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Phylogenetic Analysis and Taxonomic Revision of the Perdita Subgenera Macrotera, Macroteropsis, Macroterella and Cockerellula (Hymenoptera: Andrenidae)

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Phylogenetic Analysis and Taxonomic Revision of the *Perdita* Subgenera *Macrotera, Macroteropsis, Macroterella* and *Cockerellula* (Hymenoptera: Andrenidae)[1]

BRYAN N. DANFORTH[2]

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ABSTRACT

This paper presents a preliminary phylogenetic analysis of the 21 *Perdita* subgenera based on internal and external morphological characters. Based on this analysis, the genus *Perdita* is clearly monophyletic. The analysis yielded 6 equally parsimonious trees; a central polytomy, involving 7 groups, is the greatest source of ambiguity. These results provide the basis for a species-level phylogenetic analysis of the monophyletic group of 31 species included in the subgenera *Macrotera, Macroteropsis, Cockerellula,* and *Macroterella.* This group (referred to as the *Macrotera* group of subgenera) forms the sister group to the remaining species in the genus. Phylogenetic analysis resulted in 4 equally parsimonious trees. The greatest source of ambiguity involves the relationships among the basal species in the clade. Classificatory changes in the limits of these subgenera are made as a consequence of the species-level analysis.

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Plate I. Small-headed male of *Perdita portalis*.

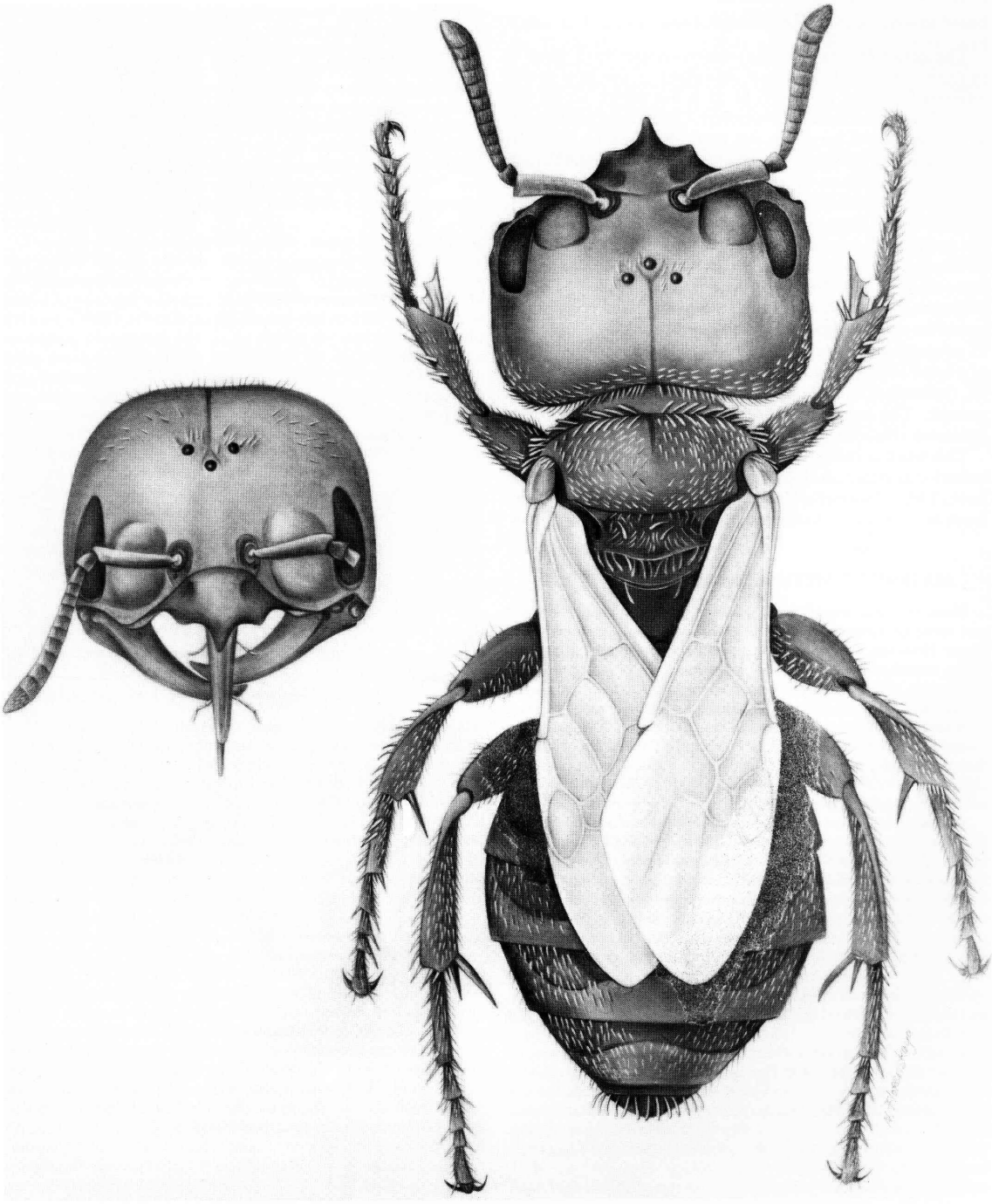

Plate II. Large-headed male of *Perdita portalis*.

INTRODUCTION

The genus *Perdita* contains numerous species of small to minute bees which are most abundant in the arid southwestern U.S. and northern Mexico but range across the United States, northward to southern Canada and as far south as Guatemala. The genus was first described by Smith in 1853 based on specimens of *Perdita halictoides* in the British Museum. Since then over 500 species have been described, the vast majority of them by P.H. Timberlake (1953-1980). Since Timberlake's revisions little work has been done on the genus and especially lacking is a phylogenetic analysis of this large genus of bees. The present work is meant as a first step in the phylogenetic analysis of the group. First, a phylogenetic hypothesis for the *Perdita* subgenera is proposed based on an investigation of representative species from all 21 subgenera. The preliminary analysis reveals the existence of a basal lineage of four subgenera (*Macrotera, Macroteropsis, Cockerellula* and *Macroterella;* herein called the *Macrotera* group). The second part of this study focuses on the evolutionary relationships among the 31 included species.

This work is meant to complement recent work on the behavior and morphology of several species of *Perdita* (Danforth, 1989b; Danforth, 1991a,b; Neff & Danforth, 1992, Danforth & Neff, 1992; Norden, et al., 1992).

MATERIALS, METHODS AND TERMINOLOGY

Many external morphological features were used in this study and some of these characters were easily visible in pinned specimens. However, internal morphological structures and characters of the mouthparts and terminal metasomal segments could only be seen in cleared, disarticulated specimens. Specimens were cleared in a weak solution of potassium hydroxide for one to two days and then repeatedly rinsed in distilled water. Cleared specimens were then stored in glycerol in plastic, 24-well tissue culture dishes. In order to see some characters in naturally pale or overly cleared sclerites it was necessary to stain the cuticle with a dilute solution of acid fuchsin.

The morphological terminology used follows that of Michener (1944), and other authors (Eickwort, 1969; Brooks, 1988). Terms used to describe surface sculpturing follow Harris (1979). Unlike Michener (1944), but as in his recent works, I have called the sternum and tergum of the first metasomal segment (homologous to the second abdominal segment) tergum 1 (abbreviated T1) and sternum 1 (abbreviated S1), respectively. The following metasomal sclerites are numbered sequentially thereafter (Fig. 1a). Terga (Fig. 1b,d) possess paired muscle attachment sites, termed apodemes, graduli, extending nearly the width of the tergum, and laterally, the paired spiracles (Fig. 1d). Sterna possess apodemes also, but, in *Perdita,* lack graduli (Fig. 1c).

In males there are seven visible terga and eight sterna, although S8 is occasionally retracted (Fig. 1a). T8 is visible only as a weakly sclerotized structure bearing apical setae on the internal surface of T7. S8 can be divided into a region proximal of the apodemal arms, the disc, and a region distal to the apodemes, the apex (Fig. 1e). S7 and S8 are highly variable in shape and are important characters for species identification.

In females there are 6 visible terga and sterna. S6 is highly variable and often useful for identifying females to species (Fig. 1f).

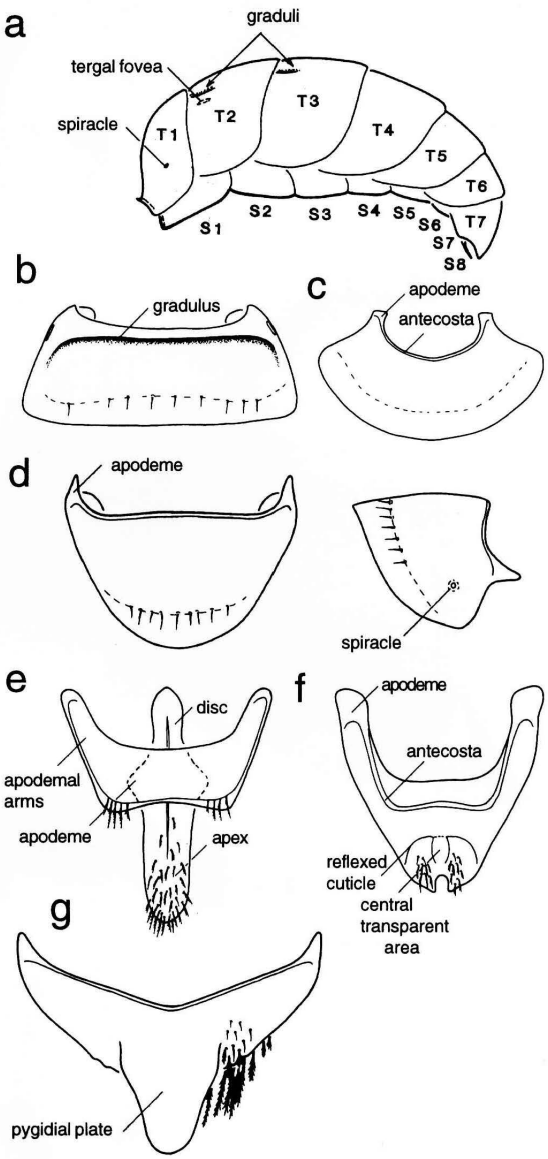

Fig. 1. Morphology of the metasoma in *P. texana:* **(a)** lateral view of male metasoma showing numbering of terga and sterna, **(b)** dorsal view of male second sternum, **(c)** ventral view of male second tergum, **(d)** dorsal and lateral views of male sixth tergum, **(e)** ventral view of male S7 and S8, **(f)** ventral view female S6, **(g)** dorsal view female T6, showing pygidial plate.

The sixth tergum in females bears the pygidial plate (Fig. 1g). The sting in *Perdita* is very weakly developed and was not studied in detail. Anteriorly the female S6 bears apodemal arms, like the preceding sterna. On the inner surface of the sterna, connecting the apodemal arms is a thickened bar of cuticle termed the antecosta (Michener, 1944). On S6 the antecosta often is separated from the anterior margin of the sterna, and can show variability between species in its shape and path. Apically, S6 often bears a thickened pad of cuticle on its internal surface, termed here the reflexed cuticle, which is highly variable in shape. In most species the reflexed cuticle is fused to the outer layer of cuticle forming a central transparent area (Fig. 1f).

The male genitalia are highly variable among species of *Perdita*. The genital capsule consists of large gonocoxites, which in some species, give rise apically to gonostyli. Ventrally one sees the paired, clasper-like volsellae. Each volsella consists of a larger, ventral cuspis which arises from the basivolsella and the smaller, dorsal digitus (Snodgrass, 1941). In *Perdita* the cuspis bears few to many papillae on its upper surface and the digitus usually has a few papillae also. Within the genital capsule is the elongate aedeagus, or penis, consisting of lateral sclerotized penis valves which, in some species, are fused into a single tube-like structure, or in others, remain separate lateral sclerites of the aeadagus. The apodemal arms of the aedagus are variable in shape, from elongate and straight to dorsally reflexed. The aedeagus sometimes contains useful characters and for this reason I have illustated the aedeagus and genital capsule separately.

Analyses of the data matrices were performed using the computer program Hennig86, version 1.5 (Farris, 1988; but see also Fitzhugh, 1989; and Platnick, 1990).

PHYLOGENETIC RELATIONSHIPS AMONG THE *PERDITA* SUBGENERA

Species Chosen for Preliminary Analysis

The species used for the preliminary analysis of the higher level relationships within the genus were selected based on Timberlake's (1954-1980) concepts of the subgenera (Table 1). At least one species was studied in detail from each of the 21 subgenera and, in some cases, more species were examined in order to evaluate the monophyly of each subgenus. The species studied in detail are listed below according to subgenus. Effort was made to examine the type species of each subgenus, but in some cases type species were poorly represented in collections and therefore could not be studied in detail. Type species which could not be examined are included in parentheses below.

