and anterior propodeum yellow with the light marks largely reduced in the male (Fig. 2-55B), and propodeum with yellow triangle dorso-anteriorly.

*Perdita yanegai* is very similar to *P. arenaria*; to distinguish these species, refer to the remarks of *P. arenaria*.

**Description of female.** Length: 3.2 mm. Forewing length: 2.0 mm.

**Coloration.** Head (Fig. 2-9I) and mesosoma base color black with greenish metallic luster; clypeus white; supraclypeal mark white, large, transverse; paraocular mark white, transverse to subtriangular, extending to level of summit of clypeus, sometimes with thin line travelling along eye to level of top of antennal socket; subantennal mark sometimes lightened along margin of antennal socket; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; frons generally with metallic tints throughout; scape white or yellowish-white; antenna more or less brown dorsally, white or tan ventrally; pronotal collar pale yellow, more or less marked with brown along medial suture; pronotal lobe white; metapleuron and anterior propodeum pale yellow (Fig. 2-55A); propodeum with narrow white or yellow triangle dorso-anteriorly; ventral surface of mesepisternum pale yellow along posterior margin, yellow
sometimes expanded medially; legs pale yellow except distal hind tarsi more or less darkened to brown; wing veins tan or light brown; metasoma white or yellowish-white with multiple lateral and medial dark brown spots (Fig. 2-7H); T1 with pair of sublateral splotches on anterior face (splotches often split into two distinct spots) and pair of sublateral spots on dorsal face; T2–T5 with five spots: one large basomedial triangle, two small baso-lateral spots, and two apico-sublateral spots, basal spots on T2 sometimes merging into continuous basal line, T2 fovea dark brown, lateral spots on T4–T5 generally reduced or absent; pygidial plate transparent white.

Structure and vestiture. Head broader than long (Fig. 2-9I); face, except for clypeus, lower supraclypeal area, and frons covered by dense recumbent white pubescence; eyes subparallel, slightly converging ventrally; facial fovea diverging dorsally, narrowly oval, extending from top of antennal socket 2/3 distance to apex of eye, generally more or less obscured by pubescence; mandible simple; labrum quadrate, slightly less than 2X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; venter of head with abundant inward-facing broadly hooked hairs; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and scutum mostly covered by combination of recumbent and erect white pubescence; fore coxa with abundant, broadly hooked hairs; apex of mid tibia with some short, thick, curved setae; forewing with second medial cell present; metasoma oval, wide basally, tapering apically, widest at T3 (Fig. 2-7H); terga tessellate and impunctate; T2 fovea linear, slightly thickened, slightly more than 1/2 length of T2; pygidial plate triangular, apex pointed (Fig. 2-24W); hairs of prepygidial fimbria thin, sparse.

Description of male. Length: 2.6 mm. Forewing length: 1.8 mm.

Coloration. Head (Fig. 2-8H) and mesosoma base color black with greenish or bluish metallic luster; clypeus white; supraclypeal mark white, large, slightly longer than broad;
paraocular mark white, ranging from transverse to triangular, generally extending in thin line to level of top of antennal socket; subantennal area typically with yellow along margin of antennal socket, sometimes entirely dark; mandible white, tip reddish; labrum white, sometimes with basomedial dark spot; scape white or yellow; antenna yellow, more or less brownish dorsally; pronotal collar yellow, more or less brown along medial suture, particularly laterally; pronotal lobe yellow or white; metapleuron and anterior propodeum with yellow band reduced, generally only yellow immediately below wing base (Fig. 2-55B); propodeum with yellow triangle dorso-anteriorly, triangle rarely reduced or absent; ventral surface of mesepisternum yellow along base of mid and hind coxae; legs entirely yellow except occasionally with faint vestigial dark mark medially on hind tibia (Fig. 2-55B); wing veins ranging from tan to brown; metasoma yellowish-white with multiple large dark brown spots (Fig. 2-6H); T1 with pair of sublateral splotches on anterior face and pair of sublateral spots on dorsal face; T2–T6 with five spots: one medial spot, two apico-sublateral spots, and two baso-lateral, medial spot often broad or subtriangular, spots on apical terga often reduced or absent; T2 fovea dark brown, merging with baso-lateral spots; pygidial plate transparent yellow.

Structure and vestiture. Head oval, broader than long (Fig. 2-8H); face, except for clypeus, lower supraclypeal area, and frons covered by dense recumbent white pubescence; eyes converging ventrally; mandible simple, extending to far side of labrum in repose; labrum quadrate, 1.5X broader than long; disc of clypeus broader than high, convex, apically protruding less than 1 OD from face; lateral extension reaching 1/3 distance to base of mandible; head with moderately dense pubescence ventrally; mesosoma strongly tessellate, impunctate, slightly shiny; pronotal collar slightly impressed, humeral angle weak; mesepisternum and margins and middle of scutum densely covered by combination of recumbent and erect white pubescence; hind tibia with sparse, short, slightly thickened hairs; metasoma narrower or equal in width to mesosoma,
suboval, wide basally, tapering apically, widest at T3 (Fig. 2-6H); terga tessellate and impunctate; T2 fovea linear, slightly thickened, 1/3 length of T2; pygidial plate narrowly triangular, apex narrowly rounded (Fig. 2-23U); hairs of prepygidial fimbria slightly thickened, sparse.

*Terminalia*. S8 (Fig. 2-57H) with spiculum bifurcate; lateral apodemes not prominent; apical portion slightly convex; much longer than broad, sides weakly converging to strongly folded over apex, apex flattened on top, forming rough C-shape (with back margin of “C” flattened rather than curved); short hairs ventrally; cuticle thinned in small circle subapically.

Genital capsule as in Figs. 2-60K–L. Gonostyli separated dorsally by narrow V-shape; gonostylus extending slightly beyond level of penis valve; dorsal lobe of gonostylus relatively short and broad; ventral lobe longer than dorsal lobe with minute hairs on apex; volsella narrow, shorter than gonostylus; cuspis with two spicules on dorsal margin of apex; digitus smaller than cuspis with single spicule on inner margin of apex; penis valve narrow, parallel, slightly expanded and turned outwards at apex; endophallus extending to level of apex of penis valve.

*Floral records*. **Boraginaceae** (59 m# 24 f#): *Cryptantha* sp. 4 m#, *Tiquilia latior* 1 m#, *T. nuttallii* 6 m# 6 f#, *T. palmeri* 13 m# 5 f#, *T. plicata* 25 m# 12 f#, *T. sp.* 10 m# 1 f#,

**Zygophyllaceae** (1 m#): *Larrea tridentata* 1 m#.

*Phenology*. Active from March to June.

*Distribution*. Mojave and Sonoran Deserts (Fig. 2-26B), USA (and likely Mexico).

*Type material*. Holotype data: m#, **CALIFORNIA**: San Bernardino Co.: Devils Playground 1850’ Sec 1 T11N R10E, 4 June 1980, T. Griswold (BBSL, accession no. 120002).
Paratype data: (19 m#) **CALIFORNIA**: Riverside Co.: 1.8 km W Wileys Well Road, 15 mi W Blythe, Chuckwalla Valley (33.60277 -114.92055): 2 m#, 7 Apr 2000, D. Yanega, *Tiquilia* sp. (UCRC): 18 mi W Blythe, Chuckwalla Valley (33.60638 -114.97361): 1 m#, 15 Apr 1958, P.H.


**Etymology.** This species is named in honor of Doug Yanega, who first recognized this species as undescribed.

**Remarks.** While this species can be separated from *P. arenaria* in some instances, in others, it is impossible to tell them apart. Both *P. yanegai* and *P. arenaria* are so variable in the extent of their light maculations, body size, and relative dimensions of the head that it is difficult to tease apart between-species variation from within-species variation. Additional specimens of both species may help resolve these issues, but it seems clear that there will always be some level of uncertainty when identifying the females.
Acknowledgements

We would especially like to thank the many people who contributed important specimens for this project: Rebekah Andrus, Stacy Higbee, Olivia and Susanna Messinger, Michael Orr, Frank Parker, Emily Sadler, Katie Weglarz, Karen Wright, and Doug Yanega. We would also like to thank Skylar Burrows for assistance with pictures, Harold Ikerd for databasing assistance, Robert Olsen for assistance measuring specimens, and Brian Rozick for databasing and making maps, and James Pitts and two anonymous reviewers for helpful comments on the manuscript.. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under grant number DGE-1147384 to ZMP. Funding was also provided by a Desert Legacy Fund grant from the Community Foundation. We acknowledge the support from the Microscopy Core Facility at Utah State University for the SEM work.

References


Tables

Table 2-1. Categorization of the different metasomal color patterns within *Perdita* (*Heteroperdita*).

<table>
<thead>
<tr>
<th>Color pattern</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellow spotted</td>
<td><em>P. arenaria</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. frontalis</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. maculosa</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. nuttalliae</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. sycorax</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. titania</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. wasbaueri</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. yanegai</em> m# and f#</td>
</tr>
<tr>
<td>Dark striped</td>
<td><em>P. optiva</em> f#</td>
</tr>
<tr>
<td></td>
<td><em>P. sexfasciata</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. trifasciata</em> m# and f#</td>
</tr>
<tr>
<td>Light striped</td>
<td><em>P. bellula</em> m#</td>
</tr>
<tr>
<td></td>
<td><em>P. coldeniae</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. optiva</em> m#</td>
</tr>
<tr>
<td></td>
<td><em>P. scutellaris</em> m# and f#</td>
</tr>
<tr>
<td>Solid amber</td>
<td><em>P. hooki</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. hippolyta</em> m# and f#</td>
</tr>
<tr>
<td></td>
<td><em>P. pilonotata</em> f#</td>
</tr>
<tr>
<td></td>
<td><em>P. rhodogastra</em> m# and f#</td>
</tr>
</tbody>
</table>
| Miscellaneous coloration (solid white, tan, brown or yellow, or vaguely spotted/striped tan or brown) | P. bellula f#  
| | P. desdemona f#  
| | P. exusta m# and f#  
| | P. prodigiosa f#  
| | P. rhodogastra m# and f# (dark form)  
| | P. vesca m# and f#  
| Ant-like | P. pilonotata m#  
| | P. prodigiosa m# |
Figure 2-1. Distribution of *Heteroperdita*. Red boxes delineate the extent of species-level maps: A – covers the Great Basin and Mojave/Sonoran Deserts, and Colorado Plateau, B – Mojave/Sonoran Deserts, C – Chihuahuan Desert. Scale bar = 200 km.
Figure 2-2. Ventral view of the head of *Perdita coldeniae* females, showing pollen basket (A) full of *Tiquilia* pollen (BBSL842342; Riverside Co., CA) and (B) empty (BBSL813845; Imperial Co., CA).

Figure 2-3. Stiff, curved setae on the apex of the outer face of the mid tibia in females. (A) *Perdita scutellaris* (DEVA55374; Inyo Co., CA). (B) *P. prodigiosa* (BBSL319173; Clark Co., NV). Scale bar = 100 micrometers (both images at the same scale).
Figure 2-4. Second submedial cell of forewing. (A) *Perdita vesca* female, present (BBSL816135; Harney Co., OR). (B) *P. prodigiosa* female, 2m-cu vein weakened dorsally (paratype, BBSL344037; Clark Co., NV). (C) *P. bellula* female, absent/weakened (BBSL316794; Clark Co., NV). (D) *P. wasbaueri* male, absent/weakened (BBSL842242; Imperial Co., CA).
Figure 2-5. Dorsal views of *Heteroperdita*. (A) *Perdita coldeniae* male with broad yellow triangle on the propodeum and the metasoma wider the mesosoma, scale = 0.5 mm (UCRC277998; Imperial Co., CA). (B) *P. arenaria* male mesosoma with narrow yellow triangle on propodeum, scale = 0.25 mm (BBSLID95733; Yuma Co., AZ). (C) *P. wasbaueri* female mesosoma with yellow scutellum and yellow along lateral margins of scutum, scale = 0.25 mm (141836; Imperial Co., AZ).
Figure 2-6. Spotted male metasomas. (A) *Perdita arenaria* (paratype, UCRC166022; Imperial Co., CA). (B) *P. frontalis* (BBSL813851; Imperial Co., CA). (C) *P. maculosa* (BBSL277846; Clark Co., NV). (D) *P. nuttalliae* (Paratype, BBSL816190; Harney Co., OR). (E) *P. sycorax* (paratype, 37225; Emery Co., UT). (F) *P. titania* (paratype, UCRC166000; Imperial Co., CA). (G) *P. wasbaueri* (BBSL842195; San Bernardino Co., CA). (H) *P. yanegai* (paratype, UCRC166011; Riverside Co., CA). All scale bars 0.25 mm.
Figure 2-7. Spotted female metasomas. (A) *Perdita arenaria* (BBSL813432; Imperial Co., CA). (B) *P. frontalis* (BBSL813797; Imperial Co., CA). (C) *P. maculosa* (BBSL638406; Clark Co., NV). (D) *P. nuttalliae* (paratype, BBSL816167; Harney Co., OR). (E) *P. sycorax* (paratype, BBSL389685; Emery Co., UT). (F) *P. titania* (paratype, BBSL342256; San Bernardino Co., CA). (G) *P. wasbaueri* (141836; Imperial Co., CA). (H) *P. yanegai* (BBSL282782; Clark Co., NV). (I) *P. bellula* with distinct spots (FDP161540; Riverside Co., CA). All scale bars 0.5 mm.

Figure 2-8. Spotted male faces. (A) *Perdita arenaria* (UCRC166001; Baja California, MEX). (B) *P. frontalis* (BBSL813803; Imperial Co., CA). (C) *P. maculosa* (BBSL277846; Clark Co., NV). (D) *P. nuttalliae* (paratype, BBSL816134; Harney Co., OR). (E) *P. sycorax* (paratype, 37234; Emery Co., UT). (F) *P. titania* (paratype, UCRC166000; Imperial Co., CA). (G) *P. wasbaueri* (BBSL842195; San Bernardino Co., CA). (H) *P. yanegai* (paratype, UCRC166011; Riverside Co., CA). All scale bars 0.25 mm.
Figure 2-9. Spotted female faces. (A) *Perdita arenaria* (BBSL813437; Imperial Co., CA). (B) *P. frontalis* with light marks on frons (BBSL813822; Imperial Co., CA). (C) *P. frontalis* without light marks on frons (BBSL813797; Imperial Co., CA). (D) *P. maculosa* (UCRC179125; Riverside Co., CA). (E) *P. nuttalliae* (142005; Box Elder Co., UT). (F) *P. sycorax* (paratype, 37239; Emery Co., UT). (G) *P. titania* (paratype, BBSL326372; San Bernardino Co., CA). (H) *P. wasbaueri* (BBSL842199; San Bernardino Co., CA). (I) *P. yanegai* (BBSL282782; Clark Co., NV). All scales bars 0.25 mm.
Figure 2-10. Striped male metasomas. (A) *Perdita optiva* (BBSL288698; Clark Co., NV). (B) *P. sexfasciata* (141743; Mojave Co., AZ). (C) *P. trifasciata* (141760; Terrell Co., TX). (D) *P. bellula* dark form (FDP161544; Riverside Co., CA). (E) *P. bellula* typical light form (BBSL817812; Mojave Co., AZ). (F) *P. coldeniae* (UCRC169099; Imperial Co., CA). (G) *P. scutellaris* (DEVA55309; San Bernardino Co., CA). All scale bars 0.5 mm.

Figure 2-11. Striped female metasomas. (A) *Perdita optiva* (BBSL813638; Imperial Co., CA). (B) *P. sexfasciata* (UCRC266156; La Paz Co., AZ). (C) *P. trifasciata* (141780; Chihuahua, MEX). (D) *P. coldeniae* (BBSL813863; Imperial Co., CA). (E) *P. scutellaris* (UCRC221793; San Bernardino Co., CA). All scale bars 0.5 mm.
Figure 2-12. Striped male faces. (A) *Perdita optiva* (BBSL813428; Imperial Co., CA). (B) *P. sexfasciata* (BBSL282900; Clark Co., NV). (C) *P. trifasciata* (BBSL844684; Culberson Co., TX). (D) *P. bellula* (BBSL842249; Imperial Co., CA). (E) *P. coldeniae*, large (BBSL813475; Imperial Co., CA). (F) *P. coldeniae*, small (BBSL813818; Imperial Co., CA). (G) *P. scutellaris* (DEVA55312; San Bernardino Co., CA). All scale bars 0.25 mm.
Figure 2-13. Striped female faces. (A) *Perdita optiva* (BBSL284979; Clark Co., NV). (B) *P. sexfasciata* (UCRC266156; La Paz Co., AZ). (C) *P. trifasciata* (BBSL347789; Eddy Co., NM). (D) *P. coldeniae* (BBSL813434; Imperial Co., CA). (E) *P. scutellaris* (DEVA55307; San Bernardino Co., CA). (F) *P. scutellaris* mandible (DEVA55062; San Bernardino Co., CA). All scale bars 0.25 mm.
Figure 2-14. Ant-like males. (A) *Perdita pilonotata* small-headed male (BBSL808042; Chihuahua, MEX). (B) *P. pilonotata* large-headed male (BBSL810335; Chihuahua, MEX). (C) *P. pilonotata* metasoma (BBSL808042). (D) *P. prodigiosa* small-headed male (paratype, BBSL813551; Clark Co., NV). (E) *P. prodigiosa* large-headed male (paratype, BBSL813549;
Clark Co., NV). (F) *P. prodigiosa* metasoma (paratype, BBSL344092; Clark Co., NV). Scale bars of heads 0.25 mm, scale bars of metasoma 0.5 mm. Note: Both species have males with intergrading medium-sized heads that are not pictured.