ALLOMACROTERA Timb. – *P. stephanomeriae* Timb. (type species); *ALLOPERDITA* Viereck – *P. mitchelli* Timb. (*P. novaeangliae* Viereck, type species); *CALLOMACROTERA* Timb. – *Perdita maritima* Timberlake (type species); *COCKERELLIA* Ashm. – *P. albipennis albipennis* Cress., *P. albipennis heliophila* Ckll., *P. baileyae* Ckll., *P. beata beata* Ckll., *P. bequaerti indianensis* Ckll., *P. coreopsidis coreopsidis* Ckll., *P. incana* Timb., *P. lepachidis lepachidis* Ckll., *P. lingualis* Ckll., *P. obscuripennis* Timb., *P. perpulchra perpulchra* Ckll., *P. purpurascens* Timb., *P. scopata* Timb., *P. tricincta* Timb., *P. utahensis* Ckll., *P. verbesinae* Ckll. (*P. hyalina* Cress., type species); *COCKERELLULA* Timb. – *P. laticauda* Timb. (*Perdita opuntiae* Ckll., type species); *EPIMACROTERA* Timb. – *P. ainsliei* Crawford (type species), *P. diversa* Timb., *P. euphorbiae* Timb., *P. nanula* Timb., *P. parvula* Timb.; *GLOSSOPERDITA* Ckll. – *P. blaisdelli* Timb., *P. giliae* Timb., *P. hurdi* Timb., *P. navarretiae* Timb., *P. pelargoides* (Ckll.) (type species); *HESPEROPERDITA* Timb. – *Perdita ruficauda ruficauda* Ckll. (type species); *HETEROPERDITA* Timb. – *P. arenaria* Timb., *P. bellula* Timb., *P. coldeniae* Timb., *P. rhodogastra* Timb. (type species), *P. scutellaris* Timb., *P. sexfasciata* Timb., *P. trifasciata* Timb., *P. wasbaueri* Timb.; *HEXAPERDITA* Timb. – *P. asteris* Timb., *P. bishoppi planorum* Timb., *P. boltoniae chrysopsina* Timb., *P. callicerata* Timb., *P. cambarella platyura* Ckll., *P. cara* Timb., *P. foveata foveata* Timb., *P. georgica* Timb., *P. heterothecae* Ckll., *P. ignota ignota* Ckll. (type species), *P. nubila* Timb., *P. pratti* Ckll., *P. xanthismae* Ckll.; *MACROTERA* F. Smith – *P. texana* (Cress.), *P. bicolor* (Smith) (type species); *MACROTERELLA* Timb. – *P. mellea* Timb., *P. nigrella* Timb. (*Perdita mortuaria* Timb., type species); *MACROTEROPSIS* Ashmead – *P. latior* Ckll. (type species); *PENTAPERDITA* Ckll. & Porter – *P. albovittata* Ckll. (type species), *P. amoena* Timb., *P. bradleyana* Timb., *P. chrysophila chrysophila* Ckll., *P. coahuilensis* Timb., *P. melanochlora* Ckll., *P. nigrifacies* Timb., *P. nigriviridis* Timb.; *PERDITELLA* Ckll. – *P. minima* Timb., *P. cladothricis* Ckll., *P. larreae* Ckll. (type species); *PROCOCKERELLIA* Timb. – *P. albonotata* Timb. (type species); *PSEUDOMACROTERA* Timb. – *P. turgiceps* Timb. (type species); *PYGOPERDITA* Timb. – *P. californica*

Table 1. List of *Perdita* subgenera and species groups based on Timberlake (1954-1980) and subsequent work, and numbers of valid species names (subspecies not counted). Numbers in parentheses give the number of species based on changes resulting from the present work.

Perdita subgenera	no. species
Allomacrotera	2
Alloperdita	7
Callomacrotera	2
Cockerellia	25
Cockerellula	9 (13)
Epimacrotera	21
Glossoperdita	5
Hesperoperdita	2
Heteroperdita	13 (14)
Hexaperdita	26
Macrotera	5 (6)
Macroteropsis	12 (6)
Pentaperdita	15
Perdita	
Halictoides Group	12
Octomaculata Group	111
Sphaeralceae Group	191
Ventralis Group	66
Zonalis Group	53
Valida Group	1
unplaced species	14
Perditella	5
Procockerellia	4
Pseudomacrotera	1
Pygoperdita	40
Xeromacrotera	1
Xerophasma	2
Total species	653 (651)

(Cress.), *P. interrupta* Cress. (type species); *XEROMACROTERA* Timb. – *Perdita cephalotes* (Cress.) (male only; type species); *XEROPHASMA* Ckll. – *P. bequaertiana* Ckll. (type species).

The subgenus *PERDITA* contains over half the species in the genus (Table 1). Representative species of each of Timberlake's five "groups" of *Perdita* s. str. were included in the detailed study: ZONALIS group – *P. zonalis zonalis* Cress.; HALICTOIDES group – *P. halictoides* Smith; OCTOMACULATA group – *P. octomaculata* (Say); VENTRALIS group – *P. wootonae* Ckll.; SPHAERALCEAE group – *P. sphaeralceae notata* Timb.

Character polarity was determined using the outgroup criterion (Lundberg, 1972; Watrous & Wheeler, 1981; and Maddison et al., 1984). Outgroup taxa were chosen based on Ruz's phylogeny of the panurgine genera (Fig. 2; Ruz, 1991), and included the following species: Calliopsini – *Calliopsis* (*Calliopsis*) *andreniformis* Smith, *C.* (*Calliopsima*) *coloradensis* Crawford, *C.* (*Verbenapis*) *nebraskensis* Crawford, *C.* (*Nomadopsis*) *linsleyi* Rozen, *C.* (*N.*) *scutellaris* (Fowler), *Callonychium mandibulare* Friese, *C. flaviventre* (Friese), *Acamptopoeum prinii* (Holmberg), *Arhysosage flava* Moure, *Spinoliella rufiventris* Toro; Melitturgini – *Melitturga clavicornis* Latreille; Panurgini – *Panurginus occidentalis* Crawford, *Epimethea kuznetzovi* Ckll.; Protandrenini – *Pterosarus albitarsus* (Cress.), *Heterosarus illinoensis* (Cress.).

Specimens for the subgeneric analysis came primarily from the Snow Entomological Museum, University of Kansas, but specimens were borrowed from other North American institutions listed in Acknowledgements.

DATA MATRIX

The data matrix used in this analysis is shown in Table 2. The codings for the ancestral taxon are based on consideration of all the panurgine outgroups listed. When the character states varied among outgroups, the most parsimonious hypothesis for the primitive condition in *Perdita* was chosen based on the rationale

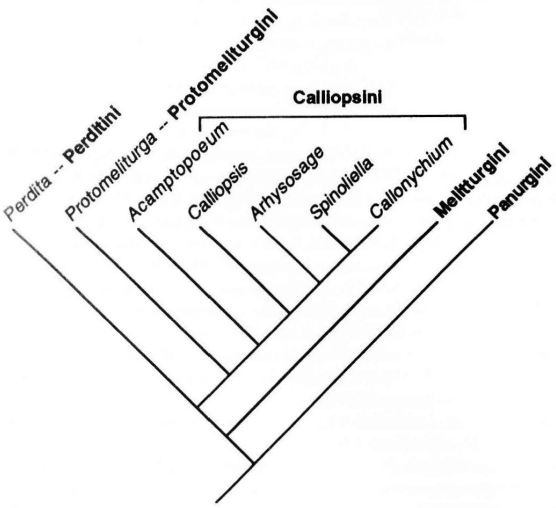

Fig. 2. Phylogeny of the Panurginae, based on Ruz (1987), showing placement of *Perdita* and relationships among outgroup taxa used.

Table 2. Data Matrix for characters of *Perdita* subgenera and species groups.

Character numbers	0000000001111111111222222222333
	1234567890123456789012345678901 2
ANCESTOR	000000000000000000000?000000000
ALLOPERDITA	10111100002011000000110110111212
CALLOMACROTERA	10011221002121021200210100011212
COCKERELLIA	10011321002221120110110101011212
COCKER. BAILEYAE	10011321001221120110110100011212
ALLOMACROTERA	1201122110?221020110?1???0011?1?
COCKERELLULA	00000000010000000000000100011100
EPIMACROTERA	10001010101001000000100110011201
GLOSSOPERDITA	1000?000101001020000100110011212
P. HURDI	10011010101001000000100110011201
HESPEROPERDITA	10001010101011010000100110011211
HETEROPERDITA	1001?01010?021000000?0011001120?
HEXAPERDITA	10?112211021?102000011011011212
MACROTERA	00000000010000000000000100011100
MACROTERELLA	00000000010000000000000100011111
MACROTEROPSIS	00000000010000000000000100011100
PENTAPERDITA	1101122?10?2?1020?00110100011212
PERDITA	
HALICTOIDES GR.	12001000101021000000100110011212
OCTOMACULATA GR.	10001101101021000000100110011212
SPHAERALCEAE GR.	10011101101001000000110110011112
VENTRALIS GR.	10111000002001000000110100011212
ZONALIS GR.	10011201101021000000110110011212
PERDITELLA	10010000101001000000110110011212
PROCOCKERELLIA	11011321102221120110110100011211
PSEUDOMACROTERA	00001100000000002000101100011010
PYGOPERDITA	
CALIFORNICA GR.	10001200101000000001100100011210
INTERRUPTA GR.	10001200101000000001100100011210
XEROPHASMA	00011000001000000000110110111212
XEROMACROTERA	?001122??02?2?0?0??0?1???00???1?

described in Watrous & Wheeler (1981). Terminal taxa included all the *Perdita* subgenera. The subgenus *Glossoperdita* was divided into two groups, the majority of *Glossoperdita* and *P.* (*Glossoperdita*) *hurdi*, because *P. hurdi* is distinct from the remainder of the subgenus *Glossoperdita* in several characters. Similarly, *Cockerellia* was broken up into the majority of *Cockerellia* species and *P.* (*Cockerellia*) *baileyae*, because *P. baileyae* lacks some of the derived characters present in the remainder of *Cockerellia*. The two groups of *Pygoperdita*, the Californica and the Interrupta groups, were treated separately, in order to test the monophyly of the subgenus.

When the plesiomorphic state of a character could be unambiguously determined based on outgroup comparison, the state was coded 0. For those characters that could not be polarized the ancestral character state was coded as unknown (? in the data matrix). Among in-group taxa, characters for which the states are not known, or which are variable within a taxon, are coded as unknown. Comments are given along with the character descriptions indicating how polarity decisions were made.

CHARACTER DESCRIPTIONS

1(0) Female paraglossa slender basally but broadening apically to form broad, brush-like apex (Fig. 3a-c); **(1)** paraglossa slender and acutely pointed to moderately broad and parallel-sided (Fig. 3d).

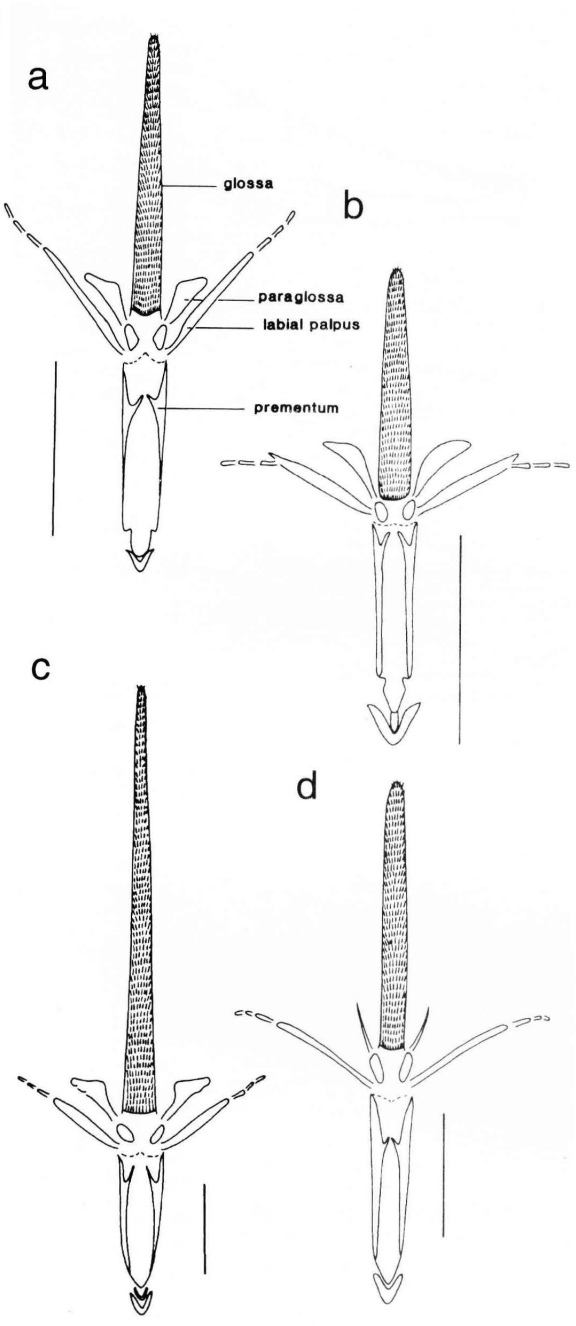

Fig. 3. Dorsal views of labia: **(a)** *P. (Cockerellula) azteca*, **(b)** *P. (Macroteropsis) echinocacti*, **(c)** *P. (Macrotera) bicolor*, **(d)** *P. (Cockerellia) albipennis*. Scale bar = 1.0 mm.

Both character states occur within *Perdita*, as well as within the outgroups studied (e.g., 1(1) in *Callonychium mandibulare* and *Pterosarus albitarsis;* 1(0) in *Calliopsis andreniformis* and *Panurginus occidentalis*). Therefore, based on outgroup morphology, it is unclear what the primitive state is for *Perdita*. However, broad paraglossae appear to be related to the application of a cell lining in species of *Perdita* studied to date. Because a cell lining is plesiomorphic for the genus, based on outgroup comparison, I assume that the broad paraglossae are also primitive for *Perdita*. Although coded 1(1) in the data matrix, *P. sphaeralceae* and *P. wootonae* (Ventralis group) show slight broadening of the paraglossae.

2(0) Female maxillary palpus with 6 segments (Fig. 4b, c); **(1)** with 5 segments (Fig. 4d); **(2)** with 3 segments (Fig. 4e).

All outgroup taxa studied have six-segmented maxillary palpi.

3(0) Acute male genal projection lacking; **(1)** acute male genal projection present (Fig. 5b), at least in some specimens.

Male genal projections are lacking in all outgroups studied and therefore 3(0) is considered plesiomorphic for *Perdita*.

4(0) Male second medial cell present (Fig. 6d); **(1)** male second medial cell lacking, i.e., veins Cu1a and 2m-cu spectral (Figs. 6c, e).

In all outgroups studied and many species of *Perdita*, the veins delimiting the male second medial cell are clearly visible in transmitted light, being well sclerotized (tubular or nebulous veins in

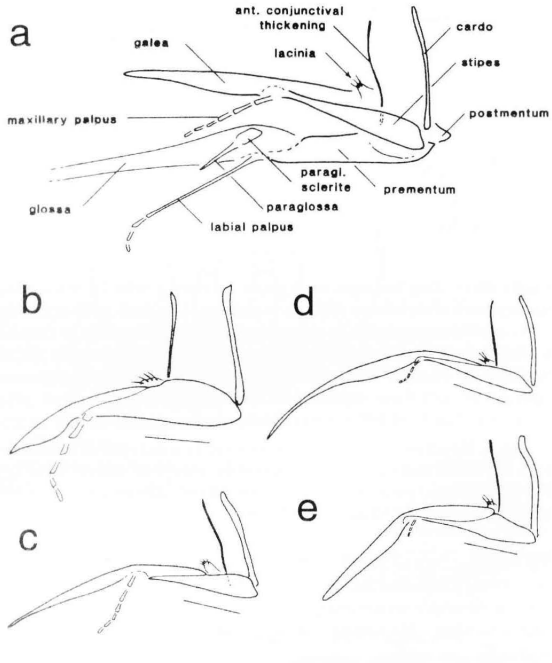

Fig. 4a. Lateral view of intact mouthparts of *Perdita texana*. **Fig. 4b-e:** Lateral views of maxillae, showing variation in the number of maxillary palpal segments: **(b)** *Panurginus occidentalis*, **(c)** *Perdita (Cockerellula) azteca*, **(d)** *P. (Procockerellia) albonotata*, **(e)** *P. (Perdita) halictoides*. Scale bar = 0.5 mm.

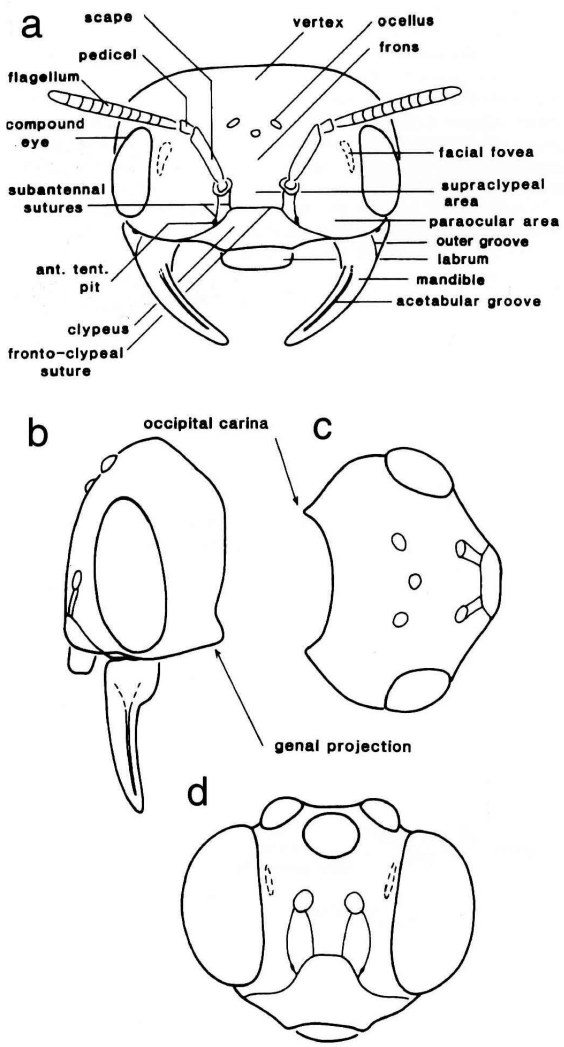

Fig. 5. Head morphology in *Perdita:* **(a)** Frontal view of head capsule in *Perdita texana,* **(b)** *P. (Hexaperdita) crawfordi,* lateral view, **(c)** *P. (Hexaperdita) crawfordi,* dorsal view, **(d)** *P. (Xerophasma) bequaertiana,* frontal view. Scale bar = 1.0 mm.

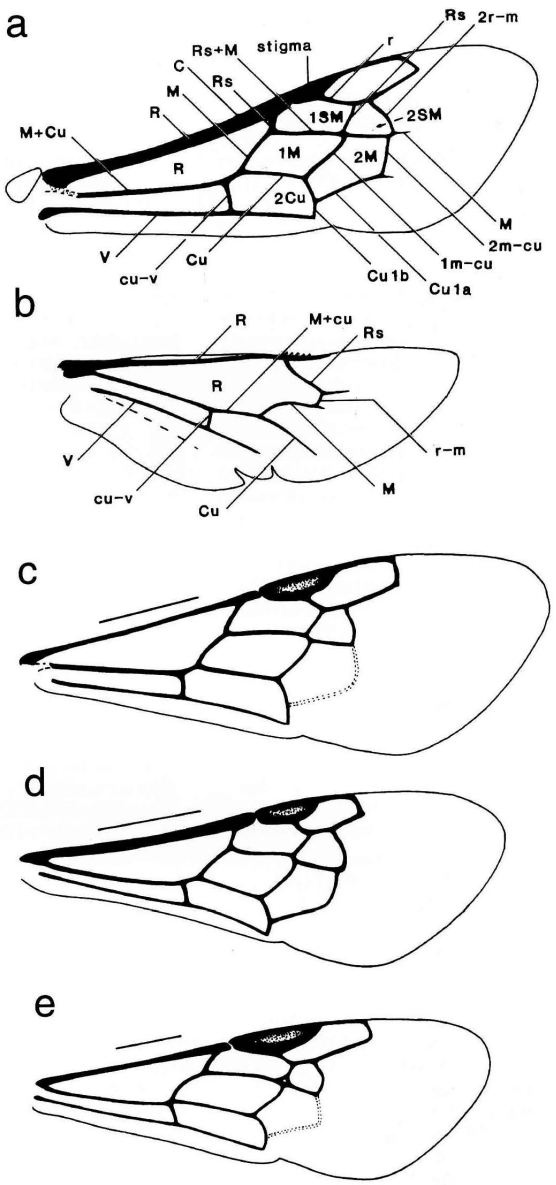

Fig. 6. Male forewings: **(a)** *P. texana* forewing with veins and cells labelled, **(b)** *P. texana* hindwing with veins and cells labelled, **(c)** *Perdita (Cockerellia) albipennis,* forewing, **(d)** *P. (Pygoperdita) californica,* forewing, **(e)** *P. (Xerophasma) bequaertiana,* forewing. Scale bar = 1.0 mm.

the terminology of Mason, 1986). In some species of *Perdita,* however, veins Cu1a and 2m-cu are invisible in transmitted light (spectral, in Mason's terminology) and therefore the second medial cell is lacking. All female *Perdita* possess a complete second medial cell.

5(0) Pre-episternal groove absent or present but not extending to scrobe (Figs. 7b); **(1)** Pre-episternal groove plus scrobal groove together forming C-shaped sulcus extending from upper edge of mesepisternum (below the forewing articulation) to scrobe (Fig. 7a).

Primitively, bees appear to possess two grooves on the mesepisternum. For example, in most Colletidae and Halictidae (excluding Nomiinae) there is a conspicuous pre-episternal groove extending downward from the upper margin of the mesepister-

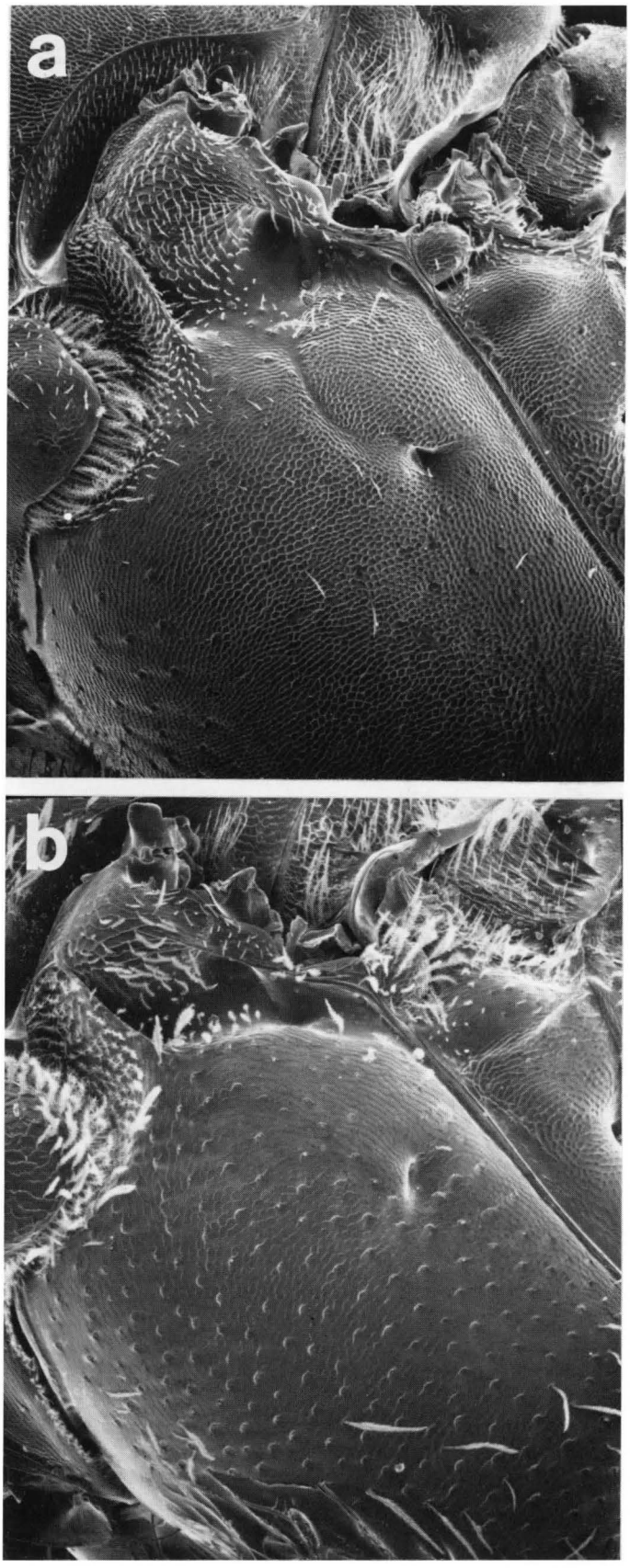

Fig. 7. Lateral views of thoraces [SEM]. **(a)** *P. (Macroteropsis) portalis* [scrobal groove present], **(b)** *P. (Perdita) octomaculata* [no groove].