Figure 2-15. Amber male metasomas. (A) *Perdita rhodogastra*, typical form (BBSL817862; Riverside Co., CA). (B) *P. rhodogastra*, dark with medial bars (paratype, UCRC185330; Imperial Co., CA). (C) *P. hippolyta* (paratype, BBSL844677 Culberson Co., TX). (D) *P. hooki* (paratype, 141837; Terrell Co., TX). (E) *P. bellula*, cyanided (BBSL315311; Clark Co., NV). All scale bars 0.5 mm.
Figure 2-16. Amber female metasomas. (A) Perdita rhodogastra, solid coloration (BBSL817856; Riverside Co., CA). (B) P. rhodogastra, with vestigial spots (FDP112655; Maricopa Co., AZ). (C) P. hippolyta (BBSL844863; Culberson Co., TX). (D) P. hooki (paratype, 141840; Terrell Co., TX). (E) P. pilonotata (BBSL810333; Chihuahua, MEX). All scale bars 0.5 mm.
Figure 2-17. Amber male faces. (A) *Perdita rhodogastra*, Sonoran (BBSL817852; Riverside Co., CA). (B) *P. rhodogastra*, Mojave (BBSL307254; Clark Co., NV). (C) *P. rhodogastra*, Mojave dark form (BBSL817150; Mojave Co., AZ). (D) *P. hippolyta* (paratype, BBSL844673; Culberson Co., TX). (E) *P. hooki* (paratype, 141837; Terrell Co., TX). All scale bars 0.25 mm.
Figure 2-18. Amber female faces. (A) *Perdita rhodogastra*, Sonoran (paratype, UCRC185307; Imperial Co., CA). (B) *P. rhodogastra*, Mojave (BBSL817814; Mojave Co., AZ). (C) *P. hippolyta*, light form (paratype, BBSL844647; Culberson Co., TX). (D) *P. hippolyta*, dark form (paratype, BBSL347060; Eddy Co., NM). (E) *P. hooki* (paratype, 141840; Terrell Co., TX). (F) *P. pilonotata* (neotype, UCRC182770; Otero Co., NM). All scale bars 0.25 mm.
Figure 2-19. Miscellaneous male metasomas. (A) *Perdita bellula*, typical form (141678; Yuma Co., AZ). (B) *P. bellula*, variation (BBSL817827; Riverside Co., CA). (C) *P. exusta* (141895; Clark Co., NV). (D) *P. rhodogastra* (BBSL309170; Clark Co., NV). (E) *P. rhodogastra*, dark form with light band (BBSL290131; Clark Co., NV). (F) *P. vesca*, light coloration (BBSL904888; Nye Co., NV). (G) *P. vesca*, spotted (BBSL816156; Harney Co., NV). (H) *P. vesca*, solid coloration (141789; Clark Co., NV). All scale bars 0.5 mm.
Figure 2-20. Miscellaneous female metasomas. (A) *Perdita bellula*, typical coloration (103744; San Bernardino Co., CA). (B) *P. bellula*, melanized (BBSL316794; Clark Co., NV). (C) *P. desdemona* (paratype, UCRC185342; San Bernardino Co., CA). (D) *P. exusta* (paratype, 141946; Clark Co., NV). (E) *P. prodigiosa*, light coloration (BBSL344016). (F) *P. prodigiosa*, dark coloration (paratype, BBSL344044; Clark Co., NV). (G) *P. rhodogastra* (BBSL271666; Clark Co., NV). (H) *P. vesca*, dark typical coloration (BBSL981672; Harney Co., OR). (I) *P. vanessa*, light coloration (BBSL904881; Nye Co., NV). All scale bars 0.5 mm.
Figure 2-21. Miscellaneous male faces. (A) *Perdita bellula*, large specimen (BBSL842249; Imperial Co., CA). (B) *P. bellula*, small specimen (BBSL817812; Mojave Co., AZ). (C) *P. rhodogastra* (BBSL817150; Mojave Co., AZ). (D) *P. exusta* (141888; Clark Co., NV). (E) *P. vesca*, dark coloration (BBSL816156; Harney Co., OR). (F) *P. vesca*, light coloration (BBSL904888; Nye Co., NV). All scale bars 0.25 mm.
Figure 2-22. Miscellaneous female faces. (A) Perdita bellula (BBSL813459; Imperial Co., CA). (B) P. desdemona (paratype, BBSL289006; San Bernardino Co., CA). (C) P. exusta (paratype, 141952; Clark Co., NV). (D) P. vesca, dark coloration (BBSL816172; Harney Co., OR). (E) P. vesca, light coloration (BBSL904881; Nye Co., NV). (F) P. prodigiosa, dark coloration (paratype, BBSL813546; Clark Co., NV). (G) P. prodigiosa, light coloration (paratype, BBSL318844; Clark Co., NV). All scale bars 0.25 mm.
Figure 2-23. Male pygidial plates. (A) *Perdita arenaria* (BBSL814703; Imperial Co., CA). (B) *P. bellula* (103717; San Bernardino Co., CA). (C) *P. coldeniae* (UCRC277998; Imperial Co., CA). (D) *P. exusta* (141888; Clark Co., NV). (E) *P. frontalis* (BBSL989204; Imperial Co., CA). (F) *P. hippolyta* (paratype, BBSL844677; Culberson Co., TX). (G) *P. hooki* (note: the pygidial plate is from a dissected specimen and the lateral edges have been artificially enhanced to give a better idea of the lateral edges, paratype, BBSL852902; Coahuila de Zaragoza, MEX). (H) *P. maculosa* (BBSL668379; Clark Co., NV). (I) *P. nuttalliae* (paratype, BBSL816190; Harney Co., OR). (J) *P. optiva* (BBSL813428; Imperial Co., CA). (K) *P. pilonotata* (CAVE17654; Eddy Co., NM). (L) *P. prodigiosa* (paratype, BBSL344085; Clark Co., NV). (M) *P. rhodogaster* (UCRC277717; Yuma Co., AZ). (N) *P. scutellaris* (DEVA55305; San Bernardino Co., CA). (O) *P. sexfasciata* (141736; San Bernardino Co., CA). (P) *P. sycorax* (note: the picture is taken at an angle but it still accurately represents the shape the pygidial plate, paratype, 37225; Emery Co., UT). (Q) *P. titania* (pygidial plate is artificially outlined for better visibility, paratype, UCRC166000; Imperial Co., CA). (R) *P. trifasciata* (141767; Chihuahua, MEX). (S) *P. vesca* (BBSL816156; Harney Co., OR). (T) *P. wasbaueri* (BBSL904842; Imperial Co., CA). (U) *P. yanegai* (UCRC50407; Riverside Co., CA). Scale bar = 0.1 mm. All images are at the same scale.
Figure 2-24. Female pygidial plates. (A) *Perdita arenaria* (BBSL289244; Clark Co., NV). (B) *P. bellula* (103744; San Bernardino Co., CA). (C) *P. coldeniae* (BBSL813873; Imperial Co., CA). (D) *P. desdemona* (holotype, BBSL289742; San Bernardino Co., CA). (E) *P. exusta* (paratype, 141946; Clark Co., NV). (F) *P. frontalis* (BBSL813797; Imperial Co., CA). (G) *P. hippolyta* (paratype, BBSL844647; Culberson Co., TX). (H) *P. hooki* (paratype, 141840; Terrell Co., TX). (I) *P. maculosa* (UCRC179125; Riverside Co., CA). (J) *P. nuttalliae* (142005; Box Elder Co., UT). (K) *P. optiva* (BBSL284974; Clark Co., NV). (L) *P. pilonotata* (neotype, UCRC182770; Otero Co., NM). (M) *P. prodigiosa* (paratype, BBSL319169; Clark Co., NV). (N) *P. rhodogastra*, pointed (FDP102612; Maricopa Co., AZ). (O) *P. rhodogastra*, rounded (BBSL271674; Clark Co., NV). (P) *P. scutellaris* (BBSL904845; Imperial Co., CA). (Q) *P. sexfasciata* (BBSL295303; Clark Co., NV). (R) *P. sycorax* (paratype, 37238; Emery Co., UT). (S) *P. titania* (holotype, BBSL326372; San Bernardino Co., CA). (T) *P. trifasciata* (FDP75046; Brewster Co., TX). (U) *P. vesca* (BBSL339200; Nye Co., NV). (V) *P. wasbaueri* (141836; Imperial Co., CA). (W) *P. yanegai* (UCRC221828; San Bernardino Co., CA). Scale bar = 0.1 mm. All images are at the same scale.

Figure 2-25. *Perdita arenaria* (A) female lateral habitus (BBSL813432; Imperial Co., CA), (B) male lateral habitus (UCRC166001; Baja California, MEX). Scale bars = 1 mm.
Figure 2-26. Distribution (males only) of (A) *Perdita arenaria* and (B) *P. yanegai*. Scale bar = 100 km.
Figure 2-27. *Perdita bellula* (A) female lateral habitus (FDP105656; Maricopa Co., AZ), (B) male lateral habitus (BBSL817812; Mojave Co., AZ). Scale bars = 1 mm.
Figure 2-28. Distribution of (A) *Perdita bellula* and (B) *P. coldeniae*. Scale bar = 100 km.

Figure 2-29. *Perdita coldeniae* (A) female lateral habitus (BBSL813873; Imperial Co., CA), (B) male lateral habitus (BBSL813859; Imperial Co., CA). Scale bars = 1 mm.

Figure 2-30. *Perdita desdemona* female lateral habitus (paratype, BBSL289006; San Bernardino Co., CA). Scale bar = 1 mm.
Figure 2-31. Distribution of (A) *Perdita desdemona* (triangles) and *P. vesca* (circles), (B) *P. exusta* (squares) and *P. frontalis* (stars). Scale bars = 100 km.
Figure 2-32. *Perdita exusta* (A) female lateral habitus (paratype, 141952; Clark Co., NV), (B) male lateral habitus (141888; Clark Co., NV). Scale bars = 1 mm.

Figure 2-33. *Perdita frontalis* (A) female lateral habitus (BBSL813820; Imperial Co., CA), (B) male lateral habitus (BBSL813803; Imperial Co., CA). Scale bars = 1 mm.

Figure 2-34. *Perdita hippolyta* (A) female lateral habitus (paratype, BBSL844647; Culberson Co., TX), (B) male lateral habitus (holotype, BBSL844675; Culberson Co., TX). Scale bars = 1 mm.
Figure 2-35. *Perdita hooki* (A) female lateral habitus (paratype, 141840; Terrell Co., TX), (B) male lateral habitus (paratype, 141837; Terrell Co., TX). Scale bars = 1 mm.
Figure 2-36. Distribution of (A) Perdita hippolyta and (B) P. hooki. Scale bar = 100 km.

Figure 2-37. Perdita maculosa (A) female lateral habitus (UCRC39927; Riverside Co., CA), (B) male lateral habitus (BBSL277848; Clark Co., NV). Scale bars = 1 mm.

Figure 2-38. Perdita nuttalliae (A) female lateral habitus (142005; Box Elder Co., UT), (B) male lateral habitus (paratype, BBSL816134; Harney Co., OR). Scale bars = 1 mm.
Figure 2-39. Distribution of *Perdita maculosa* (circles), *P. nuttalliae* (squares), and *P. sycorax* (triangles). Scale bar = 100 km.
Figure 2-40. *Perdita optiva* (A) female lateral habitus (BBSL284975; Clark Co., NV), (B) male lateral habitus (BBSL288698; Clark Co., NV). Scale bars = 1 mm.

Figure 2-41. Distribution of (A) *Perdita prodigiosa* (circles) and *P. optiva* (triangles), (B) *P. rhodogastra*. Scale bar = 100 km.
Figure 2-42. *Perdita pilonotata* (A) female lateral habitus (BBSL.810332; Chihuahua, MEX), (B) male lateral habitus (large-headed specimen, BBSL.810335; Chihuahua, MEX). Scale bars = 1 mm.
Figure 2-43. Distribution of (A) *Perdita pilonotata* and (B) *P. trifasciata*. Scale bar = 100 km.

Figure 2-44. *Perdita prodigiosa* (A) female lateral habitus (paratype, BBSL319169; Clark Co., NV), (B) male lateral habitus (paratype, BBSL813551; Clark Co., NV). Scale bars = 1 mm.

Figure 2-45. *Perdita rhodogastra* (A) female lateral habitus (BBSL817855; Riverside Co., CA), (B) male lateral habitus (BBSL817852; Riverside Co., CA). Scale bars = 1 mm.
Figure 2-46. *Perdita scutellaris* (A) female lateral habitus (DEVA55307; San Bernardino Co., CA), (B) male lateral habitus (DEVA55309; San Bernardino Co., CA). Scale bars = 1 mm.
Figure 2-47. Distribution of (A) *Perdita scutellaris* and (B) *P. sexfasciata*. Scale bar = 100 km.

Figure 2-48. *Perdita sexfasciata* (A) female lateral habitus (UCRC266156; La Paz Co., AZ), (B) male lateral habitus (141743; Mohave Co., AZ). Scale bars = 1 mm.

Figure 2-49. *Perdita sycorax* (A) female lateral habitus (paratype, 37239; Emery Co., UT), (B) male lateral habitus (paratype, 37235; Emery Co., UT). Scale bars = 1 mm.
Figure 2-50. *Perdita tithania* (A) female lateral habitus (holotype, BBSL326372; San Bernardino Co., CA), (B) male lateral habitus (paratype, UCRC166000; Imperial Co., CA). Scale bars = 1 mm.
Figure 2-51. Distribution of (A) *Perdita titania* and (B) *P. wasbaueri*. Scale bar = 100 km.

Figure 2-52. *Perdita trifasciata* (A) female lateral habitus (FDP75089; Brewster Co., TX), (B) male lateral habitus (BBSL844684; Culberson Co., TX). Scale bars = 1 mm.

Figure 2-53. *Perdita vesca* (A) female lateral habitus (BBSL816172; Harney Co., OR), (B) male lateral habitus (BBSL816156; Harney Co., OR). Scale bars = 1 mm.
Figure 2-54. *Perdita wasbaueri* (A) female lateral habitus (BBSL842199; San Bernardino Co., CA), (B) male lateral habitus (BBSL842195; San Bernardino Co., CA). Scale bars = 1 mm.

Figure 2-55. *Perdita yanegai* (A) female lateral habitus (BBSL273105; Clark Co., NV), (B) male lateral habitus (paratype, UCRC166011; Riverside Co., CA). Scale bars = 1 mm.
Figure 2-56. Male S8 in dorsal view. (A) *Perdita arenaria* (BBSL814693; Imperial Co., CA). (B) *P. bellula* (BBSL842486; Riverside Co., CA). (C) *P. coldeniae* (BBSL813338; Yuma Co., AZ). (D) *P. exusta* (BBSL578345; Clark Co., NV). (E) *P. frontalis* (BBSL813814; Imperial Co., CA).
(F) *P. hippolyta* (paratype, CAVE4578; Eddy Co., NM). (G) *P. hooki* (paratype, BBSL852902; Coahuila, MEX). (H) *P. maculosa* (BBSL638408; Clark Co., NV). (I) *P. nuttalliae* (BBSL816192; Harney Co., OR). (J) *P. optiva* (BBSL814695; Imperial Co., CA). (K) *P. pilonotata* (CAVE17654; Eddy Co., NM). (L) *P. prodigiosa* (BBSL344096; Clark Co., NV). Scale bar = 0.25 mm. All images are at the same scale.

Figure 2-57. Male S8 in dorsal view. (A) *Perdita rhodogastre* (BBSL817823; Clark Co., NV). (B) *P. scutellaris* (BBSL328151; San Bernardino Co., CA). (C) *P. sexfasciata* (BBSL295263; Clark Co., NV). (D) *P. sycorax* (2121; Emery Co., UT). (E) *P. trifasciata* (BBSL844685; Culberson Co., TX). (F) *P. vesca* (BBSL904892; Nye Co., NV). (G) *P. wasbaueri* (BBSL842247; Imperial Co., CA). (H) *P. yanegai* (BBSL904915; Nye Co., NV). Scale bar = 0.25 mm. All images are at the same scale.
Figure 2-58. Male genital capsules in ventral and dorsal view. (A) *Perdita arenaria* dorsal and (B) ventral (BBSL814693; Imperial Co., CA). (C) *P. bellula* dorsal and (D) ventral (BBSL307306; Clark Co., NV). (E) *P. coldeniae* dorsal and (F) ventral (BBSL817844; Riverside Co., CA). (G) *P. exusta* dorsal and (H) ventral (141875; Clark Co., NV). (I) *P. frontalis* dorsal and (J) ventral (BBSL813814; Imperial Co., CA). (K) *P. hippolyta* dorsal and (L) ventral (paratype, CAVE4578; Eddy Co., NM). (M) *P. hooki* dorsal and (N) ventral (paratype, BBSL852902; Coahuila, MEX). Scale bar = 0.25 mm. All images are at the same scale.
Figure 2-59. Male genital capsules in ventral and dorsal view. (A) *Perdita maculosa* dorsal and (B) ventral (BBSL638408; Clark Co., NV). (C) *P. nuttalliae* dorsal and (D) ventral (BBSL641661; Tooele Co., UT). (E) *P. optiva* dorsal and (F) ventral (BBSL814695; Imperial Co., CA). (G) *P. pilonotata* dorsal and (H) ventral (CAVE17654; Eddy Co., NM). (I) *P. prodigiosa* dorsal, (J) dorsal, and (K) lateral (BBSL344096; Clark Co., NV). (L) *P. rhodogastra* dorsal and (M) ventral (BBSL817848; Riverside Co., CA). (N) *P. scutellaris* dorsal and (O) ventral (DEVA55310; San Bernardino Co., CA). Scale bar = 0.25 mm. All images are at the same scale.