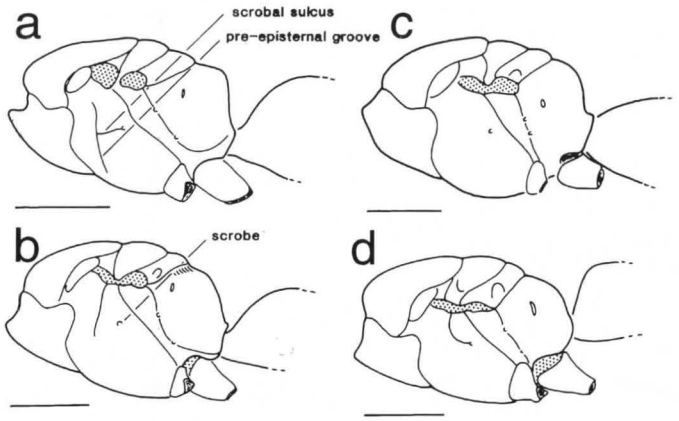

Fig. 8. Lateral views of thoraces. **(a)** *Lasioglossum zephyrum* (Halictidae), **(b)** *Pterosarus albitarsus,* **(c)** *Perdita texana,* **(d)** *Perdita albipennis.* Scale bar = 1.0 mm.

num, immediately below the forewing base (Fig. 8a). In most Colletidae this groove is very long and can reach the underside of the mesepisternum. Extending posteriorly from the pre-episternal groove and usually ending at the scrobe is the scrobal groove (Michener, 1944). Most outgroups possess only the extreme upper portion of the episternal groove and no trace of the scrobal groove (e.g., *Arhysosage flava, Pterosarus albitarsus,* Fig. 8b), while some others show no sign of either groove (e.g., some *Calliopsis*). In *Perdita* some species, like the outgroups, show no sign of a scrobal or pre-episternal groove (Fig. 8c). In the vast majority of *Perdita* species, however, there is a discrete groove extending from the upper margin of the episternum to the scrobe (e.g, *Perdita albipennis,* Fig. 8d). This groove appears to consist of both a pre-episternal groove (dorsally) and a scrobal groove (immediately anterior to the scrobe). Ruz referred to the entire groove as simply the pre-episternal groove. Because this state was not seen in any panurgine outgroups (except *Acamptopoeum*) it is considered derived for *Perdita,* in spite of the fact that similar grooves extending to the scrobe are present in many, more distantly related bees (e.g., some Apidae).

6(0) Male S7 with posterior margin straight or with weak emargination (Fig. 9a,b); **(1)** posterior margin moderately emarginate (depth of emargination equal to length of sclerite at midline) (Fig. 9c,d); **(2)** posterior margin deeply emarginate such that depth of emargination much greater than length of sclerite at midline (Fig. 9e,f); **(3)** emargination of S7 extreme, such that S7 appearing as two lateral, quadrate plates connected by thin bar of cuticle (Fig. 9g,h).

Some outgroups studied (those species in the Calliopsini and Melitturgini) have the male S7 highly modified in comparison to the anterior sterna and in comparison to those of *Perdita,* and therefore provide little information on character polarity within *Perdita.* Species in the Anthemurgini and Panurgini, however, have state 6(0), and this character state is considered plesiomorphic for *Perdita.*

7(0) Male S8 elongate and slender except for apodemal arms and with anterior end at most slightly expanded laterally (Fig. 9a,c,d,e); **(1)** apex expanded laterally and obtuse, and anterior end of disc expanded laterally or forked (Figs. 133-139, 141-153; Timberlake, 1954) (Fig. 9b); **(2)** disc of S8 expanded laterally and deeply forked anteriorly (Figs. 154-172; Timberlake, 1954) (Fig. 9f-h).

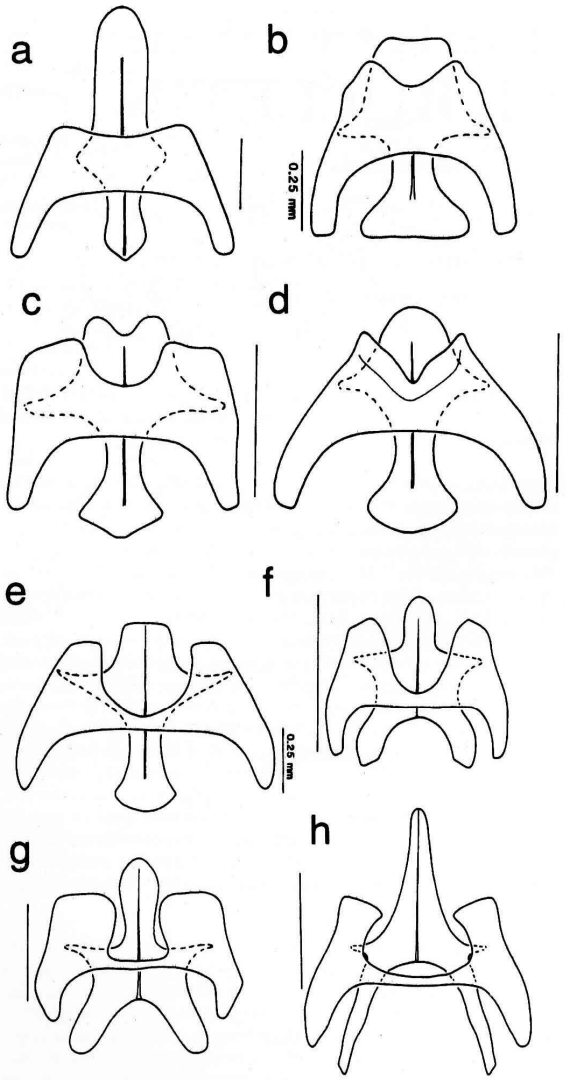

Fig. 9. Male S7 and S8, ventral views. **(a)** *Perdita (Macrotera) texana,* **(b)** *P. (Epimacrotera) euphorbiae,* **(c)** *P. (Perdita) sphaeralceae,* **(d)** *P. (Perdita) octomaculata,* **(e)** *P. (Perdita) zonalis,* **(f)** *P. (Hexaperdita) bishoppi,* **(g)** *P. (Cockerellia) coreopsidis,* **(h)** *P. (Procockerellia) albonotata.* Scale bar = 0.5 mm, except where indicated.

The male S8 can be divided into a region anterior to the apodemes (disc) and a region posterior to the apodemes (apex), which is usually exposed at the apex of the male metasoma. Because the near outgroups of *Perdita* (Calliopsini and Melitturgini) have the male S8 unlike those seen in *Perdita,* I used the Panurgini and Andreninae to polarize this character.

8(0) Antecosta of female S6 unmodified (Fig. 10c,d); **(1)** antecosta

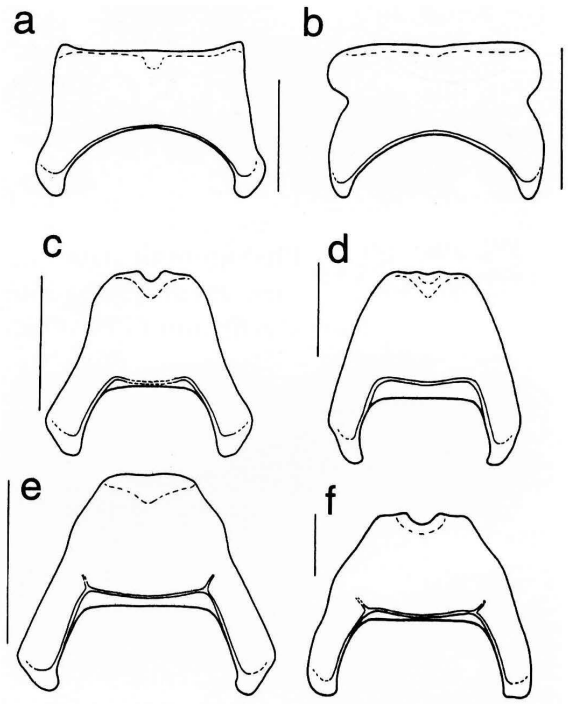

Fig. 10. Female S5 and S6. S5: **(a)** *P. (Macrotera) texana,* **(b)** *P. hurdi* (Scale bar = 1.0 mm). S6: **(c)** *Perdita (Alloperdita) mitchelli,* **(d)** *P. (Xerophasma) bequaertiana,* **(e)** *P. (Hexaperdita) bishoppi,* **(f),** *P. (Callomacrotera) maritima* (Scale bar = 0.5 mm).

of female S6 with faint, sclerotized ridge on internal surface extending posteriad from bend of antecosta (Fig. 10e,f).

Character state 8(1) can only be seen in disarticulated sixth sterna under transmitted light. The paired ridges are visible as faint lines extending posterolaterally from the angles on the antecosta at the junction of the apodemal arm and the disc of the sternum. This faint ridge is absent in all outgroups studied.

9(0) Lateral margin of female S5 straight (Fig. 10a); **(1)** lateral margin of S5 with small emargination (Fig. 10b).

The emargination is lacking in all outgroups studied and in some *Perdita.* Therefore, 9(0) is considered plesiomorphic for *Perdita.*

10(0) Outer groove of mandible as in most bees, a narrow groove apically but basally broadening to form the outer interspace (Fig. 11a) (terminology based on Michener & Fraser, 1978); **(1)** outer groove of mandible remaining discrete basally and extending diagonally across mandible to acetabulum, forming discrete outer mandibular sulcus in both sexes (Fig. 11b).

The discrete outer mandibular sulcus is absent in all outgroups studied. This character is apparently related to the dispersal of mandibular gland product because the mandibular gland opens at the base of this sulcus, near the mandibular acetabulum.

11(0) Lateral surfaces of male pronotum unmodified (Figs. 12a, 13a); **(1)** internal lateral surface of male pronotum with paired

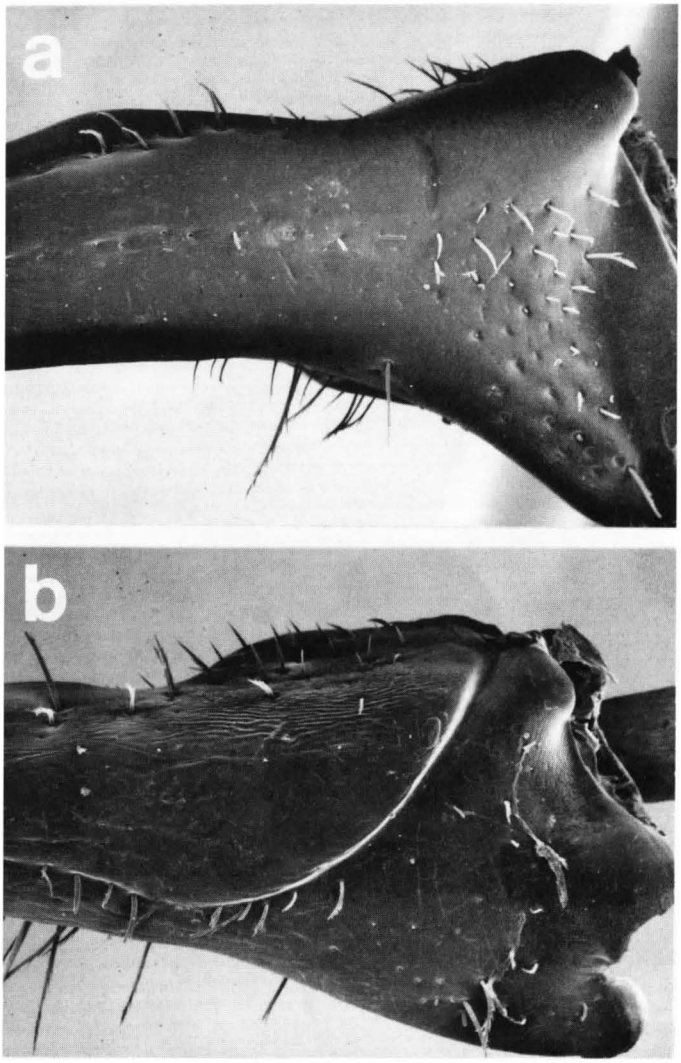

Fig. 11. Mandibles, lateral view [SEM]: **(a)** *P. octomaculata* (male) [showing lack of sulcus], **(b)** *P. texana* (male) [showing sulcus present].

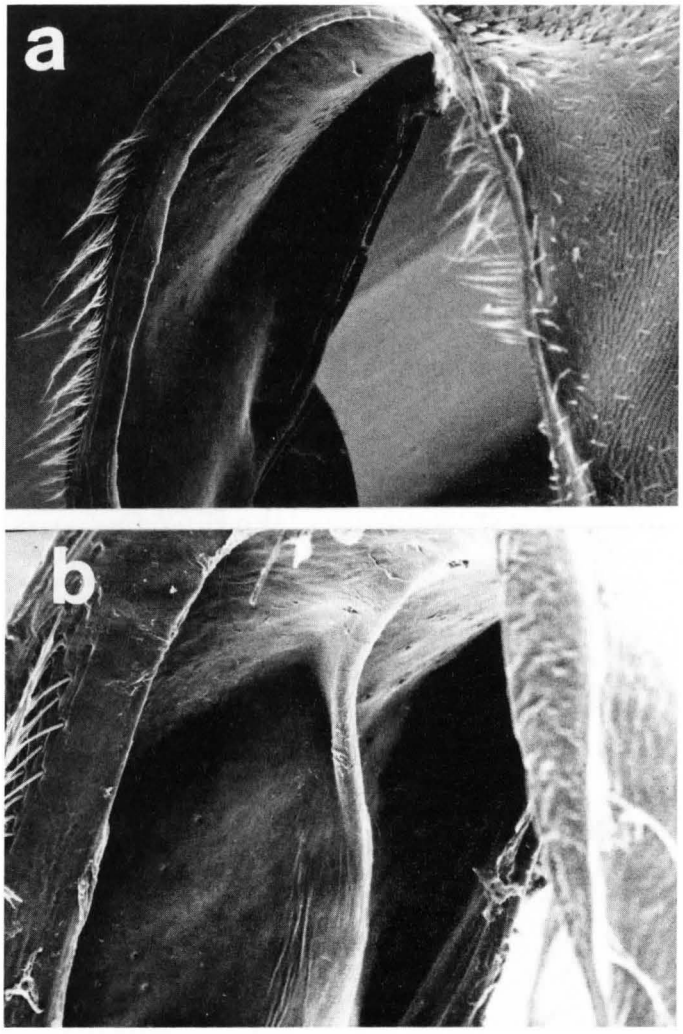

Fig. 12. Internal surfaces of male pronota [SEM] **(a)** *P. (Macrotera) texana* [pronotal carina absent], **(b)** *P. (Pygoperdita) interrupta* [pronotal carina present].

dorso-lateral carinae (Fig. 12b); **(2)** lateral surface of male pronotum with deep groove visible externally (carina may be continuous dorsally with groove) (Figs. 13b,c).