Figure 2-60. Male genital capsules in ventral and dorsal view. (A) *Perdita sexfasciata* dorsal and (B) ventral (BBSL295263; Clark Co., NV). (C) *P. sycorax* dorsal and (D) ventral (2121; Emery Co., UT). (E) *P. trifasciata* dorsal and (F) ventral (BBSL844685; Culberson Co., TX). (G) *P. vesca* dorsal and (H) ventral (BBSL817575; Washoe Co., NV). (I) *P. wasbaueri* dorsal and (J)
ventral (BBSL842247; Imperial Co., CA). (K) *P. yanegai* dorsal and (L) ventral (UCRC221814; San Bernardino Co., CA). Scale bar = 0.25 mm. All images are at the same scale.
CHAPTER 3

CONVERGENT EVOLUTION OF POLLEN TRANSPORT MODE IN TWO DISTANTLY RELATED BEE GENERA (HYMENOPTERA: ANDRENIDAE)

Abstract

Purposeful transport of pollen represents a key innovation in the evolution of bees from predatory wasps. Most bees transport pollen on specialized hairs on the hind legs or ventral metasoma in one of three ways: moist, dry, or “glazed,” which combines dry and moist transport. The evolutionary pathway among these three transport modes is unclear, though dry transport has been hypothesized to be ancestral. We address this hypothesis using museum specimens and published records of the bee genera *Perdita* (Andrenidae) and *Hesperapis* (Melittidae), two distantly related groups whose pollen transport modes appear to have converged. Most species in both genera transport moistened pollen; glazed and dry transport are limited to derived clades of specialists on floral hosts in Asteraceae and Onagraceae, with specialization on Asteraceae associated with more elaborate scopal hairs. The associations between transport mode, host plant, and hair type may be due to the sticky pollenkitt of asteraceous pollen grains and the viscin threads of Onagraceae pollen, which provide alternates to the binding properties of nectar. These findings suggest that the hypothesis that dry transport is ancestral in bees be reexamined.

Introduction

Female bees collect pollen at flowers and transport it to the nest where it serves as the primary protein source for their progeny. Although past research has explored the various adaptations of bees to gather pollen (e.g. Thorp 1979; Müller 1996a; Müller 1996b; Müller and Bansac 2004),

---

4 This chapter is written in the style of the journal Apidologie where it has been published.
fewer studies have addressed how pollen is transported to the nest. Although a few bee taxa transport pollen internally in the crop, most transport it either on the ventral metasoma (e.g., most Megachilidae) or, more commonly, on the hind legs (Michener 2007). Transport on the hind legs is facilitated by structural elaborations, mostly of the tibia and basitarsus, to include either hair brushes (scopae) or flattened plates (corbiculae).

Pollen is packed on the hind legs and transported in one of three modes: moistened with nectar or oils (Figure 3-1A–B), dry (Figure 3-2C–D), or “glazed”, a combination of dry and moist collection (Figure 3-1C–D). A glazed pollen load is initially packed dry and is then capped with nectar during the latter part of the foraging trip (Thorp 2000; Eickwort et al. 1986; Norden et al. 1992). Although most bee species transport dry pollen, five of the seven bee families also contain genera with species that transport either moistened or glazed pollen: Andrenidae, Apidae, Halictidae, Melittidae, and Stenotritidae (Malyshev 1936; Houston and Thorp 1984; Westerkamp 1996; Thorp 2000; Michener 2007).

The evolutionary sequence of external pollen transport amongst the three modes is presently unsettled. Traditionally, primitive bees were thought to transport pollen internally in the crop (Malyshev 1936; Jander 1976; Michener et al. 1978; Michener 1979). More recent hypotheses propose that primitive bees transported pollen dry on plumose hairs that covered most of the body (Roberts and Vallespir 1978; Radchenko and Pesekno 1996; Michener 2007). This hypothesis is presumably supported by the branched body hairs and plumose hindleg hairs found on the oldest known bee fossil (~100 Myr), a single male Melittosphex burmensis Poinar & Danforth (Danforth and Poinar 2011). Alternatively, others have hypothesized that plumose hairs originated as an adaptation for temperature and water regulation rather than pollen transport (Engel 2001, Michener 2007). The paucity of bees in the fossil record (Michez et al. 2012) offers little additional help in disentangling the evolution of pollen transport or of hair traits.
Bee genera that contain some species that transport moist pollen and others that transport pollen dry are particularly apt to shed light on the evolutionary sequence of pollen transport modes especially when phylogenies are available for comparison. Two examples are the genera *Perdita* (Andrenidae) and *Hesperapis* (Melittidae) (Timberlake 1954; Stage 1966), which are distantly related (Cardinal and Danforth 2013; Hedtke et al. 2013), yet have several similarities: they are restricted to North America (Michener 2007; Michez et al. 2007), are most diverse in the arid west (Michener 2007) and are comprised almost exclusively of oligoleges, i.e. species which use pollen from a small set of related floral hosts (Linsley 1958; Stage 1966; Eickwort and Ginsberg 1980; Cane et al. 1996; Minckley et al. 2013). A recent partial phylogeny is available for *Perdita* (Danforth 1996) and preliminary ones are available for *Hesperapis* (Stage 1966; Michez et al. 2009).

At present, the incidence of *Perdita* species that transport moist, dry, or glazed pollen loads is unknown. Although many are thought to transport a pollen mass that has been continuously moistened with nectar as it is packed onto the hind tibia (Timberlake 1954; Thorp 1979; Michener 2007; Neff 2008), the genus is large (>630 species, Portman et al. 2016) and the transport modes of only seven species have been studied in detail. Of these, six are moist transporters and one transports glazed pollen. Species that “glaze” their pollen loads are thought to be confined to one monophyletic section of seven subgenera (Danforth 1996; Timberlake 1954; Michener 2007). The pollen transport mode of most *Hesperapis* (~40 species, Cane et al. 1996) species is also poorly known; only three, all moist-transporters, have been investigated in depth.

At least two salient factors may influence pollen transport mode: host plant choice, scopal hair morphology and distribution, or an interaction of the two. Thorp (1979) proposed that moist pollen transport would be particularly advantageous to generalist pollen foraging species because
moistening facilitates the agglutination of pollen of diverse shapes and sizes (see also Vaissière and Vinson 1994). Paradoxically, however, many of the species that transport moistened pollen are oligolectic (Thorp 1979). In addition, there are many examples of host plant pollen being collected by different bee species that employ contrasting transport modes (e.g. Hurd and Linsley 1975, *Larrea* specialists; Hurd et al. 1980, *Helianthus* specialists). Since both dry and moist transport are exhibited by diverse generalist and specialist pollen foragers on the same host, it suggests that additional factors such as scopal hair characteristics or evolutionary limitations might be germane.

It has been previously suggested that the structure, density, and distribution of the scopae correspond to pollen properties. The scopal hairs associated with dry transport often reflect the size and ornamentation of the pollen specialized on (Linsley 1958; Thorp 1979). Examples include long simple hairs on bees specialized on Onagraceae (Michener 1944; Linsley et al. 1963; Thorp 1969; Thorp 1979), hair brushes of long, simple, curved hairs on bees specialized on Cucurbitaceae (Hurd and Linsley 1964), and dense, finely plumose or branched scopal hairs on bees specialized on small, spiny Asteraceae pollen (Linsley 1958; Linsley and MacSwain 1958; Moldenke 1979). Alternatively, other studies suggest that the simple scopal hairs of moist-transporters are adaptable to holding many pollen types (Roberts and Vallespir 1978; Thorp 1979; Thorp 2000; Michener 2007). In *Perdita*, there are clear differences in the structure of the scopal hairs between species that transport moist or glazed pollen; species that transport glazed pollen typically have longer, denser, and more structurally complex scopal hairs (Timberlake 1954; Danforth 1996).

Our objectives here are threefold: (1) expand our knowledge of the distribution of dry, moist, and glazed pollen transport in *Perdita* and *Hesperapis*; (2) determine if pollen transport mode is associated with specialization on particular floral hosts or pollen types; and (3) uncover
associations between scopal hair types and pollen transport mode. We then use extant though inchoate phylogenies to derive systematic hypotheses which address the origin and evolution of pollen transport.

**Methods**

Specimens in the genera *Perdita* and *Hesperapis* were examined from the USDA Pollinating Insect Research Unit (PIRU) collection in Logan, UT and the Entomology Research Museum, University of California, Riverside, CA using a Leica M125 or MZ12 stereomicroscope with a Techniquip ProLine 80 LED ring light. A subset of specimens were further examined using a Quanta FEG 650 Scanning Electron Microscope to confirm or refine findings on the distribution and morphology of scopal hairs and pollen grains.

Pollen transport mode was classified into three groups: moist (Figure 3-1A–B, entire pollen load moistened), dry (Figure 3-2C–D, no moistening detected), or glazed (Figure 3-1C–D, an initial layer of dry pollen covered by a layer of moistened pollen). In bees that transport glazed pollen, we estimated the proportion of the pollen load on the tibia and basitarsus that was dry. Some species were represented only by specimens with partially-filled dry pollen loads, making it impossible to distinguish between dry and glazed transport. These specimens were classified as transporting initially dry pollen.

We categorized scopal hair type by the location of hairs on different areas of the hind legs, hair-length, hair morphology, and the presence of pollen in those hairs. Although hair density and length are continuous rather than discrete characters, we were able to confidently place them into discrete categories. Hair density was estimated based on the space between scopal hairs, and was classified into three groups: sparse, medium, or dense, based on whether the integument was clearly visible, partially obscured, or fully obscured, respectively. Hair length was classified as
short, medium, or long, based on whether the hairs were less than 2X the maximum width of the hind tibia, between 2–3X, or greater than 3X, respectively. We also classified the associated pollen-transporting hairs on the anterior face of the hind tibia as either simple, branched, wavy, or corkscrew-shaped (Figure 3-3).

We used two steps to determine whether pollen in the scopae was moist or dry: a pollen load was deemed moist-packed if it was compact and extended beyond the scopal hairs. To further confirm the moist-packed designation, an insect pin was used to poke the pollen mass. Moistened pollen in museum specimens hardens into an impervious mass that resists “poking” whereas dry pollen offers no resistance and is readily penetrated. Because pollen in the scopae can be wetted passively when bees are collected in pan traps, malaise traps, or when bees regurgitate nectar in kill jars, we did not survey specimens with signs of wetting on other parts of the body such as matted hairs.

We surveyed a representative subset of species from every subgenus and major species group of the target genera (Table 3-II). Multiple specimens of each species from varying collection locations and times were surveyed whenever possible. An attempt was made to survey species that collectively specialize on a wide range of floral hosts. Particular attention was paid to bee groups thought to contain species that transport dry or glazed pollen; these groups had all available species surveyed. Records for four species not represented in the PIRU collection by specimens with pollen were compiled from the literature.

Floral specialization of *Perdita* and *Hesperapis* species was compiled from various published sources and visitation records in the PIRU database (US NPID 2016). Lastly, scopal pollen of representative specimens was compared to pollen on slides prepared from previous studies in Clark County, NV and Colorado (Tepedino et al. 1999; Griswold et al. 2006). Morphological
terminology and taxonomic classification of *Perdita* follow Michener (2007), and taxonomic classification of *Hesperapis* follows Michez et al. (2007) and includes the unnamed species from Stage (1966) and Michener (1981).

**Results**

The vast majority of both *Perdita* and *Hesperapis* species surveyed are oligolectic, specializing on floral hosts in one of 21 and 9 plant families, respectively (Table 3-I). Most species in both genera transported pollen that had been uniformly moistened with nectar (94 of 136 species of *Perdita*; 11 of 17 species of *Hesperapis*). Dry or glazed pollen transport only occurred in species of both genera that specialized on Asteraceae or Onagraceae pollen.

**Glazed or Dry Pollen Transport**

Forty-two species of *Perdita* transported either glazed or dry pollen: 24 glazed, 15 dry at least initially, and three dry (Table 3-I). Thirty-eight of those 42 species specialize on Asteraceae hosts with the proportion of dry pollen ranging from 25–80%. Bees that glaze their pollen loads do not entirely cap the basal layer of dry pollen; instead, moistened pollen is always added at a similar location on the anterior face of the hind tibia and only partially covers the dry pollen (e.g., Figure 3-1C–D). Of the four species specialized on Onagraceae hosts, three transported dry pollen loads and one transported pollen dry at least initially.

The distribution of glazed and dry pollen transport follows a clear phylogenetic pattern. Although *Perdita* species in at least eleven subgenera and species groups are specialized on Asteraceae pollen (Table 3-II), the species that transport glazed pollen fall into a single monophyletic group of seven subgenera (Fig. 3-5; Timberlake 1954; Danforth 1996). In contrast, the 18 surveyed species that transported entirely moist Asteraceae pollen are scattered across at least four
unrelated subgenera and species-groups — subgenus *Pygoperdita* (2), and the species-groups *Octomaculata* (9), *Ventralis* (2), and *Zonalis* (5) within subgenus *Perdita* s. s. (Table 3-II). All of the *Perdita* species specialized on Onagraceae are in the single monophyletic subgenus *Xerophasma* (Griswold and Miller 2010).

No *Hesperapis* transported entirely dry pollen: of six species that transported glazed pollen, five specialized on hosts in Asteraceae, and one on an Onagraceae host (Table 3-I). The proportion of dry pollen in glazed loads ranged from 10–25% for Asteraceae specialists and 50% for the lone Onagraceae specialist. As with *Perdita*, moist pollen was added by *Hesperapis* females atop dry pollen only on the anterior face of the hind tibia and did not evenly cap the dry pollen in the scopa.

**Hair types**

Pollen transport mode is associated with particular hair types in both *Perdita* and *Hesperapis* (Table 3-II, Figure 3-3). Ninety-three of 94 *Perdita* species that transport moistened pollen have simple scopal hairs. The exception is one species in the Sphaeralceae Group which transports Fabaceae pollen on minutely branched hairs. Otherwise, the hairs of the moist-transporting *Perdita* species are remarkably uniform, despite transporting pollen of 20 diverse plant families (Table 3-II). Similarly, all 11 species of *Hesperapis* that transport moistened pollen have simple scopal hairs that appear to act as generalized anchors for masses of agglutinated pollen; these species specialize on collecting pollen from nine disparate plant families.

In both *Perdita* and *Hesperapis*, glazed transport of Asteraceae pollen is associated with denser and longer hairs compared to those that transport moistened pollen (Table 3-SII). *Perdita* species that transport glazed Asteraceae pollen are also more likely to have diverse scopal hair types, including simple, branched, wavy, or corkscrew-shaped (Figure 3-3); the most common scopal
Hair type is wavy (24 species, 3 subgenera), followed by branched (10 species, 2 subgenera), corkscrew-shaped (3 species, 2 subgenera), and simple (1 species) (Table 3-II). A 2 X 2 contingency table analysis (Maxwell 1961) of hair type (simple vs. elaborate) by transport mode (moist vs. glazed or dry) for Perdita was highly significant ($X^2 = 109.2$, $df = 1$, $P << 0.0001$): moist and simple hairs are highly associated as are elaborate hairs and glazed or dry transport (Table 3-III). The Hesperapis species that transport glazed Asteraceae pollen have either branched (4 species) or simple (1 species) hairs (Table 3-II).

In both Perdita and Hesperapis, dry or glazed transport of Onagraceae pollen is associated with simple scopal hairs, although they are sometimes longer and denser than the scopal hairs of species that transport moistened pollen (Figure 3-4). Of the four surveyed Perdita species which are Onagraceae specialists, two have scopal hairs whose type, length, and spacing are similar to moist-transporting Perdita species (Figure 3-2A), although the other two species have longer and denser scopal hairs (Figure 3-2B).

**Hair distribution**

The distribution of pollen-transporting hairs on a bee’s hind legs also differs between moist and dry or glazed pollen-collectors, with scopal hairs of species that transport moist pollen tending to cover a smaller surface area than species that transport dry or glazed pollen. For example, the scopal hairs of Perdita that transport moist pollen are located only on the anterior face of the hind tibia and basitarsus (Figure 3-4A). In contrast, all Perdita examined that transport dry or glazed Asteraceae pollen have pollen-transporting hairs that also cover the lateral and posterior face of the hind tibia, the anterior side of the hind femur, and the anterior face of the hind trochanter (Figure 3-4B). The morphology of the scopal hairs on the posterior face of the tibia matches the hairs on the anterior face, but the hairs on the femur and trochanter are always branched,
regardless of the hair type on the tibia. Similar to *Perdita*, all four *Hesperapis* species that transport glazed Asteraceae pollen have scopal hairs on the posterior face of the hind tibia, and three also have branched hairs on the femur and trochanter of the hind legs. However the hairs on the femur and trochanter of those *Hesperapis* are relatively sparse and short compared to *Perdita* and appear to transport only a dusting of pollen, if any. In both *Perdita* and *Hesperapis* species that transport glazed pollen, the expanded scopal hairs on the trochanter, femur, and posterior face of the hind tibia always transport entirely dry pollen; they are never capped with moistened pollen like the scopal hairs on the anterior face of the tibia.

The differences in the distribution of the scopal hairs of bees that collect dry or glazed Onagraceae pollen are relatively minimal compared to those that transport moist pollen. All of the *Perdita* species that transport dry Onagraceae pollen have an expanded distribution of scopal hairs only on the posterior face of the hind tibia. Similarly, the one species of *Hesperapis* that transported moist-capped Onagraceae pollen has simple and sparse scopal hairs on the posterior face of the hind tibia, though they are shorter than the hairs on the anterior face.

**Discussion**

The distantly related bee genera *Perdita* (Andrenidae) and *Hesperapis* (Melittidae) (Cardinal and Danforth 2013; Hedtke et al. 2013) display convergent (Arendt and Reznick 2008) evolutionary patterns of pollen transport. In both genera, most species examined transport completely moistened pollen loads and a minority transport either glazed or dry pollen loads. Those that transport glazed or dry pollen specialize only on floral hosts in the families Asteraceae and Onagraceae, even though *Perdita* and *Hesperapis* contain species that specialize on 21 and 9 plant families, respectively (Table 3-I).
Available evidence suggests that moist pollen transport is ancestral in both genera and that the most probable evolutionary pathway is from moist to glazed or moist to dry. This hypothesis is supported in *Perdita* by the near ubiquity of moist transport in the subfamily Panurginae (Rozen 1967; Michener 2007), of which *Perdita* is a member, and by Danforth’s (1996) morphological phylogeny for *Perdita* which shows that glazed and/or dry pollen transport is limited to two derived clades (Figure 3-5). In addition, subgenera that transport the highest proportion of dry pollen fall in the more derived clades (Danforth 1996). The hypothesis that moist transport is basal in *Hesperapis* is supported by Stage’s (1966) inchoate morphological phylogeny as well as the seven species of *Hesperapis* included in the molecular phylogeny of Michez et al. (2009). Both phylogenies have the glazed and dry-transmitting species limited to derived clades, with glazed transport of Asteraceae and dry transport of Onagraceae likely arising in separate derived clades in *Perdita*. Overall, the patterns in both genera suggest that they are responding to similar selective pressures.

Evidence also suggests that the evolution of glazed or dry transport in these genera was initiated by a host switch to either Asteraceae or Onagraceae pollen. Host switches to Onagraceae by single clades of *Perdita* (*Xerophasma*) and *Hesperapis* (*Panurgomia*) do not entail modifications of scopal hairs. However, for both bee genera, host switches to Asteraceae are associated with modified scopal hairs. In *Perdita*, all but one member of the Asteraceae clade exhibits elaborate scopal hairs (corkscrew-shaped, wavy, or branched) that appear derived (Danforth 1996, Table 3-II, Figure 3-3). In contrast, moist transport of Asteraceae pollen occurs in four large, species-rich clades of *Perdita* (subgenus *Pygoperdita*, and the *Octomaculata, Ventralis*, and *Zonalis* species-groups within subgenus *Perdita s.s.*), all of which contain species that specialize on a wide variety of other plant taxa and have simple scopal hairs. The pattern is repeated in *Hesperapis*,
with both simple and branched scopal hairs found in Asteraceae specialists, suggesting that more elaborate scopal hairs are recent adaptations for transporting glazed Asteraceae pollen.

The association of Asteraceae or Onagraceae pollen with glazed or dry pollen transport and more elaborate scopal hairs may be due to the physical properties of the pollen grains, particularly those which may confer an alternative binding mode. Onagraceae pollen in particular has sticky viscin threads that attach the pollen grains together and to the scopal hairs of bees (Linsley 1958; Roberts and Vallespir 1978; Hesse 1981). A similar binding function may be provided by the copious pollenkitt and echinate projections of Asteraceae pollen. Pollen with copious pollenkitt, such as Asteraceae and Malvaceae, is more adhesive than other pollen types, and readily attaches passively to foragers in large amounts (Allard 1910; Parker 1981; Buchmann and Shipman 1990; Neff and Simpson 1997; Thorp 2000; Goulson et al. 2005). Pollenkitt’s adhesive properties may also be enhanced by pollen sculpturing, because spiny or echinate pollen grains can promote adhesion to other pollen grains or other surfaces by increasing the available surface area with which pollenkitt may interact (Roberts and Vallespir 1978; Lin et al. 2013). Pollen spines may also enhance the electrostatic binding potential of pollen (Chaloner 1986; Hesse 2000). Overall, despite being unrelated and dissimilar in morphology, the viscin threads of Onagraceae pollen and the pollenkitt and spines of Asteraceae pollen both provide an alternative to using nectar to bind the pollen grains together and to the scopae.

Although pollen types with spines and copious pollenkitt are effective at attaching to pollinators and to each other, they apparently resist being packed together with nectar by bees. Spines seem to both increase the amount of nectar required to pack individual grains together and decrease the size and stability of the final pollen mass (Vaissière and Vinson 1994). In most instances, moist-transporting bees have difficulty packing, or even reject, pollen types with large spines and
copious pollenkitt (Linsley 1960; Stephen et al. 1969; Raine and Chittka 2007; Lunau et al. 2015). In some cases, removing the pollenkitt or bending the spines increases the ability of bees to pack moistened pollen (Lunau et al. 2015). The hypothesis that pollen is kept partially dry primarily for transport purposes is supported by the fact that glazed-transporting Perdita whose nesting biology has been studied (P. albipennis, P. boharti, P. coreopsidis, P. graenicheri) still shape the pollen provisions into uniformly moistened spheres but do so in the nest (Danforth 1989; Norden et al. 1992; F.D. Parker unpubl. data).

The association of Asteraceae pollen with dry or glazed pollen transport on elaborate scopal hairs is also found in other bee groups. The subfamily Panurginae, which includes Perdita, contains multiple genera with some species that transport dry or glazed asteraceous pollen (Rozen 1989; Michener 2007). Examples include the genus Panurgus, whose members transport dry Asteraceae pollen on wavy scopal hairs (Münster-Swendsen 1970; Rozen 1971), as well as some species of Protandrena and Pseudopanurgus, which transport dry or glazed Asteraceae pollen on branched scopal hairs (Rozen 1967; Danforth 1996). Many apid bees that transport dry pollen on elaborate scopal hairs are strongly associated with Asteraceae pollen collection (e.g. Melissodes, Svastra), especially compared to related groups that transport moistened pollen such as Eucera and Centris (Moldenke and Neff 1974; Eucera: Timberlake 1969; Centris: Aguiar et al. 2003; Roubik and Villanueva-Gutiérrez 2009). Specialization on Onagraceae pollen is also commonly associated with bee genera that transport dry pollen such as Andrena, Melissodes, Sphecodogastra, Megachile, and Diadasia (Thorp 1979).

Historically, internal or dry pollen transport have been thought to be the ancestral state in bees (Michener 1944; Jander 1976; Roberts and Vallespir 1978; Radchenko and Pesenko 1996; Michener 2007). However, our results best fit a hypothesis of Perdita and Hesperapis switching
from moist to dry or glazed pollen transport due to the adhesive properties of pollen grains. This hypothesis is strengthened by the absence of apparent switches from dry to glazed or dry to moist and suggests a reconsideration of the evolutionary pathway of pollen transport in bees. For example, Melittidae, which is hypothesized to be the most basal bee family (Cardinal and Danforth 2013), contains multiple moist-transporting genera in addition to Hesperapis, including Macropis, Melitta, and Rediviva (Malyshev 1936; Cane et al. 1983; Whitehead et al. 1984; Michener 2007; Nilsson and Alves-dos-Santos 2009). The major exception, the genus Dasypoda, transports dry pollen on plumose scopal hairs and contains many Asteraceae specialists (Celary 2002; Michener 2007; Michez et al. 2008). The results of our initial investigations suggest that the question of the ancestral state of pollen transport and its evolutionary trajectory be reopened; only additional systematic and behavioral studies will settle this issue.

Acknowledgements

We thank Joe Wilson for informative discussion, Terry Griswold, James Pitts, and various anonymous reviewers for helpful comments on the manuscript, Brian Rozick and Harold Ikerd for curatorial help, Doug Yanega, Jaime Pawelek, and Glenn Hall for providing specimens, and the USDA ARS Pollinating Insect Research Unit for general support and access to the insect collection and facilities. This work is supported by a National Science Foundation Graduate Research Fellowship under grant number DGE-1147384, a Utah State University Graduate Enhancement Award, and a Utah State University Ecology Center Research Award. We acknowledge the support from the Microscopy Core Facility at Utah State University for the SEM work.

References


**Tables**

Table 3-I. The number of *Perdita* and *Hesperapis* species examined, categorized by host plant family and mode of pollen transport. Abbreviations: M = moist, G = glazed, D = dry, DI = dry initially.
<table>
<thead>
<tr>
<th>Host plant family</th>
<th>Transport mode</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>G</td>
<td>D</td>
<td>DI</td>
<td>SUM</td>
<td>M</td>
<td>G</td>
<td>D</td>
</tr>
<tr>
<td>Amaranthaceae</td>
<td>Perdita</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aquifoliaceae</td>
<td>Perdita</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asparagaceae</td>
<td>Perdita</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asteraceae</td>
<td>Perdita</td>
<td>18</td>
<td>24</td>
<td>14</td>
<td>56</td>
<td></td>
<td>1</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Boraginaceae</td>
<td>Perdita</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brassicaceae</td>
<td>Perdita</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cleomaceae</td>
<td>Perdita</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>Perdita</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabaceae</td>
<td>Perdita</td>
<td>11</td>
<td>11</td>
<td>1</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabaceae and/or</td>
<td>Perdita</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zygophyllaceae</td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydrophyllaceae</td>
<td>Perdita</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lamiaceae</td>
<td>Perdita</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Liliaceae</td>
<td>Perdita</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Loasaceae</td>
<td>Perdita</td>
<td>4</td>
<td>4</td>
<td>2</td>
<td></td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Malvaceae</td>
<td>Perdita</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onagraceae</td>
<td>Perdita</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Papaveraceae</td>
<td>Perdita</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polemoniaceae</td>
<td>Perdita</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td></td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polygonaceae</td>
<td>Perdita</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rosaceae</td>
<td>Perdita</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salicaceae</td>
<td>Perdita</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solanaceae</td>
<td>Perdita</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unknown</td>
<td>Perdita</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zygophyllaceae</td>
<td>Perdita</td>
<td>5</td>
<td>5</td>
<td>1</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hesperapis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>94</td>
<td>24</td>
<td>3</td>
<td>15</td>
<td>136</td>
<td>11</td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>
Table 3-II. Subgeneric and major species group breakdown of pollen transport mode in *Perdita* and *Hesperapis*. # of species shows the number surveyed with the total species in that group in parentheses. Additional details about specific species can be found in Table S1. Abbreviations:


<table>
<thead>
<tr>
<th>Genus</th>
<th>Subgenus</th>
<th># Species</th>
<th>Transport Mode</th>
<th>% Dry</th>
<th>Hair Type</th>
<th>Floral Hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Perdita</em></td>
<td><em>Alloperdita</em></td>
<td>4 (6)</td>
<td>M</td>
<td>0%</td>
<td>S</td>
<td>AQU, ROS</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Allomacrotera</em></td>
<td>2 (2)</td>
<td>G</td>
<td>75%</td>
<td>C</td>
<td>AST</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Callomacrotera</em></td>
<td>2 (2)</td>
<td>G</td>
<td>50%</td>
<td>B</td>
<td>AST</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Cockerellia</em></td>
<td>15 (25)</td>
<td>G</td>
<td>75%–80%</td>
<td>W</td>
<td>AST</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Epimacrotera</em></td>
<td>8 (23)</td>
<td>M</td>
<td>0%</td>
<td>S</td>
<td>BOR, EUP, FAB, LAM, POLE</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Glossoperdita</em></td>
<td>1 (4)</td>
<td>M</td>
<td>0%</td>
<td>S</td>
<td>POLE</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Hesperoperdita</em></td>
<td>2 (2)</td>
<td>M</td>
<td>0%</td>
<td>S</td>
<td>FAB</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Heteroperdita</em></td>
<td>5 (14)</td>
<td>M</td>
<td>0%</td>
<td>S</td>
<td>BOR</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Hexaperdita</em></td>
<td>9 (28)</td>
<td>G</td>
<td>25%–33%</td>
<td>B(8), S(1)</td>
<td>AST</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Pentaperdita</em></td>
<td>8 (16)</td>
<td>G</td>
<td>33%–67%</td>
<td>W</td>
<td>AST</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Perdita, Halictoides Grp</em></td>
<td>6 (11)</td>
<td>M</td>
<td>0%</td>
<td>S</td>
<td>SOL</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Perdita, Octomaculata Grp</em></td>
<td>18 (130)</td>
<td>M</td>
<td>0%</td>
<td>S</td>
<td>AST, EUP, FAB, LAM, MAL, SAL</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td><em>Perdita, Sphaeralceae Grp</em></td>
<td>19 (199)</td>
<td>M</td>
<td>0%</td>
<td>S(18), B(1)</td>
<td>BOR, BRA, CLE, FAB, LOA, MAL,</td>
</tr>
</tbody>
</table>
Table 3-III. The number of *Perdita* species falling into four categories of pollen transport mode and hair characters. Complex refers to hairs that are wavy, corkscrew, or branched. Results of contingency table analysis $X^2 = 107.5$, df = 1, $P < 0.0001$.

<table>
<thead>
<tr>
<th>Species</th>
<th>Transport Mode</th>
<th>Hair Characters</th>
<th>Simple</th>
<th>Complex</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Perdita</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td>Moist</td>
<td></td>
<td>93</td>
<td>1</td>
<td>94</td>
</tr>
<tr>
<td><em>Perdita</em></td>
<td>Glazed or Dry</td>
<td></td>
<td>5</td>
<td>37</td>
<td>42</td>
</tr>
<tr>
<td><strong>Perditella</strong></td>
<td>Moist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Procokerellia</strong></td>
<td>Moist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pseudomacrotera</strong></td>
<td>Glazed or Dry</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pygoperdita</strong></td>
<td>Moist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Xeromacrotera</strong></td>
<td>Moist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Perdita</strong></td>
<td>Glazed or Dry</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Carinapis</strong></td>
<td>Moist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Disparapis</strong></td>
<td>Moist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Hesperapis</strong></td>
<td>Moist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Panurgomia</strong></td>
<td>Glazed or Dry</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Xeralictoides</strong></td>
<td>Glazed or Dry</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Zacesta</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

POLE, SAL, ZYG
ASP, AST, LOA, POLY, ROS, ZYG
AST
AMA, EUP, ZYG
AST
FAB/ZYG
AST, LIL, PAP, ROS
AST
ONA
FAB, POLE, ROS, ZYG
AST, MAL
AST
HYD, POLE
ONA
LOA
POLE
Figures

Figure 3-1. Lateral views of moist and glazed transport. **a** Moist transport of Loasaceae pollen by *Perdita perplexa* Timberlake on simple hairs. **b** Moist transport of Asteraceae pollen by *P. n. sp. 2 aff. laticincta* on simple hairs. **c** Glazed (25% dry) transport of Asteraceae pollen by *Hesperapis hurdi* Timberlake on branched hairs. **d** Glazed (80% dry) transport of Asteraceae pollen by *P. albonotata* Timberlake on corkscrew-shaped hairs.
Figure 3-2. Dry transport of Onagraceae pollen. a Sparse, simple scopal hairs of *P. pallida* Timberlake. b Denser and longer scopal hairs of *Perdita vespertina* Griswold & Miller. c Dry transport Onagraceae pollen on *P. pallida*. d Closeup of c showing viscin threads binding pollen together.
Figure 3-3. Optical and SEM examples of the different hair types. a and b Simple hairs on moist-transporting *Perdita koebelei* Timberlake. c and d Branched hairs on *P. asteris* Cockerell. e and f Wavy hairs on *P. lingualis* Cockerell and *P. albovittata* Cockerell, respectively. g and h Corkscrew-shaped hairs on *P. moabensis* Timberlake. All SEM scale bars = 50 micrometers.
Figure 3-4. Dry pollen covers an expanded area compared to moist pollen. a Moisten Malvaceae pollen limited to the tibia and basitarsus of *Perdita xanthochroa* Timberlake. b An incomplete load of dry Asteraceae pollen transported on the femur and trochanter in addition to the tibia and basitarsus of *P. albipennis* Cresson.
Figure 3-5. Morphological phylogeny of *Perdita* subgenera adapted from Danforth (1996).

Clades that transport dry or glazed pollen are highlighted with red.
A REVIEW AND UPDATED LEXICON OF POLLEN GATHERING
BEHAVIOR IN BEES (HYMENOPTERA: APOIDEA)

Abstract

Pollen is the primary protein and nutrient source for bees and they employ many different behaviors to gather it. A large number of terms have arisen to describe pollen gathering behaviors, creating confusion as new terms overlap with, or are not clearly differentiated from, existing terms. There is a need for a clear yet flexible lexicon that allows for accurate, succinct descriptions of pollen gathering behaviors in order to enable meaningful discussion and comparison. Here, we classify the different pollen gathering behaviors into two main classes: active and incidental pollen collection. Active pollen collection is subdivided into six behaviors: scraping with the extremities, buzzing, rubbing with the body and/or scopae, rubbing with the face, tapping, and rasping. In addition to the active and incidental pollen gathering behaviors, many bees have an intermediate step in which they temporarily accumulate pollen on a discrete patch of specialized hairs. Each behavior is described and illustrated with video examples. Many of these behaviors can be further broken down based on the variations found in different bee species. Different species or individual bees mix and match these pollen collecting behaviors depending on their behavioral plasticity and the morphology of the host plant. Taken together, the different behaviors are combined to create complex behavioral repertoires built on a foundation of simple and basic steps. This classification sets the groundwork for further research on various

---

5 This chapter is written in the style of the journal Functional Ecology.
topics, including the breadth of behaviors in different species, comparisons between generalists and specialists, and the relative effectiveness of different pollen gathering behaviors.

**Keywords**

Pollinators, pollen collection, foraging, behavior, floral hosts, Anthophila

**Introduction**

Bees visit flowers primarily for nectar and pollen, which they use to provision their young and meet their own energetic and nutritional requirements (Michener 2007, Cane et al. 2016). Pollen is the primary resource in the larval provisions of most species, and bees have evolved behaviors to efficiently collect large amounts of pollen (Thorp 2000). Unsurprisingly, not all bees gather pollen identically, and many different pollen gathering behaviors exist. For example, even on the same floral host, different bee species often use different pollen gathering behaviors (Thorp 1979). In addition, flexibility exists at the individual level, with individual bees using different pollen gathering behaviors depending on the floral host and the availability of pollen (Heinrich 1976b, Prosi et al. 2016, Russell et al. 2017). The type of behavior that bees use can influence their floral preferences and may impact their effectiveness as pollinators. Due to the importance of pollen gathering behavior and the growing interest in bee biology and pollination ecology, the number of research papers that describe or mention pollen gathering behavior have rapidly proliferated. As a result, it is necessary to produce a standardized terminology which both accurately describes the different behaviors and facilitates their effective communication.

Pollen-gathering behavior in bees is divided up into two main types: active and incidental (or passive) collection (Parker 1926, Doull 1970, Inouye et al. 1994, Westerkamp 1996, Thorp 2000). Active pollen collection refers to the purposeful uptake of pollen, generally through the use of the
forelegs and mandibles, directly from anthers or other floral surfaces. Incidental (or passive) pollen collection refers to pollen that accumulates on bees as they forage for nectar — this pollen may either be packed into the pollen transporting structures or groomed and discarded (Doull 1970). However, such broad categories oversimplify the diversity of pollen gathering behaviors exhibited by bees. Previous researchers have broken down active pollen gathering into numerous variants, but these attempts often lack a broader framework and conflate, or overlap with, existing definitions. For example, a single species — *Osmia montana* — has had its pollen gathering behavior variously coined as “thumping,” “tapping,” “patting,” and “drumming” (Rust 1974, Cripps and Rust 1989, Cane 2011, Cane 2016). Conversely, the same term can have multiple meanings, such as “scrabbling,” which has been variously used to describe bees that scrape with the forelegs or run over a plane of flowers (Percival 1955, Thorp 2000). These numerous, overlapping, and poorly-defined terms illustrate the need for more precise and consistent terminology to describe pollen gathering behavior.