Like the corresponding female pronotal character (character 21), this character is best seen in cleared specimens. The character states are similar to those of character 21, but because the taxonomic distribution of the two characters differs they are not redundant. For example, although the presence of a deep groove in female pronota is found in only one subgenus (*Callomacrotera*), deeply grooved male pronota are found in at least four subgenera. All outgroups studied had 11(0).

12(0) Scopal hairs arising from flattened outer surface of tibia simple; **(1)** branched; **(2)** finely crinkled and unbranched.

In many species the hairs on the outer edges of the tibia are minutely branched but this character relates only to the setae on the flattened central portion. All outgroups examined had simple scopal hairs. Finely crinkled scopal hairs occur in some species within *Pterosarus* and *Pseudopanurgus,* and appear in these genera, as in *Perdita,* to be associated with carrying pollen of Asteraceae (J. Neff, pers. comm.).

13(0) Male hind basitibial plate present and well defined; **(1)** weak (rim, though complete, weakly distinguished from surrounding area); **(2)** absent (rim delineating plate incomplete).

All outgroups possess well-developed basitibial plates.

14(0) Female hind basitibial plate present and well defined; **(1)** absent.

15(0) Male tarsal claw pattern 2-2-2; **(1)** 2-2-1.

A "2" indicates a bifid claw and "1" indicates a simple claw. All outgroups have bifid tarsal claws, both in males and females (Character 16).

16(0) Female tarsal claw pattern 2-2-2; **(1)** 2-1-1; **(2)** 1-1-1.

17(0) Upper margin of male mandible lacking medial dilation; **(1)** upper margin with single acute projection originating at base (as

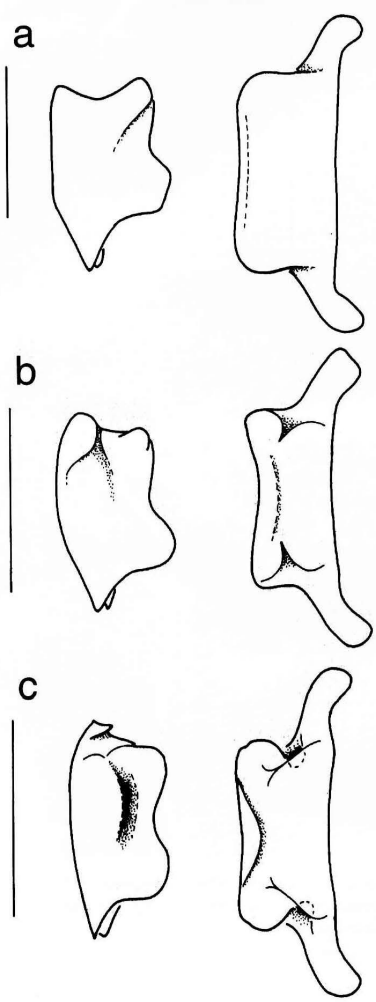

Fig. 13. Male pronota, lateral and dorsal views: **(a)** *P. (Macrotera) texana,* **(b)** *P. (Procockerellia) albonotata,* **(c)** *P. (Cockerellia) coreopsidis.* Anterior is to the left. Scale bar = 1.0 mm.

in *Callomacrotera*); **(2)** upper surface with paired acute projections arising at about midpoint along length (as in *P. turgiceps*).

18(0) Upper margin of female mandible lacking medial dilation; **(1)** upper margin dilated obtusely; **(2)** upper margin dilated acutely.

19(0) Female mandible gradually curving to apex; **(1)** female mandible abruptly angled beyond middle (angle > 45 degrees).

20(0) Apical margin of male T7 lacking ventral processes; **(1)** apical margin with median, longitudinal lamellate keel projecting ventrally or with two submedial, longitudinal lamellae projecting ventrally.

In most species of *Perdita,* and all outgroups studied, the male T7 differs from the previous terga in that the lateral edges are wrapped more ventrally, giving it a more tubular shape. There is a very weakly defined pygidial plate in some species, and there are usually stout, finely branched setae apically. In constrast, species in the subgenus *Pygoperdita* possess conspicuous single or paired ventrally-directed lamellae along the distal margin. Timberlake (1956:275) distinguished two groups within the subgenus *Pygoperdita* (Californica and Interrupta groups) based on this character, but the distinction between the two groups is weak. Based on outgroup comparison, 20(0) is plesiomorphic for *Perdita.* (See Timberlake, 1956:337-367 for illustrations of male T7 in *Pygoperdita.*)

21(0) Female pronotum lacking internal dorso-lateral carinae and grooves; **(1)** acute, lamellate internal dorso-lateral carinae present; **(2)** deep, dorso-lateral impression present.

In cleared pronota of *P. laticauda* one can see distinct internal carinae continuous dorsally with the dorsal internal carina. The lateral carinae end at about 1/4 to 1/3 the height of the pronotum in lateral view (21[1]). In some species (*P. maritima*) the internal carina is lacking, but at roughly the same position one sees a deep inpocketing of the cuticle to form an interior projection (21[2]). The similarity in the positions of the deep impression and of the lateral carina lead me to believe they are homologous. Finally, in other species there is no indication of a carina or deep impression (e.g., *P. texana;* 21[0]). At first glance *P. turgiceps* apparently lacks the internal carina; however, on close inspection one can see a minute carina. All outgroups studied possess 21(0).

22(0) Antero-dorsal rim of male pronotum unmodified (Fig. 13a); **(1)** antero-dorsal rim of male pronotum with small transverse projection or collar (Fig. 13b,c).

In lateral view, the male pronotum of some species (e.g., *P. mitchelli, P. maritima, P. zonalis*) has a prominent dorsal projection or bump at the leading edge of the pronotum (just behind the head). This projection is formed as a result of a deep transverse sulcus passing very near the anterior rim of the pronotum. When the transverse sulcus passes across the pronotum roughly at the midpoint of the pronotum, no prominent projection is formed anterior to the sulcus. The trait is especially pronounced in males, but a similar character is found in female pronota. All outgroups studied lack the projection.

23(0) Antero-medial angle of the prosternal apophysis in females prominent, acute and located more dorsally; **(1)** inconspicuous, obtuse and located more ventrally.

In lateral view of the female prosternum, one sees two sets of paired processes projecting anteriorly from the dorsal, anterior corner of the sternal apophysis. The postero-dorsal angle of each propleuron articulates with the prosternum at a broad, depressed area, set off from the rest of the prosternal apophysis by a low carina, between these two processes. Michener (1944) called these processes the antero-medial angle of the apophyseal arm (the more ventral process) and the antero-dorsal angle of the apophyseal arm. In most species of *Perdita* (e.g., *P. lacteipennis* and *P. halictoides*), the antero-medial angle is prominent, acutely pointed and located close to the antero-dorsal angle. However, in the subgenus *Pseudomacrotera* the antero-medial angle is much less prominent, obtuse and is located more ventrally, as in some outgroups (e.g., *Acamptopoeum prinii* and *Meliturga clavicornis*). Both states of this character are present in the outgroups so it is impossible to polarize this character.

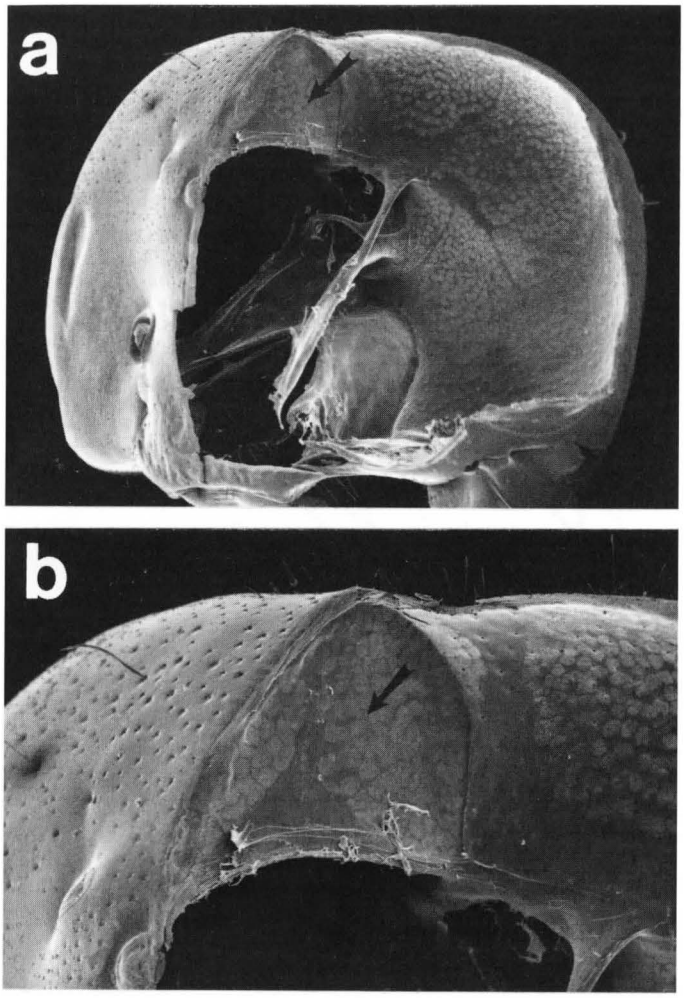

Fig. 14. Internal anatomy of male head capsule in *P. texana* [SEM]: **(a)** oblique view of head capsule showing median cephalic lamella (indicated by arrow), **(b)** close-up of median cephalic lamella (indicated by arrow), showing sites of muscle attachment.

24(0) Median internal cephalic lamella absent; **(1)** lamella present along midline of head capsule (Figs. 14a, b).

A median internal cephalic lamella, extending from the anterior ocellus nearly to the occipital foramen, is present in both males and females of all species of *Perdita* studied, and is lacking in all outgroups. The presence of this lamella is considered a synapomorphy of *Perdita*. The median cephalic lamella serves as a site of attachment for the mandibular adductors.

25(0) In females, tentorial bridge separated from roof of proboscidial fossa; **(1)** tentorial bridge broadly fused to roof of proboscidial fossa.

In some species (e.g., *P. texana, P. lacteipennis* and *P. californica*) the bridge of the tentorium lies distinctly above the roof of the proboscidial fossa and the two are connected by a thin vertical lamella of cuticle. In ventral view, the roof of the proboscidial fossa, has a dark line running along its midline which corresponds to the internal vertical lamella. In other species (e.g., *P. zonalis, P. bequaertiana*) the tentorial bridge is fused broadly to the inner surface of the roof of the proboscidial fossa and no lamella is visible in lateral view. All outgroups studied, except *Acamptopoeum prinii,* have the tentorial bridge dorsal to the proboscidial roof, with the two separated by a thin lamella (25[0]).

26(0) Occipital region in male unmodified; **(1)** occipital region with paired arcuate carinae on either side of occipital foramen (preoccipital carinae) (Fig. 5c).

In dorsal view of the occipital region of the head one sees two sharp carinae on either side of the occipital foramen in the males of some species (e.g., *P. (Hexaperdita) bishoppi*). Most species of *Perdita* and all outgroups studied lack such carinae.

27(0) Second submarginal cell lacking (two submarginal cells; Fig. 6c, d); **(1)** small, triangular, intercalary second submarginal cell present (three submarginal cells; Fig. 6e).

In five species of the subgenus *Alloperdita* and in all species of *Xerophasma,* a small second submarginal cell is present. In all other species of *Perdita* there are only two submarginal cells. Based on their shape and position, it is likely that the two submarginal cells present in most species of *Perdita* are homologous to the first and third submarginal cells in those species possessing three submarginal cells. Because all outgroups, except *Melitturga clavicornis,* lack the second submarginal cell, it is most likely a derived state within *Perdita.* Timberlake (1956:271-273), however, considered the possession of three submarginal cells primitive for *Perdita.* For bees as a whole three submarginal cells is certainly plesiomorphic, but the second submarginal cell of many bees and the small triangular cell seen in a few *Perdita* species are probably not homologous.