While pollen gathering behavior has previously been reviewed by others, these have tended to focus such disparate fields as the phenological, chemical, and morphological adaptations of bees to flowers (Müller 1996b, Thorp 1979, 2000). In addition, the recent proliferation of high-speed, high-definition video technology enables the efficient study and communication of previously inaccessible or complex. Here, we propose a comprehensive terminology to categorize and describe the full range of pollen-gathering behaviors. Our approach builds on the existing schema of active vs. incidental pollen gathering. Active pollen gathering is broken down into six types, which can be further subdivided based on the nuances of particular bee groups and the morphology of floral hosts. Our updated lexicon systematizes pollen gathering behavior and facilitates the description and communication of behavioral observations. In addition, it will allow
researchers to better address questions on the breadth, limitations, evolution, and convergence of pollen gathering behaviors.

**Methods**

Pollen gathering videos were recorded by ZMP and MCO as well as gathered from other researchers or sources (e.g. youtube.com) and used with permission. To record behavior, we used a Sony A65 with a 90mm macro lens and a Pentax Optio WG-2. Morphological terminology generally follows Michener (2007); for simplicity, abdomen is used to refer to the metasoma and thorax is used to refer to the mesosoma. Bees were identified using either collected specimens or still images from videos.

Every pollen gathering behavior has been referred to by multiple different terms. Three main considerations were taken into account in selecting the most appropriate terminology for the different pollen gathering behaviors: priority, usage, and accuracy. Priority refers to the first known instance of use, usage refers to the prevalence of a term in the scientific and popular literature, and accuracy refers to how well a term describes a given behavior. In general, terms with priority were used, though exceptions were made for usage and accuracy, particularly when terms had conflicting or multiple meanings, or when use is widely accepted.

**Results and Discussion**

**The different types of pollen gathering behavior**

We define pollen gathering behaviors as the movements bees use to acquire pollen from anthers or other pollen presenting structures. Pollen gathering is related to, but separate from, pollen transport, which refers to the carrying of accumulated pollen back to the nest in specialized transport structures (Roberts and Vallespir 1978, Portman and Tepedino 2017. The different pollen gathering behaviors (listed below) may be used individually or in combination,
concurrently or sequentially, creating composites from a set of simple, well-defined building blocks. Taken together, our definitions offer a useful guide to the full set of major behaviors used by bees when gathering pollen.

In foraging from flowers bees have three possible primary purposes on each trip: nectar (or oil), pollen, or both. We term pollen gathering **active** when pollen is the primary objective or when nectar (or oil) and pollen are co-objectives. Active pollen gathering is broken down into the set of six pollen gathering behaviors described below. We term pollen gathering **incidental** when nectar is the primary objective and pollen is passively accumulated on the body. The bee then “decides,” based on pollen and floral characteristics, and on need, to discard or keep the pollen. Bees may also incidentally collect pollen on non-target areas of the body while actively gathering pollen. Such pollen may or may not be gathered into the pollen transporting structures.

**Active** pollen gathering behaviors can be broken up into six types, listed loosely in order of prevalence:

- **Scraping with the extremities**: use of the legs or mouthparts to remove pollen directly from anthers, or, less commonly, to glean pollen from flowers.
- **Buzz pollination, or buzzing**: vibrating a flower to release pollen onto the body.
- **Rubbing with the body and/or scopae**: the gathering of pollen through direct and more or less continuous contact with the anthers by the main trunk of the body (thorax, abdomen) and/or the scopal hairs.
- **Rubbing with the face**: continuous and more or less direct contact with the anthers by the face.
- **Tapping**: picking up pollen from anthers by a rapid up and down motion of the abdominal venter.
- **Rasping:** rubbing of the dorsum of the thorax against anthers, causing the anthers to vibrate and release the pollen

**Incidental** pollen gathering (not broken down into types): the use of pollen that has accumulated on the body through nectar gathering or on non-target areas as a result of a primary pollen gathering behavior. A major component of incidental behavior is the degree of movement by the bee, which increases the amount of pollen that adheres to the bee through contact.

- **Scraping with the extremities**

Scraping with the extremities refers to the use of the legs and/or mouthparts (including the mandibles) to gather pollen with a repetitive unidirectional motion (Figure 4-1). The term “scraping” is generally accepted by most authors, though other terms, such as “brushing,” “raking,” “scrabbling,” “stroking,” “wiping,” etc. have also been used (Casteel 1912, Jander 1976, Michener et al. 1978, Thorp 1979, Thorp 2000). Scraping pollen directly from the anthers or other pollen-presenting structures with the basitarsal brushes of the forelegs is the most common pollen gathering method used by bees (Grinfel’d 1962, Michener et al. 1978, Westerkamp 1996, Michener 2007).

Typically the forelegs and mandibles are used in unison to scrape pollen, though the midlegs may also assist the forelegs. The forelegs may also be used to glean pollen from other surfaces, such as flower petals, or even the scopae of other bees (termed “cleptolecty;” Thorp and Briggs 1980, Snelling and Stage 1995). One elaboration is seen in bees which “strike” poricidal anthers with the forelegs to loosen pollen. Striking has been observed in *Bombus* and *Ptiloglossa* on *Solanum* (Linsley 1962), *Osmia ribifloris* on blueberry (Torchio 1990), and *Apis mellifera* on cranberry (“drumming;” Cane et al. 1993). In *Bombus* and *Ptiloglossa*, striking is accompanied by buzzing.

The mouthparts, especially the mandibles, are also frequently used to gather or loosen pollen. The mandibles are used to bite anthers to loosen the pollen in association with scraping with the
forelegs (Sladen 1912, Thorp 1979). Some bees, including *Apis*, *Colletes* (Buchmann et al. 1977), *Bombus* (Todd 1882, Robertson 1890, Bowers 1975) and various halictines (Thorp and Estes 1975), use the mandibles in a “milking” motion to gather pollen from poricidal flowers, such as *Cassia* and *Solanum* (however, the observations of *Bombus* from the late 1800’s may just be misinterpretations of buzzing behavior). This behavior is often combined with buzzing to release the pollen (Thorp and Estes 1975). The mandibles can also be used to chew open poricidal anthers in order to render the pollen more accessible, a behavior observed repeatedly in *Trigona* (Wille 1963, Inouye 1980, Renner 1983).

The midlegs are generally used to assist the forelegs in scraping pollen (Westerkamp 1996). However, some megachilid bees have specialized hair brushes on the femur of the middle and/or hind legs that appear to be used to scrape pollen from Asteraceae flowers (Müller and Bansac 2004). Although the exact pollen gathering movements remain unclear, the mid or hind legs appear to bend at the femoral-tibial joint to scrape pollen from individual anthers, mirroring the movements used to scrape pollen off the foreleg by the midleg.

Scraping movements are also made with the hind legs, particularly with keel-shaped flowers. In these cases, the hind legs appear to be used because the front and middle legs are occupied in obtaining a purchase and spreading open the wing petals to expose the anthers. Various *Andrena*, *Anthophora*, *Apis*, *Bombus*, and megachilids use these behaviors on keel-shaped flowers such as *Collinsia* (Plantaginaceae) and *Lupinus* (Fabaceae) (Rust and Clement 1977, Wainwright 1978). One particularly interesting example is *Samba turkana* (Melittidae), which uses an enlarged and curved hind tibial spur to scrape pollen from anthers of *Crotalaria* (Fabaceae) (Packer and Martins 2015).

In bees that gather pollen primarily by rubbing with the abdomen (discussed in a later section), the hind legs are often used in an accessory fashion to gather a clump of anthers and draw them to
the body, as well as to help scrape pollen from the gathered anthers. This gathering and scraping behaviors is seen in Megachilidae such as *Osmia cornuta* (Monzón et al. 2004) and *O. lignaria* (Rust and Clement 1977). It should be noted that scraping with the hind legs is distinct from rubbing with the scopae, which are often located on the hind legs. Scraping with the hind legs entails removal of pollen from anthers with a repeated, one-directional movement, and then the pollen is quickly removed from the hair brushes. In contrast, rubbing with hindleg scopae involves rubbing the scopal hairs back and forth on the anthers, and the continuous contact with the pollen works the pollen directly into the scopal hairs.

Bees that scrape with the extremities often possess morphological features that improve their efficiency. There are many examples of hooked hairs on the forelegs and foretarsi which are typically associated with specialization on flowers with narrow corollas and allow the bees to efficiently extract pollen (Thorp 1979), although exceptions to the narrow-corolla association exist (Neff 2004). Examples have been well-reviewed by Thorp (1979, 2000); more recent examples include two species of European *Colletes* on hosts in Boraginaceae (Müller and Kuhlmann 2003), multiple species of North American *Colletes* on various hosts (Neff 2004), and a species of European *Hoplitis* specialized on Boraginaceae (Sedivy et al. 2013).

Similar to the forelegs, the mouthparts (primarily the stipes, galea, labial and maxillary palpi) can be modified, often with hooked hairs, to extract pollen from flowers with narrow corollas. The presence and use of modified hairs on the mouthparts has been well-reviewed by Thorp (1979, 2000). Some more recent examples include various visitors of Pontederiaceae (Alves-dos-Santos 2003), *Ceblurgus longipalpis* (Halictidae) on *Cordia* (Boraginaceae) (Milet-Pinheiro and Schlindwein 2010), various Anthophora (Micranthophora) on various hosts (Orr and Griswold In Press), and multiple megachilid species, including *Haetosmia vechti* on *Heliotropium* (Gotlieb et al. 2014) and multiple *Hoplitis* on various hosts (Müller 2006, Sedivy et al. 2013). In addition to
modified hairs, other bees show additional structural modifications that presumably assist in pollen removal such as enlarged or elongated labial palpi. Examples include *Perdita heliotropii*, a specialist on *Heliotropium* (Boraginaceae) (Timberlake 1958) and *Hesperapis “palpalis”* (Stage manuscript name), a specialist on Polemoniaceae (Stage 1966).

- **Buzz Pollination or “Buzzing”**

Buzz pollination is the use of the thoracic flight muscles to generate audible vibrations that aide in accessing and collecting pollen from a flower (Figure 4-2, Buchmann 1983, Thorp 2000). Buzzing induces the release of pollen from the anthers, which the bee usually receives on the venter. The adhesion of pollen to bees is aided by the electrostatic attraction of the pollen to the bee’s body and hairs (Buchmann and Hurley 1978, Corbet et al. 1982, Buchmann 1983, Vaknin et al. 2000). The legs are subsequently used to groom pollen from the body into the pollen transporting structures. A variant of buzz pollination, “buzz milking” (Cane and Buchmann 1989); is performed by *Protandrena mexicanorum* (Andrenidae), which buzzes anthers of *Solanum* while gradually sliding up the upward-facing anthers before curling over the tips of the anthers to receive pollen.

Although it is clear what “buzz pollination” refers to, many different terms have been used to describe it (Table 1). Observations of buzz pollination have been made for over 70 years (e.g. Meidell 1944, Rick 1950), but it remained poorly-defined until Michener (1962) and Wille (1963) described the behavior in-depth and referred to it as “buzzing.” Buchmann (1974, 1983) later codified the term “buzz pollination,” though he and others have often used alternative terminologies, often within a single paper (Table 1). Starting in the mid 1980’s, the term “floral sonication” has also been used to refer to this behavior (Cane 1985, Cane et al. 1985), though this term is a misnomer since mechanical vibrations, rather than sound waves, cause the pollen to be expelled. Due to their priority (Michener 1962, Wille 1963, Buchmann 1983) and widespread
usage, we recommend using the term “buzz pollination” to refer broadly to the behavior, and variants of “buzz” (e.g. “buzzed,” “buzzing,” “buzzes”) to refer to the specific act of buzzing flowers. However, it is important to note that “buzz pollination” is also a misnomer because it does not necessarily effect pollination as the name implies.

Members of all bee families have been documented using buzz pollination, though it is uncommon or rare in Andrenidae, Melittidae, and Megachilidae (Meidell 1944, Buchmann and Hurley 1978, Buchmann 1983, Houston and Thorp 1984, Cane et al. 1985, Neff and Simpson 1988, Thorp 2000). Interestingly, some of the most generalized bees, such as the honey bee and *Trigona* spp. (*sensu lato*), do not buzz pollinate (Buchmann 1983, King and Buchmann 2003, Michener 2007). Although a wide variety of plants are buzz pollinated (>72 families, reviewed in Buchmann 1983), this behavior was traditionally considered exclusive to plants with poricidal, or hidden, anthers (Michener 1962). Buzzing propels pollen from within these complex flowers, allowing bees to access otherwise unavailable resources. However, there are many exceptions to this, and bees buzz a variety of flowers in the families Asteraceae, Cucurbitaceae, Fabaceae, Papaveraceae, Rosaceae, Scrophulariaceae, and others (Heinrich 1976a, Buchmann 1985, Bernhardt 1989, Avery et al. 2017).

- **Rubbing with the body and/or scopae**

Rubbing refers to the use of direct, more or less continuous contact between the anthers and the scopae and/or venter of the main body segments (thorax or abdomen). The defining character of rubbing is the curling of the abdomen, which generally moves in an up and down motion, or less often, a back-and-forth or telescoping motion (Figure 4-3). There are two types of bees that use this behavior: those that transport pollen in scopae on the ventral abdomen, and those that transport pollen on hind leg scopae. Bees that transport pollen in ventral scopae gather pollen directly into the scopal hairs, whereas bees that transport pollen with hind leg scopae must transfer pollen from the
venter into the scopa. Despite this difference, the general pollen gathering movements are largely the same, and further, many bees have diffuse scopa that cover both the ventral abdomen and hind legs (e.g. *Ptilothrix*). Rubbing behavior has been observed in a wide variety of species in every bee family (except Stenotritidae) on numerous floral hosts (Table 2), and is likely more common than the relatively few observations suggest. Gathering pollen directly with the abdomen, in particular, has been known since at least the late 1800's (Müller 1883, Robertson 1889, Robertson 1899).

Rubbing behavior has been referred to by a wide variety of inconsistent descriptions and terms. Rubbing has often been referred to as, or lumped together with “tapping,” which we consider a separate behavior. In addition, observations of the same bee species rubbing on the same plant species often result in quite different descriptions: *Hoplitis anthocopoides* on *Echium vulgare* (Boraginaceae) has been reported as “she vibrates [the abdomen] back and forth rapidly against the anthers while her hind legs also move back and forth against the anthers and scopa” (Eickwort 1973) and alternatively described as “rapidly contracts and expands her abdomen, accordion fashion, over the anthers” (Strickler 1979). Similarly, *Dieunomia triangulifera*, while foraging on *Helianthus annuus* (Asteraceae) has been reported as “waggling the abdomen vigorously from side to side” (Cross and Bohart 1960), as well as “tapping the heads of the disc flowers with the ventral surface of the [abdomen]” (Minckley et al. 1994). We use the term “rubbing” to refer to these behaviors because the term is succinct, accurate, and paraphrases the earliest descriptions, which typically overlap with other more well-known behaviors (e.g. “scraping,” “vibrating,” and “wagging”).

Most bees that gather pollen via rubbing take up the pollen directly with the abdominal scopa (e.g. Megachilidae) or by a combination of the hind leg scopae and abdomen (e.g. *Ptilothrix* and *Andrena* sp.). Rubbing is used by a wide variety of bees that perform additional variants at
different speeds. For example, *Melissodes* spp. and *Andrena helianthi* both collect pollen from *Helianthus* by repeatedly rubbing the curled-over apex of their abdomen against the anthers with the hind leg scopae periodically scraping the abdomen to transfer the gathered pollen. The basic movements of the legs and abdomen of the different species are more or less the same even though the speeds of the abdominal movements can appear quite different. Further examples of the variation in rubbing behavior are seen in *Ptilothrix bombiformis* gathering pollen from *Hibiscus* as well as *Andrena* sp. gathering pollen from *Camissonia*, both of which curl the abdomen over a clump of anthers that have been grabbed by the legs. In addition, the venter of the thorax can be used for rubbing in tandem with the abdomen or scopae. Examples include bees in the genus *Macropis*, which use rubbing to accumulate pollen on corkscrew-shaped hairs on the venter of the thorax and abdomen (Cane et al. 1983, Vogel 1992). Despite the different variations in movement and speed, all of the aforementioned rubbing variants appear derived from the universal abdominal grooming and pollen-packing movements which involve tamping the legs against the sides and base of the abdomen (Michener et al. 1978), and any attempt to draw a clear dividing line between these variations will likely become increasingly futile as more observations are made.

Finally, various mentions in the literature suggest that rubbing behavior has been observed in additional species but precise descriptions are lacking. This includes suggestions of rubbing by *Osmia lignaria, O. indeprensa, and O. kincaidii* (“the anthers are drawn to the scopal hairs by the hind legs,” Cripps and Rust 1989), as well as *Osmia rufa* on *Ranunculus*, and *O. leaiana* and *O. coerulescens* on Asteraceae, which were observed “walking over the anthers so that the ventral scopae touched them while they probed the nectaries” (Raw 1974). In addition, various Megachilidae have been reported to gather pollen by “seesawing” the scopae directly against anthers: *Hoplitis robusta* on *Potentilla* (Rosaceae), *H. zanderi* on various hosts, *Pseudoanthidium*
eximium on Asteraceae, and Protosmia minutula on Lamiaceae (Müller 1996a, 1996b, Müller and Mauss 2016). Lastly, various bees visiting Clarkia (Onagraceae) perform a “pollen dance” on the flowers and potentially rub to pick up pollen, though only one species — Megachile gravita, which “settle on the stamens and rapidly vibrate the abdomen laterally” — is described in enough detail to confidently identify it as rubbing (MacSwain et al. 1973).