28(0) In females, graduli present, in some form, on S2-S5 (Fig. 15a); **(1)** graduli entirely lacking on S2-S5 (Fig. 15b).

All species of *Perdita* studied lack graduli on S2-S5. Because all panurgine outgroups studied have either medial, paired lateral, or complete (continuous medial and lateral portions) graduli, the lack of sternal graduli is considered a synapomorphy of *Perdita.*

29(0) Broad pale membranous line on antero-lateral corner of female T5 absent or present but not reaching the spiracle (Fig. 16a); **(1)** slender pale membranous line reaching, or nearly reaching, spiracle (Fig. 16b, c).

In all species of *Perdita* the female T5 in lateral view has narrow transparent membranous lines extending from the antero-lateral corners, just beneath the apodemes, posteriorly to the spiracles. Homologous pale regions are present in other terga but are most easily seen in T5. These pale regions are membranous and allow the lateral portions of the terga to move with respect to the dorsal part, possibly allowing dorso-ventral expansion and contraction of the metasoma. Since these membranous areas are small and do not reach the spiracle in any of the outgroup taxa studied, their presence is considered a synapomorphy of *Perdita.*

30(0) Pale membranous line on female T1 narrow and passing beneath spiracle; **(1)** line broad, enclosing spiracle; **(2)** line absent or present but not reaching spiracle.

In all outgroup taxa studied there are paired transparent membranous lines extending backwards from the antero-lateral corners of T1, passing beneath the spiracle and ending somewhat posterior of each spiracle. This state has been found in only one species of *Perdita, P. turgiceps,* and is considered primitive for *Perdita.*

31(0) Pale membranous line on antero-lateral corners of male T6

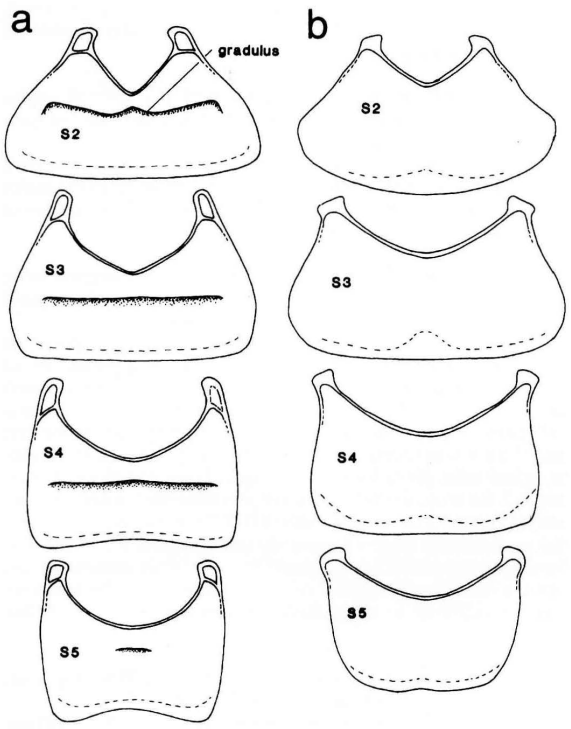

Fig. 15. Female sterna 2-5. **(a)** *Pterosarus albitarsus,* **(b)** *Perdita (Callomacrotera) maritima.*

absent (Fig. 16d, e); **(1)** pale membranous line reaching, or nearly reaching, spiracle (Fig. 16f).

Because the outgroup taxa studied lack the membranous line, 31(0) is considered primitive.

32(0) Posterior margin of female S1 straight or very slightly emarginate medially (Fig. 17a) ; **(1)** margin deeply but gradually and obtusely emarginate (Fig. 17b); **(2)** margin deeply and acutely emarginate medially (Fig. 17c).

All outgroups lack a pronounced medial emargination and therefore 32(0) is considered primitive.

PHYLOGENETIC ANALYSIS

The data matrix was analyzed two ways. In the initial analysis, all of Timberlake's subgenera were included except for the monotypic *Xeromacrotera* (*P. cephalotes*), which is only known from the male. The placement of *P. cephalotes is* discussed in a second analysis, presented below. In the analyses, all characters were treated as unordered (non-additive) except for multistate characters 2, 6, 13 and 32, for which the character states could be logically connected by a linear sequence (e.g., character 2: maxillary palpi 6-segmented -> 5-segmented -> 3-segmented).

In the first analysis the m*, bb* options of Hennig86 resulted in 12 equally parsimonious trees of length 84 and con-

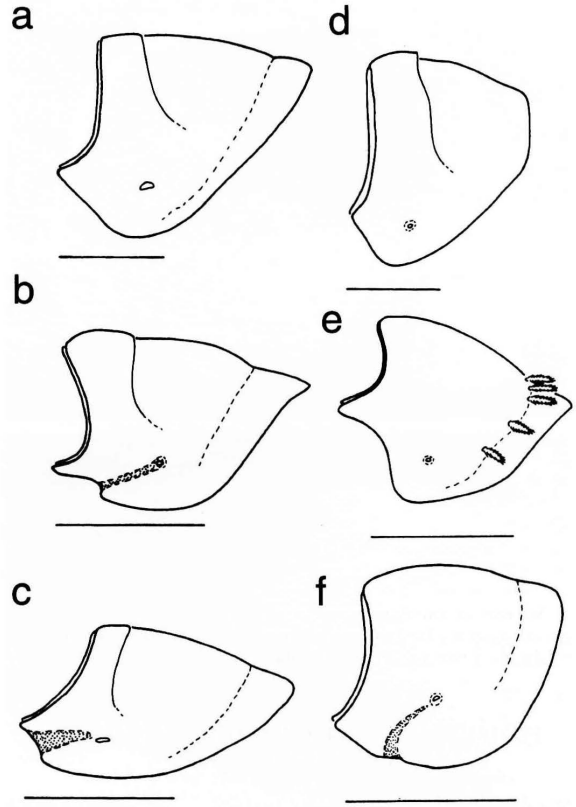

Fig. 16. Lateral views of female T5 and male T6. Female T5: **(a)** *Pterosarus albitarsus,* **(b)** *Perdita (Cockerellula) anthracina,* **(c)** *P. (Cockerellia) albipennis.* Male T6: **(d)** *Pterosarus albitarsus,* **(e)** *Perdita latior,* **(f)** *P. (Glossoperdita) pelargoides.* Scale bars = 0.5 mm.

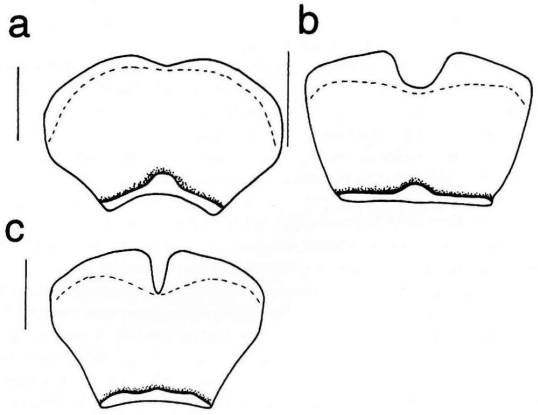

Fig. 17. Female S1. **(a)** *P. (Cockerellula) laticauda,* **(b)** *P. (Epimacrotera) euphorbiae,* **(c)** *P. (Perdita) zonalis.* Scale bar = 0.25 mm.

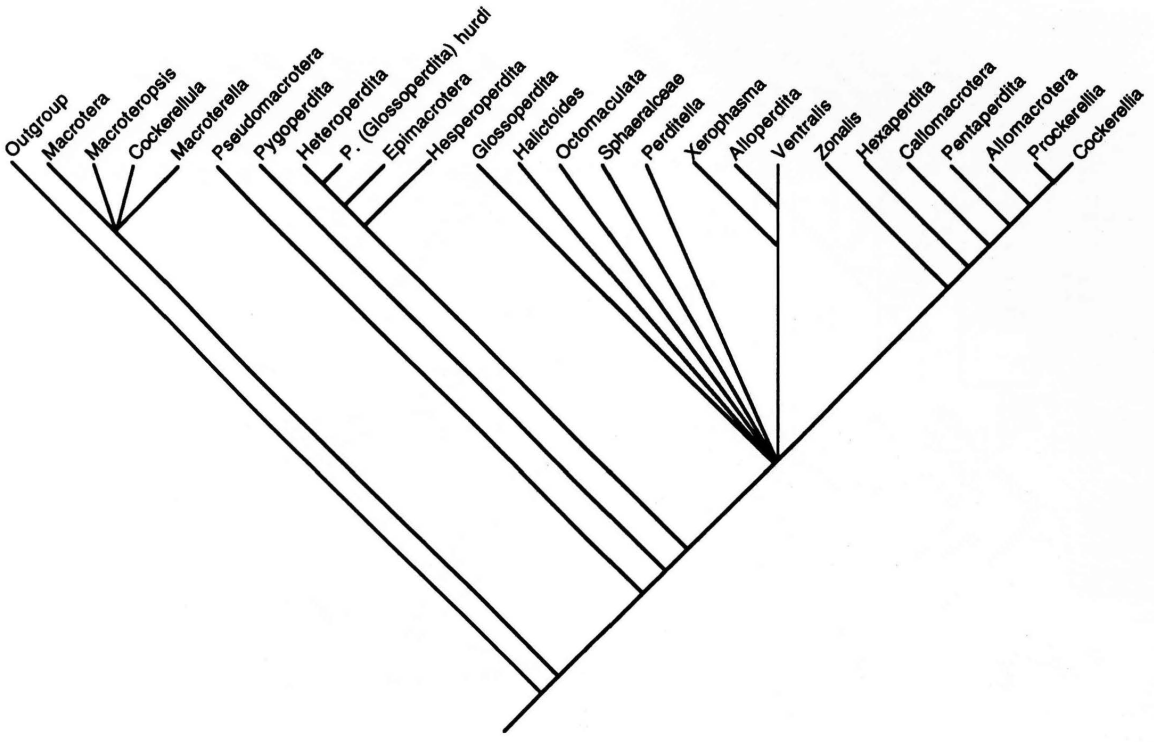

Fig. 18. Consensus tree of 6 equally parsimonious trees for subgeneric analysis. The subgenus *Perdita* includes the Halictoides, Octomaculata, Sphaeralceae, Ventralis and Zonalis groups.

sistency index of 54 for the 32 characters and 28 taxa (*Xeromacrotera* excluded). Among these 12 trees there were 6 distinct topologies. Figure 18 shows the consensus tree, Fig. 19 a-f show the 6 equally parsimonious resolutions of the single polytomy, and Fig. 20 shows the characters mapped on the preferred tree, as discussed below.

Monophyly of *Perdita*. The monophyly of the genus is supported by three unique and un-reversed characters (Fig. 20): the presence of an internal median cephalic lamella, not known to occur in any other bees (24[1]; Fig. 14); the lack of sternal graduli in females (28[1]); and (3) the presence of a pale membranous line extending to the spiracle on the lateral edges of the female S6 (29[1]).

Based on Luisa Ruz's phylogeny of the Panurginae (Ruz, 1991), the monophyly of *Perdita* is supported by three additional unique and unreversed characters: (1) the male sixth sternum is three or more times broader than long (90[1]), whereas in the remainder of the panurgines S6 is at most only slightly broader than long (Fig. 21a), (2) the marginal cell is shorter than the distance from its apex to the wing tip (46[2]) and (3) the first valvifer is elongate rather than triangular (129[1]), as it is in the other panurgines. The first of these characters is variable within *Perdita*. While some species show a very slender male S6 (Fig. 21a,c,d), others (e.g., *P. echinocacti*, Fig. 21b) have a male S6 which is only twice as broad as long. Therefore, this character cannot be considered a synapomorphy of the genus. The marginal cell character holds for all species I studied. I did not investigate the third character so I cannot reject it as a synapomorphy of *Perdita*.

Relationships among the *Perdita* Subgenera. The monophyly of the subgenera *Macrotera, Macroteropsis, Macroterella,* and *Cockerellula* (herein called the *Macrotera* group) is supported by two characters (Fig. 20). Character 10(1), the presence of a discrete sulcus on the outer surface of the mandibles of both males and females, is a unique and unreversed synapomorphy of these four subgenera. Character 30(1) also supports the *Macrotera* group but arose convergently in the Sphaeralceae group of *Perdita* sensu stricto as well. The *Macrotera* group appears to form the sister group to a monophyletic group including all the remaining subgenera (*Pseudomacrotera,* plus all the taxa to its right; Fig. 20). The species-level phylogenetic relationships of the *Macrotera* group will be presented below.