- **Tapping**

Tapping refers to the act of picking up pollen through a rapid up and down motion of the metasomal venter directly against the anthers (Figure 4-4). It is characterized by the horizontal orientation of the rigid abdomen and the rapidity of movement. The term “tapping” comes from what appears to be the original use by Pasteels and Pasteels (1974): “l’abdomen qui tapote de haut en bas sur étamines” (“the abdomen tapped up and down on the stamens”). In the same year, Rust (1974) used “thumping” to describe the behavior. However, Rust subsequently switched to the term “tapping” (Cripps and Rust 1989) to describe the behavior in the same species (Table 3).

Historically, “rubbing” and “tapping” with the abdomen have often been lumped together (e.g. Müller 1883, Simpson and Neff 1987, Westerkamp 1996, Thorp 2000). However, there are distinct differences between tapping and rubbing with the scopae and/or abdomen: in tapping, the rate of movement is faster (Cane 2016), the abdomen is kept more rigid, and the orientation of the abdomen is parallel to the plane of anthers (compared to curled over in typical rubbing). Further, rubbing entails nearly continuous contact, while tapping is specifically defined by intermittent contact. In rubbing behavior especially, the legs are often used to grab a clump of anthers and rake them against the scopal hairs. Despite these differences, additional exploration of this behavior may reveal that rubbing and tapping fully intergrade. Currently, tapping has been observed solely in bees of the family Megachilidae (Ashmeadiella, Heriades, Lithurgus, Pseudoanthidium, Osmia, Megachile, and Trachusa) on asteraceous hosts (Table 3).
• Rubbing with the face

The face (anterior head) is used to gather pollen through direct, continuous rubbing contact with the anthers (Figure 4-5). Facial collection (reviewed in Müller 1996a, Thorp 2000) is found in numerous unrelated species in the families Apidae, Andrenidae, Halictidae, Megachilidae, and the wasp subfamily Masarinae (Vespidae). In most cases, the hairs on the clypeus and/or frons are thickened, hooked, or corkscrew-shaped, but they can also be unmodified (Müller 1996a, Prosi et al. 2016). Rubbing with the face is associated with the collection of pollen from nototribic flowers, which have the stamens and styles facing downwards from the dorsum of the corolla, thereby promoting contact with the dorsum of floral visitors (Müller 1996a, Thorp 2000).

More recent examples of bees with modified facial pilosity that gather pollen from nototribic flowers include *Osmia brevis*, *O. cyaneonitens*, and *O. ednae* (Megachilidae) on *Penstemon penlandii* (Scrophulariaceae) (Tepedino et al. 1999), *Anthophora walteri* (Apidae) on *Salvia* (Lamiaceae) (Gonzalez et al. 2006), *Osmia calaminthae* on *Calamintha* (Lamiaceae) (Rightmyer et al. 2011), *Chalicodoma riyadhense* (Megachilidae) which has been seen visiting *Blepharis* (Acanthaceae) (Alqarni et al. 2012), and *O. pilicornis* on *Ajuga* and *Glechoma* (both Lamiaceae) (Prosi et al. 2016). Both *O. calaminthae* and *O. pilicornis* — two species for which detailed observations of pollen gathering are available — rapidly move their heads and bodies up and down against the anthers to remove pollen (Rightmyer et al. 2011, Prosi et al. 2016).

Interestingly, *O. pilicornis* also has hooked hairs on the mouthparts, which it uses to scrape pollen from flowers of *Pulmonaria* (Boraginaceae). In some cases, such as in *Rophites algirus* (Halictidae), rubbing with the face is combined with buzzing (Müller 1996a).

• Rasping

Rasping is defined as rubbing with the thoracic dorsum in order to mechanically vibrate anthers in order to release pollen. Rasping is a specialized behavior that has only been observed in bees
foraging on *Penstemon* flowers that have partially concealed anthers with dentate tips (Table 4). Various Hymenoptera — including the pollen wasp *Pseudomasaris vespoides* (Vespidae), *Osmia brevis* (Megachilidae), *O. penstemonis*, and potentially other *Osmia* species — have been observed rubbing their thoracic dorsum against the dentate anthers to release the pollen (Torchio 1974, Wilson et al. 2006, Cane 2014 – Apidologie, Cane 2016). Rasping is associated with a roughened or punctate integument on the scutum of *P. vespoides*, which assists in vibrating the anthers (Torchio 1974, Cane 2014). Cane (2014) coined the term “rasping” due to the noise produced by the behavior. This noise was also observed by Torchio (1974), who reported the noise produced as a “clicking” sound. Interestingly, *O. brevis* also collects pollen from *Penstemon* by buzzing (Cane 2014) as well as by rubbing with the face (Tepedino et al. 1999).

The different pollen gathering behaviors of *Osmia* on *Penstemon* may be related to the size of the *Penstemon* flowers, with rasping performed in larger flowers and other strategies used in smaller-flowered species. So far, rasping has only been observed on *Penstemon* flowers; it remains to be seen whether this pollen gathering is found in additional taxa or is performed on other nototribic flowers.

- **Incidental**

When pollen accumulates on bee bodies as a by-product of another behavior without any obvious deliberate pollen gathering movements related to that area, it is termed incidental (Doull 1970, Buchmann and Shipman 1990, Thorp 2000). The terms “incidental” and “passive” pollen collection have been used more or less interchangeably in the past (Thorp 2000); “incidental” has been more prevalent historically (e.g. Parker 1926, Doull 1970) and “passive” has been used more often recently (e.g. Westerkamp 1996, Williams 2003). We prefer the term incidental because passive implies that the pollen is picked up unintentionally, which is often not the case,
since many bees engage in behaviors that appear to maximize the amount of pollen picked up incidentally.

Incidental pollen collection is always a secondary behavior that occurs when a bee performs a primary behavior such as nectar collecting, oil collecting, or another pollen collecting behavior. Incidental pollen gathering is further characterized by the accumulation of pollen on generalized body hairs rather than a specialized brush or patch of hairs. This is particularly relevant when incidental occurs during other primary behaviors such as rubbing or tapping, where pollen is incidentally accumulated on non-target areas. The amount of pollen actually picked up depends on the degree of contact with the anthers and the hairiness of the bee (Stavert et al. 2016). That the hairs specifically function to enhance pollen collection seems clear, since cleptoparasitic bees tend to undergo a reduction in overall hairiness along with the loss of their pollen-collecting behavior (Müller 1883, Robertson 1899).

A major component of incidental pollen gathering is the degree of movement exhibited by the bee, since the act of moving over or through anthers invariably results in the incidental accumulation of pollen. The degree of movement represents a continuum, encompassing bees that move simply to reach the next anther or nectary, while other bees seem to use it as a means to rapidly accumulate additional pollen on their bodies. For example, on open flowers such as *Daucus*, *Cornus*, and *Spiraea*, *Bombus* wade rapidly over flowers with their mid and hind legs and abdomen appressed in a way that maximizes the incidental collection of pollen, although the primary mode of pollen gathering is still scraping with the forelegs (Heinrich 1976b). Many different terms have been used to describe the movement of bees on flowers, e.g., “wallow,” “run,” “wade,” “crawl,” “sweep,” “scramble,” “walk,” “scurry,” “rotate,” and “scramble” (Malyshev 1936, Bohart and Nye 1960, Cross and Bohart 1960, Heinrich 1972, Houston 1975, Heinrich 1976b, Houston and Thorp 1984, Buchmann and Shipman 1990, Thorp 2000). We
prefer the term “wade,” since it is the earliest term to describe moving over or through a flower that also does not imply a specific speed (Bohart and Nye 1960). In addition, it accurately describes the behavior of how a bee moves both over and through floral structures.

Most bees appear to use incidental pollen collection to supplement their primary pollen gathering behaviors. For example, many groom off the incidentally accumulated pollen between flower visits. However, some species appear to collect the majority of pollen incidentally. For example, Megachile fortis gathers pollen by accumulating it on the body while foraging for nectar (Neff and Simpson 1990), while other species — including bees in the genera Dasypoda (Melittidae), Panurgus (Andrenidae), and Protoxaea (Andrenidae) — “wallow” in anthers whilst nectaring to gather pollen (Malyshev 1936, Linsley and Cazier 1972). Incidental collection of pollen is often used by honey bees and bumble bees, which gather nectar without making any special effort to gather pollen, yet still pack accumulated pollen into the corbiculae (Parker 1926, Heinrich 1976b).

**Temporarily accumulating pollen**

In addition to the seven main pollen gathering behaviors, temporarily accumulating pollen on a specialized patch of hairs represents an important transitional step in the pollen gathering behavior of many bee species. Traditionally, most bees are thought to gather pollen with the legs and immediately transfer it to the scopae, or, alternatively, take the pollen which has adhered to generalized body hairs and groom it into the scopae (Michener et al. 1978, Michener 2007). However, many bees perform a third method in which they temporarily accumulate large amounts of pollen onto a discrete patch of specialized hairs before transferring it to the scopae. These specialized hairs are generally simple (unbranched) and are often hooked or bent apically (Figure 4-6). The use of a temporary holding area does not appear to be limited to certain flowers, as bees with a temporary holding area collectively specialize on a wide array of floral families and flower
types (Table 5). In addition, a temporary holding area is not an adaptation to flowers that restrict pollinator movement and make immediate transfer of pollen impossible; numerous species use a temporary holding area even though they gather pollen from open flowers such as *Sphaeralcea* (Malvaceae) or *Prosopis* (Fabaceae).

Temporarily accumulating pollen in a specialized hair patch is well-documented in Panurginae (Table 5) and appears to be used by a majority of species in the subfamily. Based on observations on species in the genera *Perdita* and *Macrotera* (Andrenidae), pollen is initially gathered by scraping with the forelegs, which immediately load it into the discrete holding area after each scrape. Once a sufficient quantity of pollen has accumulated in the holding area, the forelegs pick it back up and transfer it to the scopae via the midlegs (e.g. Eickwort 1977, Norden et al. 2003).

*Trigona sensu lato* (Apidae) also load the specialized hair patch with the forelegs, but transfer pollen to the corbiculae while hovering (Wille 1963, Michener et al. 1978, Renner 1983). The presence of similar modified hair patches on the venter of other bees (e.g. *Monoeca* (Apidae); Michener 2007, Torretta and Roig-Alsina 2016) suggests that this method of temporarily accumulating pollen may occur in a wider variety of bee groups than is generally reported.

Similar to Panurginae, bees in the genus *Macropis* (Melittidae) also accumulate pollen on their venter, but use specialized corkscrew-shaped hairs (Cane et al. 1983, Vogel 1992, Schäffler and Dötterl 2011). However, in this group, the pollen is loaded directly into the temporary holding area via rubbing with the thorax and abdomen. This behavior may have arisen because the legs are simultaneously occupied by dabbing up oil from the flowers (Vogel 1992). Similar corkscrew-shaped hairs have been found in various anthidiine bees, but their pollen gathering behavior has not been observed (Müller 1996b). In addition, temporarily accumulating pollen in genal hair baskets has been observed in some bee groups, but it is not clear whether these baskets are loaded by directly scraping against pollen or are loaded with the forelegs. This is seen in the
Perdita subgenus Heteroperdita, specialists on Tiquilia (Boraginaceae) (Portman et al. 2016); Hesperapis laticeps (Melittidae), a specialist on Mentzelia (Loasaceae); and both species of Xeralictus (Halictidae) — X. bicuspidariae and X. timberlakei — also specialists on Mentzelia (Snelling and Stage 1995).

**Flexibility in pollen gathering behavior**

The pollen gathering behaviors of bees are not rigid and stereotyped actions performed in isolation. Instead, bees combine different behaviors, mixing and matching them depending on their behavioral repertoires and the morphology of their host plants. The use of different behaviors on flowers with different morphologies has been well-demonstrated in *Apis* and *Bombus*, which will switch between collecting pollen either actively via scraping or incidentally depending on the floral host (Parker 1926, Heinrich 1976b). Another example is found in *Osmia pilicornis*, which uses the proboscis to gather pollen from Pulmonaria (Boraginaceae) and rubs with the face on flowers of Ajuga (Ajugoideae) and Glechoma (Lamiaceae) (Prosi et al. 2016). Using different behaviors on different hosts is also found in specialist bees, such as the Asteraceae specialist *O. montana*, which taps for pollen on most asteraceous flowers, but scrapes with its legs on *Taraxacum* (Cane 2016). More impressively, *O. brevis* uses three distinct behaviors when gathering pollen from Penstemon – rasping, buzzing, and rubbing with the face (Tepedino et al. 1999, Cane 2014). Another example is seen in *Tetraglossula bigamica* (Colletidae) a specialist on Ludwinda elegans (Onagraceae); when anthers are closed, the bees open them with the mandibles and gather pollen by scraping with the fore- and mid-legs. However, when anthers are open and full, the bees gather pollen by rubbing the scopa directly against them (Gimenes 1997).

In addition to using different behaviors on the same or different hosts, many bees perform multiple pollen gathering behaviors simultaneously. For example, *Andrena* sp. on Camissonia
(Figure 4-3E–F) simultaneously scrapes pollen with the forelegs and rubs the abdomen and scopa against the anthers, and *Ashmeadiella buconis* on Asteraceae (Figure 4-4) taps with the metasoma while at the same time probing for nectar and incidentally picking up pollen on the face and body, which is subsequently groomed into the scopa during flight.

**Implications for diet breadth**

While some bees display flexibility in pollen gathering behavior, others have more limited behavioral suites. This has implications for which floral hosts they use (Thorp 1979). Social bees in particular are expected to be more versatile in their pollen gathering behavior compared to solitary bees because their colonies are active for longer periods and must therefore utilize a broad array of successively blooming plants (Heinrich 1976b). However, the opposite appears to be true; instead of having a broad breadth of behaviors, social bees use variations on a small suite of basic behaviors to collect pollen from a variety of different host plants (Table 6). This basic repertoire of various social Apidae and Halictidae is comprised of scraping with the extremities, buzz pollination, and incidental collection. Further, *Apis mellifera* and *Trigona* spp. (*sensu lato*) — likely the most generalized pollinators — are even more restricted, since they cannot buzz pollinate (Table 6, Wille 1963, Buchmann 1983).

The specialized behaviors of bees may limit their ability to collect pollen from alternative hosts despite the fact that their larvae can develop on alternative pollen sources (Cripps and Rust 1989, Williams 2003). This is particularly apparent in Megachilidae; for example, *Hoplitis anthocopoides* (which rubs directly with the scopa) only gathered pollen from *Echium vulgare*, and refused to gather pollen from either the related *Anchusa* sp. or alternative hosts in eight other plant families (Strickler 1979). In addition, the Asteraceae specialist *Heriades truncorum* (which taps with the scopa) refused to gather pollen from *Echium* (Boraginaceae) (Praz et al. 2008). Similarly, Williams (2003) observed that the Asteraceae specialist *Osmia californica* (which taps
with the scopa) refused to gather either *Phacelia* (Boraginaceae) or *Brassica* (Brassicaceae) pollen when it was the only host present, but, in an interesting twist, did gather some *Phacelia* pollen when its normal asteraceous host was also present. When *O. californica* gathered *Phacelia* pollen, it used the same tapping behavior it used on its normal Asteraceae host, but its attempts were clumsy and inefficient, particularly compared to the more generalized *O. lignaria* (Williams 2003). These examples support the hypothesis that the specialized behaviors of these bees (rubbing or tapping) mean that they are either incapable of gathering non-host pollen or can do so only inefficiently.

In contrast, other specialist bees readily gather pollen from alternative hosts. For example, an individual of *Diadasia australis* (Apidae), whose normal host is *Opuntia* (Cactaceae), was observed gathering pollen from *Phacelia* (Boraginaceae) after the local cactus blooms were exhausted (Linsley and MacSwain 1958). Another *Diadasia* cactus-specialist, *D. rinconis* was experimentally induced to gather pollen from *Sphaeralcea* (Malvaceae), but only after nesting was initiated by the temporary introduction of *Opuntia*, the preferred host (McIntosh 2001). Similarly, *Hesperapis pellucida* (Melittidae) was observed gathering pollen from *Gilia capitata* (Polemoniaceae) and other flowers when its normal host, *Eschscholtzia californica* (Papaveraceae), was mowed (Stage 1966). When the normal host recovered and flowered a month later, the bees switched back to gathering pollen from it. *Andrena erythronii* (Andrenidae) gathers pollen from *Erythronium* (Liliaceae) while it is in bloom, but readily switches to other sources once bloom has ended (Michener and Rettenmeyer 1956). Thorp (1969) also reported multiple species of *Andrena* subgenus *Diandrena* gathering pollen from their non-preferred hosts, particularly in times of pollen shortage. All of these bees apparently gather pollen primarily by scraping with the forelegs; this generalized pollen gathering behavior could allow them to more easily exploit non-preferred hosts.
Given the diversity of pollen gathering behaviors, even on the same host plant, it is clear that there is not necessarily a “right way” to gather pollen from a particular host plant. For example, on *Helianthus*, honey bees gather pollen incidentally while nectaring, generalist *Lasioglossum* gather pollen by scraping with the forelegs, *Osmia californica* gather pollen by tapping with the scopae, and *Melissodes* gather pollen by rubbing with the abdomen and scopae. The behavioral differences could be explained by a number of reasons. For example, specialist behaviors such as tapping could be more efficient at particular hosts but less efficient at gathering from alternative hosts (Williams 2003). Conversely, more generalized behaviors could represent a compromise that allows for less efficient utilization of a wider variety of hosts. Lastly, different behaviors on the same host could represent different ecological niches, with some behaviors allowing bees to rapidly skim off accessible pollen while leaving the less accessible pollen untapped, whereas other behaviors could allow bees to meticulously gather the remaining pollen (Simpson et al. 1977).

**The evolution of pollen gathering behavior**

It is widely recognized that the pollen gathering behaviors of bees are derived from ancestral grooming behaviors (Jander 1976, Michener et al. 1978, Westerkamp 1996, Michener 2007). This is particularly apparent for the two most generalized pollen gathering behaviors: scraping with the extremities and incidental pollen gathering. The primary tool used in both of these behaviors is the foreleg, which has a specialized brush used for manipulating pollen, either by scraping up pollen directly from anthers or by grooming pollen from the body. Well-developed brushes on the foreleg are widespread in aculeate Hymenoptera, where they are used for grooming (Grinfel’d 1962). Therefore it is a simple step between scraping pollen for grooming purposes and scraping it in order to collect it into transport structures.
The origin of many other behaviors, including scraping with the other extremities, rubbing with the face, rasping, and rubbing with the body can likely be explained as developing through a series of steps, starting with incidental contact with pollen and progressing into behaviors that maximize pollen uptake. These parts regularly contact pollen during pollen or nectar gathering, and as a result, relatively small behavioral modifications could allow these parts to assist in gathering pollen, or even develop into the primary pollen gathering extremities. For example, the face and mouthparts often come into contact with anthers during nectaring, and certain bees have evolved specialized morphological and behavioral adaptations that assist in the uptake of this pollen, leading to scraping with the tongue or rubbing with the face (Thorp 1979, Müller 1996a). Similarly, rasping likely evolved as a result of bees taking advantage incidental contact by the dorsum of the thorax with anthers.

Rubbing with the body or scopae also appears to have developed through incidental contact that progressed into active pollen uptake. Rubbing behavior likely originated from the typical grooming movements used when bees groom the venter of the abdomen with the hind legs (described by Jander 1976), since these two behaviors are incredibly similar. However, these same movements are used by many bees to tamp down the pollen in the scopae (Michener et al. 1978), making a clear progression difficult to pin down. The universality of this abdomen-cleaning and pollen-tamping behavior makes it likely that rubbing behavior has evolved separately on numerous occasions. Further, which body parts are involved in rubbing depends strongly on the morphology of the flower. For example, rubbing with the apex of the abdomen occurred on flat-topped disk flowers, while rubbing with the abdomen, scopae, and thorax developed on flowers with protruding stamens such as various Malvaceae.

Two behaviors which have unclear origins are tapping and buzzing. Tapping may have developed from ancestors that rubbed with the abdominal scopa. Additional documentation of the
prevalence and host association of this behavior are needed. In particular, it remains to be seen whether this behavior is limited to bees in the family Megachilidae and whether rubbing with the abdomen and tapping intergrade in any bee groups. In terms of buzzing, the origin remains a mystery. However, buzzing is common in multiple other contexts, including thermoregulation, communication, alarm sounds, and nest excavation (Buchmann 1983). Presumably, buzzing was coopted from one of these other behaviors, such as bees using buzzing to thermoregulate on flowers (Heinrich 1972, Thorp 1979).

A major innovation in pollen gathering behavior is the direct use of the pollen-transporting scopal hairs to gather pollen. Using the scopal hairs for both pollen gathering and transport reduces the number of steps involved, which is presumably more efficient than gathering with the extremities and passing the pollen to the. Gathering pollen directly with the scopae is most prominent in the Megachilidae, which have the scopa centrally located on the venter of the abdomen, allowing easier access to anthers compared to bees that have the scopae located on the outer face of the hind legs. However, whether or not gathering pollen directly into the scopa is actually more efficient awaits experimental testing.

Conclusion and Future Directions

Pollen gathering behavior in bees is a complex process that involves the mixing and matching of different behaviors depending on the behavioral repertoire of a given bee species and the floral morphology of host plants. Here, we classify the different uses, breaking down pollen gathering behaviors into “active” and “incidental” categories, further subdividing “active” pollen gathering into six subtypes. In addition, we document an intermediate step in certain bees which temporarily accumulate pollen on a discrete patch of specialized hairs. It is our hope that this updated lexicon and review will allow for the effective communication and comparison of future research, particularly given the rise of low cost, high definition video recording devices.
Despite the abundance of behavioral observations, the breadth and flexibility of pollen gathering behaviors remain poorly understood. This is particularly true in basal groups such as the Rophitini, Fideliinae, and the family Melittidae. Learning more about these groups and others can help shed light on the evolution of pollen gathering, particularly how behaviors such as rubbing, tapping, and rasping evolved and whether they are consistently associated with specific hosts or floral morphologies. Further, it is not clear why some specialists have broad behavioral flexibility, while other specialists, appear to have much more rigid behaviors. Similarly, it’s not clear why generalists tend to have a smaller breadth of behaviors, particularly the lack of buzz pollination in *Apis* and *Trigona*. Examining the tradeoffs between behavioral breadth and pollen gathering efficiency, as well as the genetic and physiological bases of these behavioral limitations, could shed light on these questions.

One of the biggest unanswered questions is whether specialized behaviors increase the efficiency of pollen gathering, either by increasing the efficiency of pollen uptake or by allowing bees to perform to behaviors at once (i.e. gather pollen and nectar simultaneously). It seems probable that specialized behaviors (e.g. rubbing with the abdomen/scopae or tapping) are more efficient than generalized behaviors (e.g. scraping with the forelegs) on the same host, but this remains to be experimentally tested. Conversely, more work is needed to understand whether pollen gathering behavior limits the floral hosts that bees can use.

**Acknowledgments**

We thank the many people who engaged in discussions or pointed to further resources: Skyler Burrows, Jim Cane, Brian Rozick, Avery Russell, Irmgard Schäffler. We also thank Robert Klips and sigma1920HD who contributed videos from YouTube, Corey Andrikopolous for the opportunity to observe the bees in his greenhouse experiments, and Vince Tepedino for reviewing early drafts of the manuscript.
References


Linsley EG, Cazier MA (1963) Further observations on bees which take pollen from plants of the genus Solanum. Pan-Pac Entomol 39:1–18.


Robertson C (1889) Flowers and Insects. III. Bot Gaz 14:297–304.

Robertson C (1890) Flowers and Insects. V. Bot Gaz 15:199–204.

Robertson C (1899) Flowers and Insects. XIX. Bot Gaz 28:27–45.


Stage GI (1966) Biology and systematics of the American species of the genus *Hesperapis* Cockerell. University of California, Berkeley


Vogel S (1992) Ölblumen und ölscammelnende Bienen [Oil Flowers and Oil-collecting Bees]. IWF (Göttingen)


Tables

Table 4-1: Terminology used to refer to buzz pollination. This list is not comprehensive; instead, it focuses on the first usage of terms and the major works on buzz pollination.

<table>
<thead>
<tr>
<th>Term used</th>
<th>Genus or Species</th>
<th>Floral Host</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>“vigorous whirrings” and “whirring method”</td>
<td>Bombus (Apidae) and</td>
<td>Melampyrum (Orobanchaceae)</td>
<td>Meidell 1944 (posthumously published notes)</td>
</tr>
<tr>
<td></td>
<td>Megachile (Megachilidae)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>“vibrating the flowers with rapid leg movements accompanied by a high pitched hum”</td>
<td>Not specified</td>
<td>Lycopersicon (Solanaceae)</td>
<td>Rick 1950</td>
</tr>
<tr>
<td>Buzzing Behavior</td>
<td>Insects</td>
<td>Flower Genus</td>
<td>Year</td>
</tr>
<tr>
<td>------------------</td>
<td>---------</td>
<td>--------------</td>
<td>------</td>
</tr>
<tr>
<td>“buzz,” “buzzing,” “buzzing behavior,” and “vibrate”</td>
<td>Various Andrenidae, Apidae, and Halictidae</td>
<td>Cassia (Fabaceae) and Solanum (Solanaceae)</td>
<td>Michener 1962</td>
</tr>
<tr>
<td>“buzzing,” “buzzing behavior,” and “buzzing technique”</td>
<td>Various Apidae, Colletidae, and Halictidae</td>
<td>Cassia (Fabaceae)</td>
<td>Wille 1963</td>
</tr>
<tr>
<td>“vibrate”</td>
<td>Various Apidae, Andrenidae, and Colletidae</td>
<td>Solanum (Solanaceae)</td>
<td>Linsley and Cazier 1963</td>
</tr>
<tr>
<td>“vibratory pollen collection” and “wing vibration”</td>
<td>Bombus (Apidae) and various Halictidae</td>
<td>Dodecatheon (Primulaceae)</td>
<td>Macior 1964</td>
</tr>
<tr>
<td>“buzz,” “buzzing,” and “buzzing behavior”</td>
<td>Agapostemon (Halictidae)</td>
<td>Chamaecrista (Fabaceae) and Solanum (Solanaceae)</td>
<td>Roberts 1969</td>
</tr>
<tr>
<td>“buzzed the anthers” and “vibrate the anthers”</td>
<td>Caupolicana and Ptiloglossa (Colletidae)</td>
<td>Datura and Solanum (Solanaceae)</td>
<td>Linsley and Cazier 1970</td>
</tr>
<tr>
<td>“vibrate their wings”</td>
<td>Bombus terricola</td>
<td>Solanum (Solanaceae) and Spiraea (Rosaceae)</td>
<td>Heinrich 1972</td>
</tr>
<tr>
<td>“buzz” (vibratile pollination), “buzzing,” and “buzzing technique”</td>
<td>Centris and Melipona (Apidae)</td>
<td>Cassia (Fabaceae)</td>
<td>Buchmann 1974</td>
</tr>
<tr>
<td>“vibratory behavior” and “vibrated anthers”</td>
<td>Various Apidae and Halictidae</td>
<td>Chamaecrista [as Cassia] (Fabaceae)</td>
<td>Thorp and Estes 1975</td>
</tr>
<tr>
<td>“vibration of the thorax”</td>
<td>Anthophora, Bombus, and Xylocopa (Apidae), Augochlorella (Halictidae), Psanethia (Andrenidae)</td>
<td>Solanum (Solanaceae)</td>
<td>Bowers 1975</td>
</tr>
<tr>
<td>“buzz,” “buzzing,” and “vibrated the anthers while emitting a buzzing sound”</td>
<td>Bombus spp. (Apidae)</td>
<td>Rosa (Rosaceae), Solanum (Solanaceae), and Vaccinium (Ericaceae)</td>
<td>Heinrich 1976b</td>
</tr>
<tr>
<td>“buzz,” “buzz pollination,” “buzzing,” “buzzing behavior,” and “vibratile pollination”</td>
<td>Anthophora, Bombus, and Xylocopa (Apidae), Colletes (Colletidae) and Volucella (Syrphidae)</td>
<td>Solanum (Solanaceae)</td>
<td>Buchmann et al. 1977</td>
</tr>
<tr>
<td>“buzz,” “buzz pollination,” “buzzing,” “shivering,” “vibratile pollination,” and “vibrational pollination”</td>
<td>Not specified</td>
<td>Solanum (Solanaceae)</td>
<td>Buchmann and Hurley 1978</td>
</tr>
<tr>
<td>“wing vibration” and “wing vibration method”</td>
<td>Bombus (Apidae)</td>
<td>Echeandia (Liliaceae)</td>
<td>Bernhardt and Montalvo 1979</td>
</tr>
<tr>
<td>“buzz pollination,” “buzzing,” “buzzing behavior,” and “vibratory behavior,”</td>
<td>Not specified</td>
<td>Not specified</td>
<td>Thorp 1979</td>
</tr>
<tr>
<td>“buzzing” and “vibratile behavior”</td>
<td>Not specified</td>
<td>Not specified</td>
<td>Eickwort and Ginsberg 1980</td>
</tr>
<tr>
<td>“buzz pollination,”</td>
<td>Euglossa and</td>
<td>Mouriri</td>
<td>Buchmann and</td>
</tr>
<tr>
<td>Buzzing Behaviors</td>
<td>Genera/Species</td>
<td>Families/Techniques</td>
<td>Authors/Year</td>
</tr>
<tr>
<td>---------------------------------------------------------------------------------</td>
<td>----------------------------------------------------</td>
<td>-----------------------------------------------</td>
<td>--------------</td>
</tr>
<tr>
<td>“thoracic vibration” and “vibrate”</td>
<td>Lasioglossum (Halictidae)</td>
<td>Vibratile methodology</td>
<td>Bernhardt 1984</td>
</tr>
<tr>
<td>“buzz-pollination” and “floral sonication”</td>
<td>Bombus (Apidae)</td>
<td>Thoracic vibration and vibrate</td>
<td>Cane 1985</td>
</tr>
<tr>
<td>“buzz,” “buzz pollination,” “buzzing,” “buzzing behavior,” “floral buzzing,” “floral vibration,” “vibratile methods,” “vibratile pollen-collecting behavior,” “vibratile pollen harvesting,” “vibratile foraging behavior,” “vibrating,” vibratory pollen-collecting behavior, vibratory manner, and vibratory pollen harvesting</td>
<td>Bombus, Xenoglossa, and Xylocopa (Apidae) and Megachile (Megachilidae)</td>
<td>Asteraceae, Cucurbitaceae, Papaveraceae, Rosaceae, Scrophulariaceae</td>
<td>Buchmann 1985</td>
</tr>
<tr>
<td>“buzz,” “buzz pollination,” “buzzing,” and “vibratory pollen collection”</td>
<td>Bombus (Apidae)</td>
<td>Actinidia (Actidiniaceae), Borago and Symptum (Boraginaceae), and Polygonatum (Asparagaceae)</td>
<td>Corbet et al. 1988</td>
</tr>
<tr>
<td>“buzz,” “buzzing,” and “sonicate”</td>
<td>Bombus and Habropoda (Apidae)</td>
<td>Vaccinium (Ericaceae)</td>
<td>Cane and Payne 1988</td>
</tr>
<tr>
<td>“thoracic vibration,” “vibratile behavior,” and “vibratile pollen-harvesting”</td>
<td>Megachile (Megachilidae)</td>
<td>Chamaecrista (Fabaceae)</td>
<td>Neff and Simpson 1988</td>
</tr>
<tr>
<td>“buzz,” “buzz-harvesting,” “buzz-milking,” “buzz pollination,” “buzzing,” and “sonicate”</td>
<td>Protandrena mexicanorum (Andrenidae)</td>
<td>Solanum (Solanaceae)</td>
<td>Cane and Buchmann 1989</td>
</tr>
<tr>
<td>“buzz,” “buzzing,” “floral sonication,” “sonicate,” and</td>
<td>Bombus (Apidae) and Ptiloglossa (Colletidae)</td>
<td>Solanum (Solanaceae)</td>
<td>Buchmann and Cane 1989</td>
</tr>
</tbody>
</table>
“vibratile buzzes”
“buzzing”
“floral sonication” and “sonicate”
“buzz,” “buzz pollination,” “buzzing behavior,” “sonication,” “sonication behavior,” “vibratile or buzz pollination,” and “vibrating”

<table>
<thead>
<tr>
<th>Genus or Species</th>
<th>Behavior Description</th>
<th>Floral Host</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Family Andrenidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Protoxaea gloriosa</em></td>
<td>Holding the anthers against the abdominal venter and hind legs and shaking them while rotating the body</td>
<td><em>Kallstroemia</em> (Zygophyllaceae)</td>
<td>Cazier and Linsley 1974</td>
</tr>
<tr>
<td><em>Andrena erigeniae</em></td>
<td>“pollen was … rubbed from the anthers onto the bee’s body and legs”</td>
<td><em>Claytonia</em> (Montiaceae)</td>
<td>Davis and LaBerge 1975</td>
</tr>
<tr>
<td><strong>Family Apidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucerine spp.</td>
<td>“tummy-tapping”</td>
<td>Asteraceae</td>
<td>Simpson and Neff 1987</td>
</tr>
<tr>
<td><em>Ptilothrix bombiformis</em></td>
<td>“pollen was worked into the scopae”</td>
<td><em>Hibiscus</em> (Malvaceae)</td>
<td>Rust 1980</td>
</tr>
<tr>
<td><em>Ptilothrix fructifera</em></td>
<td>“brush the anthers [between the midlegs, hindlegs, and abdomen]”</td>
<td><em>Opuntia</em> (Cactaceae)</td>
<td>Schlindwein and Wittmann 1997</td>
</tr>
<tr>
<td><em>Svastra obliqua</em></td>
<td>“tummy-tapping … with the distal portion of the abdominal venter”</td>
<td>Asteraceae</td>
<td>Simpson and Neff 1987</td>
</tr>
<tr>
<td><em>Svastra oblique</em> and <em>Melissodes agilis</em></td>
<td>“rhythmically tapping … with the distal venter of their slightly decurved”</td>
<td>Asteraceae</td>
<td>Cane 2016</td>
</tr>
</tbody>
</table>

Tables 4-2: Rubbing with the abdomen, scopae, and/or venter of the thorax.
<table>
<thead>
<tr>
<th>Family Colletidae</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Tetraloniella fulvescens [as Tetralonia dufouri]</td>
<td>“tummy-tapping”</td>
</tr>
</tbody>
</table>

| Tetraglossula bigamica | “rubbing the abdomen against the anthers” | Ludwigia (Onagraceae) | Gimenes 1997 |

<table>
<thead>
<tr>
<th>Family Halictidae</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Dieunomia triangulifera</td>
<td>“waggling the abdomen vigorously from side to side”</td>
</tr>
</tbody>
</table>

| Dieunomia triangulifera | “tapping the heads of the disc flowers with the ventral surface of the metasoma” | Helianthus (Asteraceae) | Minckley et al., 1994 |


| Systropha planidens | “they rapidly moved their abdomen up and down” | Convolvulus (Malvaceae) | Gonzalez et al., 2014, S. Burrows pers. comm. |

<table>
<thead>
<tr>
<th>Family Megachilidae</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Megachile gravita</td>
<td>“females settle on the stamens and rapidly vibrate the abdomen laterally.”</td>
</tr>
</tbody>
</table>

| Hoplitis anthocopoides | “she vibrates [the metasoma] back and forth rapidly against the anthers while her hind legs also move back and forth against the anthers and scopa” | Echium (Boraginaceae) | Eickwort 1973 |

| Hoplitis anthocopoides, H. producta, Megachile relativa, Osmia coerulescens | “rapidly contracts and expands her abdomen, accordion fashion, over the anthers” | Echium (Boraginaceae) | Strickler 1979 |

| Osmia lignaria, Megachile spp. | “filaments are held between the hind legs and … raked against the scopal hairs” | Collinsia (Plataginaceae) | Rust and Clement 1977 |

| Ochreriades fasciatus | “repeatedly tap their metasomal scopae directly against the anthers” | Ballota (Lamiaceae) | Rozen et al. 2015, G. Pisanty pers. comm. |

<p>| Family Melittidae |  |</p>
<table>
<thead>
<tr>
<th>Genus or species</th>
<th>Behavior Description</th>
<th>Floral Host</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heriades spp.</td>
<td>“l’abdomen qui tapote de haut en bas sur les étamines” = “the abdomen taps up and down on the stamens”</td>
<td>Asteraceae</td>
<td>Pasteels and Pasteels 1974</td>
</tr>
<tr>
<td>Osmia montana</td>
<td>“a rapid thumping movement of the abdomen”</td>
<td>Helianthus</td>
<td>Rust 1974</td>
</tr>
<tr>
<td>O. californica and O. montana</td>
<td>“very rapidly tapping the abdominal scopal against the composite disk anthers”</td>
<td>Asteraceae</td>
<td>Cripps and Rust 1989</td>
</tr>
<tr>
<td>O. californica</td>
<td>“tamp their abdomens”</td>
<td>Helianthus, Balsamorhiza, Helianthella (Asteraceae)</td>
<td>Williams 2003</td>
</tr>
<tr>
<td>Megachile melanopyga and M. octosignata</td>
<td>“rapid up and down movements of the abdomen”</td>
<td>Centaurea  (Asteraceae)</td>
<td>Müller and Bansac 2004</td>
</tr>
<tr>
<td>O. californica</td>
<td>“patting the flowers with their abdominal venters”</td>
<td>Balsamorhiza (Asteraceae)</td>
<td>Cane 2005</td>
</tr>
<tr>
<td>Heriades truncorum</td>
<td>“moving the abdomen rapidly up and down”</td>
<td>Asteraceae</td>
<td>Praz et al. 2008</td>
</tr>
<tr>
<td>O. californica and O. montana</td>
<td>“rapidly drumming or patting their abdomens up and down against the pollen-bearing floral”</td>
<td>Balsamorhiza (Asteraceae)</td>
<td>Cane 2011</td>
</tr>
</tbody>
</table>

Table 4-3: Tapping behavior in the literature.
Table 4-4: Rasping behavior in the literature.