Interestingly, the placement of the *Macrotera* group at the base of the tree is consistent with the existence of ple-

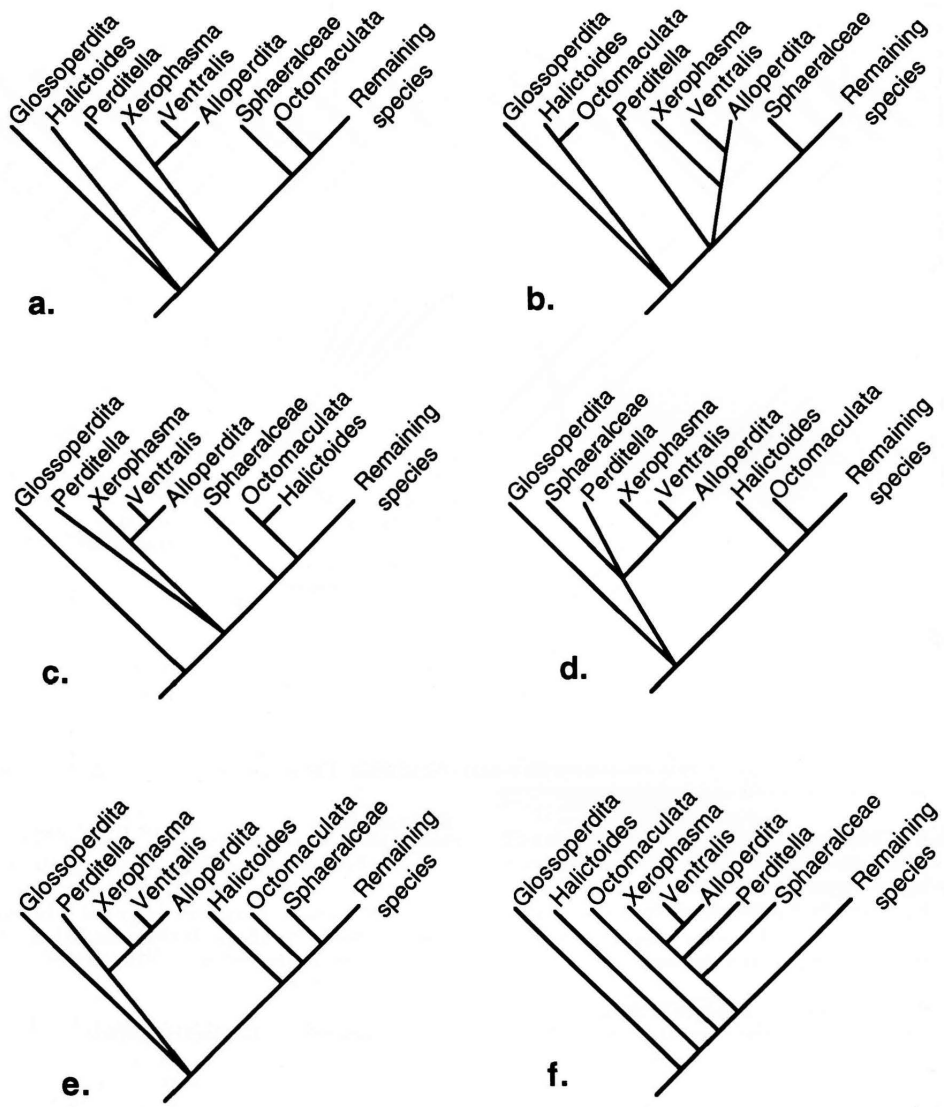

Fig. 19 a-f. Six equally parsimonious resolutions of the consensus tree shown in Fig. 18.

siomorphic behavioral characters in the species which have been studied so far. The placement of larval fecal material on the rear wall of the cell in *P.* (*Macrotera*) *texana* (Neff & Danforth, 1991), *P.* (*Macrotera*) *pipiyolin* (Rozen & Michener, pers. comm.), *P.* (*Macroteropsis*) *portalis* (Danforth, 1991a) and *P.* (*Macroterella*) *mellea* (Rozen, pers. comm.) is similar to the placement of fecal material in the non-*Perdita* Panurginae (Rozen, 1967). However, in species of the more derived *Perdita* that have been studied (e.g., the subgenera *Perdita* and *Cockerellia*), feces are placed on the venter of the larva (Rozen, 1967; Danforth, 1989b). Similarly, the presence of a hydrophobic lining on the inner surface of the cell is shared by *P. texana, P. bullocki, P.* (*Macroteropsis*) *latior* (Danforth, pers. obs.), *P. portalis* and *P. mellea,* as well as the non-*Perdita* panurgines (Rozen, 1989).

The monophyly of the group *Pseudomacrotera* plus all the groups to its right, is supported by three characters: the presence of a c-shaped pre-episternal groove extending from the forewing base to the scrobe (5[1]), the presence of internal dorso-lateral carinae in the female pronotum (21[1])

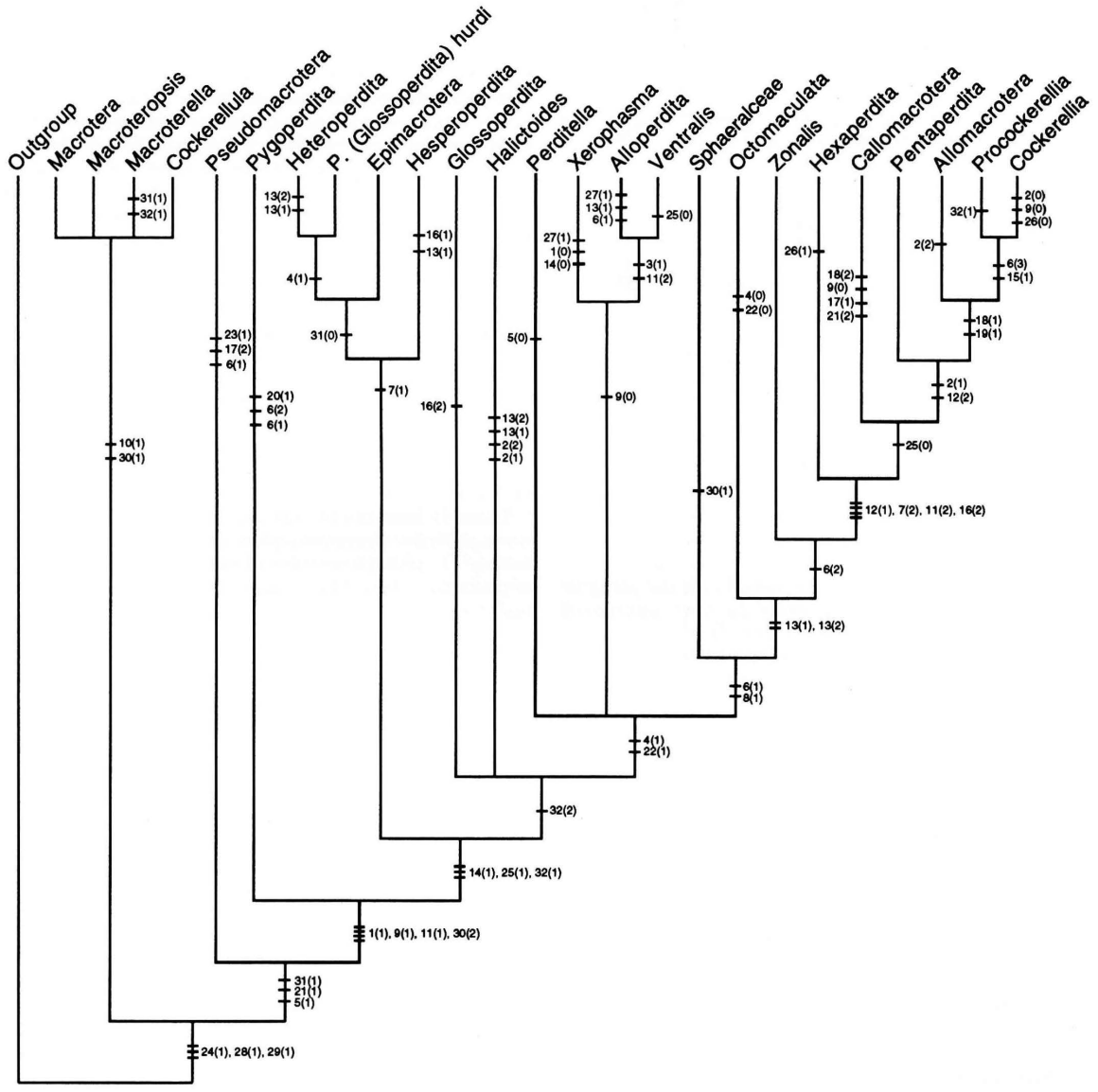

Fig. 20. Preferred tree of the six equally parsimonious resolutions of the consensus tree (Fig. 18); characters mapped onto tree.

and the presence of a pale, membranous line which reaches the spiracle on the male T6 (31[1]), although this last character is reversed in the group *Heteroperdita* + *P. hurdi* + *Epimacrotera*.

The group including the subgenus *Pygoperdita* and the subgenera to its right in Fig. 20 is also well supported by unique features. This group I refer to below as the "higher *Perdita*." Character 1(1), the possession of slender, acutely pointed female paraglossae, is present in all of the higher *Perdita*, except the subgenus *Xerophasma*. Although the outgroups were variable for this character, the derived state for *Perdita* appears to be 1(1). It is likely that the broad, brushlike paraglossae (1[0]), seen in the subgenera belonging to the *Macrotera* group, are used in the application of the hydrophobic coating to the cell wall. I have seen female *P. portalis* construct cells in observation nests and in the final

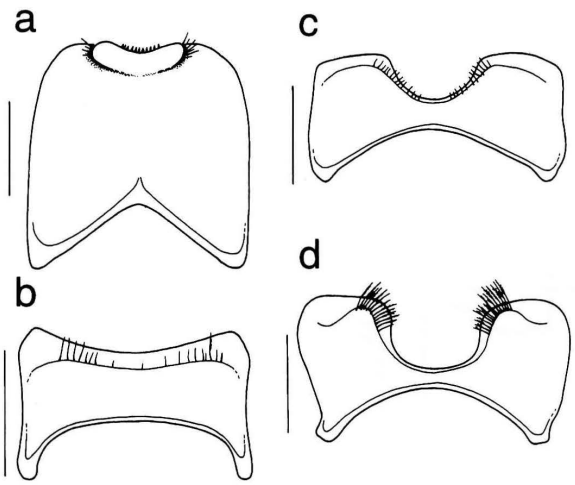

Fig. 21. Male S6, showing depth of emargination along posterior margin: **(a)** *Panurginus occidentalis,* **(b)** *Perdita (Macroteropsis) echinocacti,* **(c)** *P. (Perdita) zonalis,* **(d)** *P. (Procockerellia) albonotata.* Scale bar = 0.5 mm.

stages the walls of the cell were brushed with the paraglossae, apparently in the application of the hydrophobic cell coating (Danforth, 1991a)

Other characters which support the monophyly of the "higher Perdita" are 30(2), 9(1), the small emarginations on the lateral margins of the female S5, and 11(1), the carinae on the internal surface of the male pronotum, although the latter two characters had low consistency (ci = 25 and 50, respectively).

The subgenus *Pygoperdita* is clearly monophyletic based on the present analysis. In all species the seventh tergum in the male (character 20) has either paired, ventrally-directed lamellate lobes (in the Californica group) or a single, ventrally-directed bifid lobe (in the Interrupta group). Because these two states intergrade (making placement of some species difficult for Timberlake [1954]), and because there are no similar structures in other members of *Perdita,* these two conditions are considered homologous and synapomorphic for the subgenus *Pygoperdita.* The monophyly of this subgenus is further supported by the deeply divided male S7 (6[2]). Although a similarly divided S7 occurs elsewhere in the tree (uniting the Zonalis group and the subgenera to its right in Fig. 20), numerous characters support the hypothesis that these states have arisen independently.

The subgenera *Hesperoperdita, Epimacrotera, Heteroperdita* and one species previously placed in the subgenus *Glossoperdita, P. hurdi,* form a monophyletic group united by the uniquely shaped male S8 (7[1]). It is clear from this analysis that *P. hurdi* does not belong with members of *Glossoperdita.* The shape of the male S8 (7[1]) and the lack of the male second medial cell (4[1]) place *P. hurdi* as the sister group to *Heteroperdita.* Although this group of three subgenera plus *P. hurdi* appears to be monophyletic, the subgenera included in it are not all necessarily monophyletic.

According to Timberlake (1954:377), *Epimacrotera* is "similar and closely allied to *Glossoperdita.*" Timberlake later stated that "it is now becoming evident that *Glossoperdita* and *Epimacrotera* may intergrade more or less completely" (1960:129). I have found no synapomorphies for *Epimacrotera.* A possible synapomorphy mentioned by Timberlake (1954:377) is the presence of upturned hairs along the lower margin of the scopa, but I was unable to see such hairs. Females of *P. diversa* have a very unusual hind basitibial protuberance, which does not appear to be homologous to the basitibial plate in other species. This character may prove useful for resolving the relationships within this subgenus.

Hesperoperdita is apparently a monophyletic subgenus. *P. ruficauda* possesses an unusual tarsal claw pattern in the female, with a very small basal tooth on the mid and hind tarsal claws, making them appear simple, and a larger basal tooth on the fore-tarsal claws, giving them a bifid appearance (16[1]). According to the phylogenetic analysis, the weakly defined basitibial plate in *Hesperoperdita* (13[1]) is also a synapomorphy of the subgenus, but this character had rather low consistency (ci=20).