<table>
<thead>
<tr>
<th>Genus or species</th>
<th>Behavior Description</th>
<th>Floral Host</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pseudomasaris vespoides</em> (Masaridae)</td>
<td>“[the anthers] rub against the thoracic surface”</td>
<td><em>Penstemon</em> (Plantaginaceae)</td>
<td>Torchio 1974</td>
</tr>
<tr>
<td>Hymenoptera spp.</td>
<td>“the anthers have teeth that rasp against the back and wings of the pollinator”</td>
<td><em>Penstemon</em> (Plantaginaceae)</td>
<td>Thomson et al. 2000</td>
</tr>
<tr>
<td><em>Osmia</em> spp.</td>
<td>“the deliberate rubbing of their backs against the anthers”</td>
<td><em>Penstemon</em> (Plantaginaceae)</td>
<td>Wilson et al. 2006</td>
</tr>
<tr>
<td><em>Osmia brevis</em></td>
<td>“rasping”</td>
<td><em>Penstemon</em> (Plantaginaceae)</td>
<td>Cane 2014</td>
</tr>
<tr>
<td><em>Osmia brevis and O. penstemonis</em></td>
<td>“rasping”</td>
<td><em>Penstemon</em> (Plantaginaceae)</td>
<td>Cane 2016</td>
</tr>
</tbody>
</table>
Table 4-5: Panurgine bees known to temporarily accumulating pollen.

<table>
<thead>
<tr>
<th>Genus or species</th>
<th>Floral hosts</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Anthemurgus passiflorae</em></td>
<td><em>Passiflora</em> (Passifloraceae)</td>
<td>Neff 2003a</td>
</tr>
<tr>
<td><em>Calliopsis subalpina</em></td>
<td><em>Sphaeralcea</em> (Malvaceae)</td>
<td>Pers. Obs.</td>
</tr>
<tr>
<td><em>Panurginus polytrichus</em></td>
<td>Polyleptic</td>
<td>Neff 2003b</td>
</tr>
<tr>
<td><em>Macrotera opuntiae</em></td>
<td><em>Opuntia</em> (Cactaceae)</td>
<td>Bennett and Breed 1985</td>
</tr>
<tr>
<td><em>Macrotera texana</em></td>
<td><em>Opuntia</em> (Cactaceae)</td>
<td>Neff and Danforth 1991</td>
</tr>
<tr>
<td><em>Perdita floridensis</em></td>
<td><em>Ilex</em> (Aquifoliaceae)</td>
<td>Norden et al. 2003</td>
</tr>
<tr>
<td><em>Perdita gerhardi</em></td>
<td><em>Monarda</em> (Lamiaceae)</td>
<td>Miliczky 1991</td>
</tr>
<tr>
<td><em>Perdita halictoides</em></td>
<td><em>Physalis</em> (Solanaceae)</td>
<td>Sullivan 1984</td>
</tr>
<tr>
<td><em>Perdita minima</em></td>
<td><em>Chamaesyce</em> (Euphorbiaceae)</td>
<td>Pers. Obs.</td>
</tr>
<tr>
<td><em>Perdita multiflorae</em></td>
<td><em>Mentzelia</em> (Loasaceae)</td>
<td>Pers. Obs.</td>
</tr>
<tr>
<td><em>Perdita octomaculata</em></td>
<td><em>Solidago</em> (Asteraceae)</td>
<td>Eickwort 1977</td>
</tr>
<tr>
<td><em>Perdita sphaeralcea</em></td>
<td><em>Sphaeralcea</em> (Malvaceae)</td>
<td>Pers. Obs.</td>
</tr>
<tr>
<td><em>Perdita spp.</em></td>
<td><em>Prosopis</em> (Fabaceae)</td>
<td>Simpson et al. 1977</td>
</tr>
</tbody>
</table>
Table 4-6: Comparison of the repertoire of pollen gathering behaviors found in different bee species and groups (? = unclear if the bee has that behavior or not).

<table>
<thead>
<tr>
<th>Species</th>
<th>Scraping</th>
<th>Buzzing</th>
<th>Body Rubbing</th>
<th>Face Rubbing</th>
<th>Tapping</th>
<th>Rasping</th>
<th>Incidental</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generalist Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Apis mellifera</em></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Trigona spp.</em></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bombus impatiens</em></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Halictus ligatus</em></td>
<td>X</td>
<td>?</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Specialist Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Andrena helianthi</em></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Osmia brevis</em></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>Perdita spp.</em></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Ashmeadiella bucconis</em></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Macropis spp.</em></td>
<td>?</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>
Figures

Figure 4-1: *Andrena chlorogaster* biting with the mandibles and scraping with the forelegs: A) foreleg extended and B) foreleg scraping towards the body.

Figure 4-2: *Bombus impatiens* buzzing a *Solanum* flower. The rapid vibrations expel the pollen from the anthers. Image adapted from Russell et al. (2016)
Figure 4-3: Rubbing with the body and/or scopae. A) *Andrena* sp. on *Camissonia* rubbing with the scopae and abdomen. B) *Ptilothrix bombiformis* on *Hibiscus* rubbing with the scopae and abdomen. C–D) *Melissodes* sp. rubbing with the abdomen on *Helianthus*. E–F) *Andrena helianthi* rubbing with the abdomen on *Helianthus*. G–H) *Macropis* sp. rubbing with the thorax and abdomen on *Lysimachia*.

Figure 4-4: *Ashmeadiella bucconis* tapping on Asteraceae. The directionality of the rapid movement of the abdomen is denoted by A) down, B) up, and C) down arrows.
Figure 4-5: *Osmia pilicornis* gathering pollen by rubbing the face against the anthers of *Ajuga reptans* (shown here in contact with the face). The bee repeatedly jerks the whole body A) up and B) down. Image adapted from Prosi et al. (2016).

Figure 4-6. Specialized ventral hairs of A) *Perdita turgiceps* and B) *Protandrena maculata* (belly-up view, head to the left). Scale bars = 200 micrometers.
My dissertation broadly addresses the biodiversity and floral relationships of bees. Bee biodiversity and their floral relationships are intimately related, because with the exception of cleptoparasitic bees, provisioning young is one of the most important behaviors that bees perform. Overall, the different parts of this dissertation combine to suggest that plant morphology, particularly the structure of the flower, and the morphology of the pollen influence how bees utilize those resources.

The relationships between bees and plants have been identified as a primary driver in bee evolution and diversification at both broad and fine scales (Sipes and Tepedino 2005, Cardinal and Danforth 2013). In particular, oligolecty, or specialization on the pollen of a group of related host plants, plays a major role in bee ecology and evolution (Minckley et al. 2000, Michener 2007). Floral specialization may allow bees to partition their environment in a way that reduces competition between species. Alternatively, specialization may be beneficial in extreme habitats by allowing specialists to sync with the phenology of their preferred host (Moldenke 1975, Minckley et al. 2000). However, many questions remain on underlying factors that cause bees to specialize, as well as the mechanisms that bees use to specialize on their preferred hosts (Strickler 1979, Roulston and Cane 2000, Sedivy et al. 2008).

Chapter two adds to our knowledge of the relationship between bee diversity and floral specialization because *Hetero Pere dita* contains many closely related species that often co-occur on host plants, and are all specialized on pollen of the genus *Tiquilia* (Boraginaceae). Indeed,

---

6 This chapter is written in the style of the journal Zootaxa.
fieldwork from that study found up to six *Heteroperdita* species co-occurring at the same time and place. Given the overlap in their distribution and floral preferences, it remains an open question of how these bees are able to coexist. One factor that is likely important is the small size and narrow corolla of *Tiquilia* flowers, which may limit other pollinators from accessing their pollen. *Heteroperdita* are able to access *Tiquilia* pollen through a combination of their minute size and a specialized basket of hairs on the venter of their head. The matchup between the minute, narrow *Tiquilia* flowers, and the minute, specialized *Heteroperdita* species suggests that there may be a coevolved relationship between these two groups. The taxonomic groundwork laid in chapter two will hopefully allow future exploration of this fascinating system.

Despite the groundwork that has been laid, there are almost certainly additional discoveries to made in this group. For example, *Perdita desdemona*, is only known from the female sex and the male remains unknown. In addition, there are many areas where *Heteroperdita* are likely to occur, but have not been well-surveyed. For example, in the United States, northern and eastern Arizona remain poorly sampled. In Mexico, collections of *Heteroperdita* are extremely limited, particularly in the south and Baja California. *Tiquilia* is known to occur in these areas, and targeted collections of the visitors of these plants will likely yield new species.

Finally, in addition to the insights *Heteroperdita* can provide into bee biodiversity and specialization, the subgenus also contains multiple beautiful and rare species. Two species in particular, *Perdita frontalis* and *Perdita titania*, both appear to be limited to dune habitats and have incredibly limited distributions. These two species in particular should be considered for future conservation work in order to ensure that these incredibly rare species continue to persist in an era of pervasive anthropogenic change.
In chapter three, I examined the different types of external pollen transport in bees. Bees can externally transport pollen in one of three ways: either dry, moistened, or glazed, which combines both dry and moist transport. I found that, at least in the genera *Perdita* (Andrenidae) and *Hesperapis* (Melittidae), the mode of pollen transport is related to the floral host that the bees specialize on. Specifically, dry and glazed transport of pollen are associated with specialization on either Asteraceae or Onagraceae. These two plant families, although very different in many respects, are both similar in that they have adhesive pollen. This adhesive pollen potentially provides a mechanism for bees to transport the pollen either entirely or partially dry.

If the adhesive properties of host pollen are indeed driving the evolution of pollen transport in these bees groups, it has implications for general patterns of evolution in bees. For example, it suggests that bees are specializing, at least in part, on the properties of host pollen. This hypothesis was historically accepted by many researchers, who observed a relationship between the morphology of pollen and the scopal hairs of various bee groups (Robertson 1914, Linsley 1958, Roberts and Vallespir 1978, Thorp 1979), though in recent years, the relationship between pollen properties and scopal hairs has received less attention. Bees that specialize on floral hosts in the family Asteraceae in particular have often presented an evolutionary puzzle. For example, the “Asteraceae paradox” states that although specialist species of *Colletes* (Colletidae) gather Asteraceae pollen, closely related generalists avoid it (Müller and Kuhlmann 2008). Hypotheses that explain the odd evolutionary and ecological patterns revolving around specialization on Asteraceae have generally focused on potentially toxic secondary plant compounds found in Asteraceae pollen (Praz et al. 2008, Sedivy et al. 2012). However, the adhesive properties of Asteraceae pollen could explain why many bees appear to avoid collecting it, especially if bees need specialized tools in order to effectively carry the sticky pollen.
In chapter four, I documented the different types of pollen gathering behavior used by bees. I combined a careful review of existing literature with modern video technology to build up a base of knowledge on the different types of pollen gathering behavior. From this, I created an updated lexicon for the different behaviors and built them into a broader framework. This chapter is in many ways preliminary, laying the necessary groundwork needed to advance future research. Previous reviews of pollen gathering largely skipped over the specific behavioral steps of gathering pollen, either focusing on the broader aspects of foraging in bees or instead compiling previous work without attempting to synthesize it. In chapter four, I have synthesized the diverse and disparate pollen gathering behaviors in order to create a base of work that will facilitate further research in the burgeoning field of pollination biology.

There will no doubt be those who disagree, either with the definitions of specific behaviors, or with the classification of specific behavioral examples into certain groups. Indeed, the breadth and variety of behaviors resist classification into tidy groups. These different pollen gathering strategies are often varied between different species and may use different areas of the body and occur at different speeds. However, in most cases, the similarities between the behaviors outnumber the differences, and the behaviors are likely functionally similar, especially from an ecological standpoint. Further, from the work presented here, it is clear that there are convergent pollen gathering strategies that occur in many different unrelated bee groups. Overall, this work sets a baseline from which others can agree, disagree, or propose their own alternate classifications. This is a step forward from the current state of affairs, which often encourages observations in isolation and the coining of novel terms for previously-described behaviors.

References


Zachary M. Portman

Education

2011–Present  Ph.D. Candidate in Ecology
Research Adviser: Terry Griswold
Utah State University, Logan, UT

2009  B.S. with honors, Biology and Computer Science
Thesis: A 3-Dimensional Model of Bryophyte Canopy Light Interaction
Union College, Schenectady, NY

Publications

2017

Portman, Z.M., Tepedino, V.J., Tripodi, A.D., Szalanski, A.L., & Durham, S.L. Local extinction of a rare plant pollinator in southern Utah (USA) associated with invasion by Africanized honey bees. Biological Invasions. DOI: 10.1007/s10530-017-1559-1


2016


Portman, Z.M., Griswold, T. & Pitts, J.P. Association of the female of *Perdita* (*Xeromacrotera*) cephalotes (Cresson), and a replacement name for *Perdita bohartorum* Parker (Hymenoptera: Andrenidae). Zootaxa 4097, 567–574.


**Non Peer-Reviewed Publications**


**Grants, Fellowships, and Awards**

2017 Utah State University Graduate Enhancement Scholarship – $4,000.


2015 Utah State University Ecology Center Research Award – $3,000.

2015 "Mapping the evolution of pollen transport in *Perdita*,” Utah State University Doctoral Dissertation Enhancement Award – $9,800.

2014 Utah State University USUSA Research and Project Grant – $1,000.


2011 NSF GRFP Fellowship – $134,500 over three years.


**Presentations**

05/2017  Portman, Z.M. & Tepedino, V.J. Oral Presentation. A tale of two poppies: recent studies of the pollinators of *Arctomecon humilis* in Utah and *A. californica* in Nevada. Washington County Rare Plants Meeting, St. George, UT.

04/2017  Portman, Z.M. Oral Presentation. Specialization and pollen gathering behavior in bees. Entomological Society of America Pacific Branch Meeting, Portland, OR.


**Professional Experience**

2016–2017  Graduate Research Assistant, USDA-ARS Pollinating Insect Research Unit, Logan, UT.

2016  Independent Research Scientist, funded by the US Fish and Wildlife Service.
2015  Bee Identification Consultant, University of Wisconsin, Madison, WI.

2012–2015 NSF GRFP Fellow, Utah State University, Logan, UT.

2011–2012 Graduate Research Assistant, USDA-ARS Pollinating Insect Research Unit, Logan, UT.

2011 Field Technician, Rutgers University, New Brunswick, NJ. PI: Dr. Rachel Winfree.

2010 Research Assistant, Washington University in St. Louis, St. Louis, MO. PI’s: Dr. Tiffany Knight and Dr. Laura Burkle.

**Teaching Experience**

2017 Graduate Teaching Assistant, Biology and the Citizen. Utah State University, Logan, UT.

2017 Guest Instructor, Native American Bee Course, USDA-ARS Pollinating Insects Research Unit, Logan, UT. June 12–16.

2017 Guest Lecture, “Biology and Conservation of Bees,” Biology and the Citizen, Utah State University, Logan, UT. June 8th.

2015–2016 Graduate Teaching Assistant, Biology I Laboratory. Utah State University, Logan, UT.

2013 Volunteer Teaching Assistant, Software Carpentry Programming Bootcamp, Utah State University, Logan, UT. March 23–24.


**Training and Skills**

Programming languages: Proficient in Python, Java. Familiar with SQL, C/C++, R.

2014 Getting Started as a Successful Proposal Writer and Academician Grant Writing Workshop. Utah State University, Logan, UT.
2012  Allies on Campus Training. Utah State University Access and Diversity Center, Logan, UT.

2012  The Bee Course. Southwest Research Station, Portal, AZ.

2009  Identification and Ecology of Midwestern Bees. Tyson Research Center, St. Louis, MO.


**Service and Outreach**

2013–Present  Entomology outreach at USU Science Unwrapped events (6x yearly).
2017  Volunteer, Gardeners Market Pollinator Booth, Logan, UT.
2016  Finalist, Utah State University Val R. Christensen Service Award.
2013–2016  Member, USU Graduate Student Advisory Council.
2012–2013  Graduate Representative, USU Student Association, Utah State University.
2012–2013  Chair, USU Student Health Advisory Committee.
2011–2013  Volunteer, USU Student Organic Farm.
2011–2012  Secretary, USU Biology Graduate Student Association.
2009  Americorps Volunteer, Rocky Mountain Youth Corps, Steamboat Springs, CO.