There is little doubt that the subgenus *Heteroperdita* is monophyletic. Synapomorphies of the group are the following: (1) postero-ventrally directed setae on either side of proboscidial fossa in females, (2) yellow maculation on male metanotum and/or propodeum, and (3) white, closely appressed hairs over the head and mesosoma.

The greatest source of ambiguity in this analysis involves the polytomy in Fig. 18 that includes the Halictoides, Octomaculata and Sphaeralceae groups, *Perditella, Glossoperdita,* the monophyletic group of *Xerophasma* + (*Alloperdita* + Ventralis group) and the monophyletic group including the Zonalis group and the subgenera to its right. The monophyly of this entire group is supported by the acutely emarginate posterior edge of the female S1 (32[2]; Fig. 17c). Figures 19a-f show the six equally parsimonious resolutions of the polytomy. I prefer the tree shown in Fig. 19a as the most likely resolution because the characters whose homologies I am most confident of (6 and 8) have the highest consistency indices in this resolution (ci = 42 and 100, respectively). Intuitively, I believe that the Sphaeralceae and Octomaculata groups are closely related to the monophyletic group of Zonalis and the groups to its left. The fact that there are several resolutions of this polytomy indicates real uncertainty about the relationships among these groups, and a need for more characters at these nodes.

Based on the characters included in this study, *Glossoperdita* is clearly polyphyletic, with at least one species, *P. hurdi,* belonging elsewhere, as discussed above. Timberlake originally considered this group distinct because of the elongate glossae; many species visit flowers in the Polemoniaceae. As mentioned above, he later conceded (1960:129) that the distinction between *Glossoperdita* and *Epimacrotera,* based primarily on glossa length, was weak. *P. hurdi* differs from other members of *Glossoperdita* studied in lacking a second medial cell in the male, in lacking a pollex on the male mandible and in having a short galeal comb (*P.*[*G.*] *pelargoides* lacks

a galeal comb). *P. hurdi* is larger than other members of *Glossoperdita*. Synapomorphies of *Glossoperdita*, excluding *P. hurdi*, are a distinctive pattern of metasomal maculation in males (a central yellow bar and two lateral yellow spots along the posterior margin of each tergum) and a rectangular head longer than wide.

The Halictoides group of *Perdita* sensu stricto is united by the greatly reduced maxillary palpi (2[2]), and, in this analysis, by the reduced male basitibial plates (13[2]).

The subgenus *Xerophasma*, which contains two highly apomorphic, nocturnal species, is clearly monophyletic. Both species are very large, entirely pale and have enlarged compound eyes and ocelli (Fig. 5d).

Alloperdita is united by three characters; however, none provides very convincing evidence that this subgenus is monophyletic. Characters 6(1) and 13(1) have arisen elsewhere in the tree. Character 27(1), the presence of a small, triangular, intercalary submargical cell (Fig. 6e), may have arisen independently in *Alloperdita* and *Xerophasma* (Fig. 20) or, equally parsimoniously, may have arisen once in the common ancestor of *Xerophasma, Alloperdita* and the Ventralis group, and then reversed to the plesiomorphic state in the Ventralis group. This character is variable within some species and even in some individuals, with one wing showing three submarginal cells and the other just two. The elongate, stout antennae of males is the strongest synapomorphy of *Alloperdita*.

Alloperdita and the Ventralis group are united by two characters: 3(1), the presence of male genal projections and 11(2), deep, acute grooves in the lateral surfaces of the male pronota. The latter character is also found in the monophyletic group including *Hexaperdita* plus all the groups to its right.

The subgenus *Perditella* is apparently polyphyletic. At least two species (*P. larreae* and *P. cladothricis*) possess characters which are shared by members of the *Cockerellia* group: deep impressions in the lateral surfaces of the male pronotum and male occipital carinae. The characters used by Cockerell and Timberlake to recognize this group were small size, enlarged stigma, small, triangular second submarginal cell and shortened marginal cell (Timberlake, 1956:267). All the wing venational characters are highly correlated with body size and therefore may be poor indicators of phylogenetic relationship (Danforth, 1989a). For the purposes of this preliminary phylogenetic analysis, I used *P. minima* as a representative species.

The monophyletic group of the Zonalis group plus the 6 subgenera to its right in Fig. 20 is supported by the deeply emarginate male S7 (6[2]). The group of subgenera including *Hexaperdita, Callomacrotera, Pentaperdita, Allomacrotera, Procockerellia* and *Cockerellia* clearly form a monophyletic group which I will refer to below as the *Cockerellia* group. Characters supporting this group include male S7 morphology (7[2]), male pronotal morphology (11[2]), scopal hair structure (12[1]) and the female tarsal claw pattern (16[2]). The relationships among the members of the *Cockerellia* group are well supported; the characters in this portion of the tree have high consistency and in all previous analyses of these data, this group showed virtually the same pattern of relationships.

The hypothetical transformation series shown in Fig. 20 for character 2 deserves some explanation. According to the present analysis, reduction in the number of maxillary palpal segments is considered a synapomorphy of the group including *Pentaperdita, Allomacrotera, Procockerellia* and *Cockerellia*, with a reversal to the 6-segmented condition in *Cockerellia*. Although such a reversal seems unlikely, the alternative hypothesis, that reduced maxillary palpi is a synapomorphy of *Pentaperdita, Procockerellia* and *Allomacrotera*, is incongruent with characters 6(3) and 15(1), which unite *Procockerellia* and *Cockerellia*. Analysis of the data matrix with character 2 treated as unordered resulted in the same pattern of relationships.

While the *Cockerellia* group of subgenera is clearly a monophyletic group, the subgenera which make up this group are not necessarily themselves monophyletic. For example, no unique and unreversed characters were found to support the monophyly of the subgenus *Hexaperdita*. *Hexaperdita* is united by the possession of an occipital carina in males (26[1]; Fig. 5c), although this character has arisen in *Cockerellia* as well. A character of many, though not all, species of *Hexaperdita* is the possession of a carina at the posterior margin of the male mandible, near the base. This carina was not seen in members of any other subgenera or outgroups.

One species, *P. cara*, lacked both preoccipital carinae and deep grooves in the lateral surfaces of the male pronotum. *P. cara* is also very small in comparison to other species of *Hexaperdita*. Placement of *P. cara* remains unclear, but it most likely belongs elsewhere in the genus.

The subgenus *Callomacrotera*, containing only two described species, is clearly monophyletic. Synapomorphies include the acute basal tooth on the inner surface of the female mandible, the large, robust body form, and the depressions on the dorso-lateral corners of the female pronotum (21[2]). Both species also have a highly modified male clypeus. In *P. maritima* the male clypeus is densely clothed with erect setae. In *P. acapulcona* the male clypeus is depressed and with an apical fringe of long setae overhanging the labrum.

Timberlake referred to the reduced number of maxillary palpi and the bifid metatarsal claws as features uniting *Pentaperdita* (Timberlake, 1954:404). In the present analysis the tarsal claw character is considered plesiomorphic (15[0]), and reduction in the number of maxillary palpal segments is considered a synapomorphy of the group including *Pentaperdita, Allomacrotera, Procockerellia* and *Cockerellia*, with a reversal to the 6-segmented condition in *Cockerellia*. I was unable to find any convincing synapomorphies of *Pentaperdita*.

Although the members of *Cockerellia* are a seemingly homogeneous group, there were few obvious synapomorphies uniting them. In Fig. 20, although three characters appear as synapomorphies of *Cockerellia*, 2(0), 9(0) and 26(1), two are reversals to the plesiomorphic state and one occurs elsewhere on the tree (26[1] has arisen independently in

Hexaperdita as well). One potential synapomorphy of *Cockerellia,* not included in the analysis, can be seen in the shape of the male genital capsule in lateral view. In all species studied (excluding *P. baileyae*) there are paired, acutely pointed projections on the ventro-medial surfaces of the apices of the gonocoxites (see Figs. 75-90 in Timberlake, 1954).

Because only one species of *Procockerellia* was studied, it is impossible to comment on the monophyly of the group. However, a possible synapomorphy is the deeply divided male sixth sternum with paired apical protuberances clothed in elongate setae (Fig. 21d). *Procockerellia* and *Cockerellia* are united by the shape of the male S7 (6[3]) and the unique male tarsal claw pattern (15[1]).

It is clear from this analysis that the subgenus *Perdita,* represented in Figs. 18-20 by the Halictoides, Ventralis, Sphaeralceae, Octomaculata and Zonalis groups, is not monophyletic. Although some of the species groups within *Perdita* s. str. (e.g., Halictoides and Octomaculata groups) are likely to be monophyletic, the subgenus as a whole is made paraphyletic by the *Cockerellia* group.

Placement of the Subgenus *Xeromacrotera*. The placement of the subgenus *Xeromacrotera* is problematic because this subgenus is known only from the males of *P. cephalotes.* Therefore, many of the characters are unknown for this subgenus, and, in the initial analysis, it was left out. Based on overall appearance and size, *P. cephalotes* appears closely related to *Procockerellia* and/or *Allomacrotera.* However, *P. cephalotes* lacks the derived tarsal claw pattern which unites *Cockerellia* and *Procockerellia* (15[1]) and lacks the reduced number of maxillary palpal segments shown by *Pentaperdita, Procockerellia* (5-segmented) and *Allomacrotera* (3-segmented). Timberlake considered this species to be closely related to *Pentaperdita* because "the maxillary palpi tend to be five jointed" (1954:412). The one male whose mouthparts I dissected clearly has 6-segmented maxillary palpi.

In order to make a preliminary hypothesis of the relationships between *Xeromacrotera* and the other *Perdita* subgenera, I included *Xeromacrotera* in a second analysis of the subgeneric data matrix (Table 2). In this analysis characters were treated as in the first analysis. Using the m*, bb* options of Hennig86 I found 60 trees of length 79, and a consistency index of 56, as in the original analysis. The same resolutions of the polytomy involving *Glossoperdita,* the Halictoides group, *Perditella,* etc. were found, and the trees produced by the two analyses are identical except for the relationships within the *Cockerellia* group. There were 5 equally parsimonious placements of *Xeromacrotera* (Fig. 22a-e). The consensus tree of these five equally parsimonious resolutions is shown in Fig. 22f.

Based on the analysis, *Xeromacrotera* clearly belongs to the monophyletic *Cockerellia* group, which is united by male characters 7(2) and 11(2) and female characters 12(1) and 16(2). The placement of *Xeromacrotera* at the base of this group is essentially determined by three characters. Characters 7(2) and 11(2) place *Xeromacrotera* within the monophyletic *Cockerellia* group and the possession of six-segmented maxillary palpi requires that this species be allied to the basal members of the clade (*Callomacrotera* and *Hexaperdita*), which retain the plesiomorphic, six-segmented condition.

The variable placement of *Xeromacrotera* within the *Cockerellia* group is due more to lack of data than to conflicting characters. This is indicated by the fact that of the seven characters responsible for altering the topology of the trees shown in Fig. 22 (characters 9, 12, 16, 18, 21, 25) all are unknown for *P. cephalotes.*

PHYLOGENETIC RELATIONSHIPS AMONG SPECIES IN THE *MACROTERA* GROUP OF SUBGENERA

Having established the monophyly and the position of the four subgenera *Macrotera, Macroteropsis, Cockerellula* and *Macroterella,* I present a phylogeny of the 31 species in these four subgenera. A revised classification is presented, based on this phylogeny, along with a key to species and diagnoses of species and subgenera.

Table 3 lists the species included in this study, based on Timberlake's classification, and a revised classification, based on results presented below.

DATA MATRIX

The data matrix for this analysis is shown in Table 4. The first three taxa are outgroups. "Panurginae" refers to the non-*Perdita* Panurginae used as outgroups in the subgeneric phylogeny. A second outgroup taxon, "*Perdita,*" represents the members of *Perdita* which belong to the "higher *Perdita*" discussed above. Finally, *P.* (*Pseudomacrotera*) *turgiceps* was included as an outgroup, because, although this species does not belong to the groups here treated, it is clearly near the base of the *Perdita* phylogeny, and is useful for character polarization.

The remaining 27 taxa listed in Table 4 are members of the ingroup. Although there are a total of 31 species in this group (see species diagnoses), 4 species are known only from female specimens, and hence could not be included in the phylogenetic analysis because of lack of data. It was nevertheless possible to place them within the classification based on female characters.

As in the subgeneric data matrix, plesiomorphic character states are all coded 0. For those characters which could not be polarized based on outgroup comparison, the ancestral character state was coded as unknown (? in the data matrix). *P. seminigra* is known only from the holotype male, so female characters are missing for this species.

CHARACTER DESCRIPTIONS

(0) Female paraglossae slender basally but broadening apically to form broad, brush-like apex; **(1)** paraglossae slender and acutely pointed to moderately broad and parallel-sided.

This character was used in the subgeneric analysis (character 1).

2(0) Outer groove of mandible as in most bees, a narrow groove apically but basally broadening to form the outer interspace; **(1)** outer groove of mandible remains discrete basally and extends di-

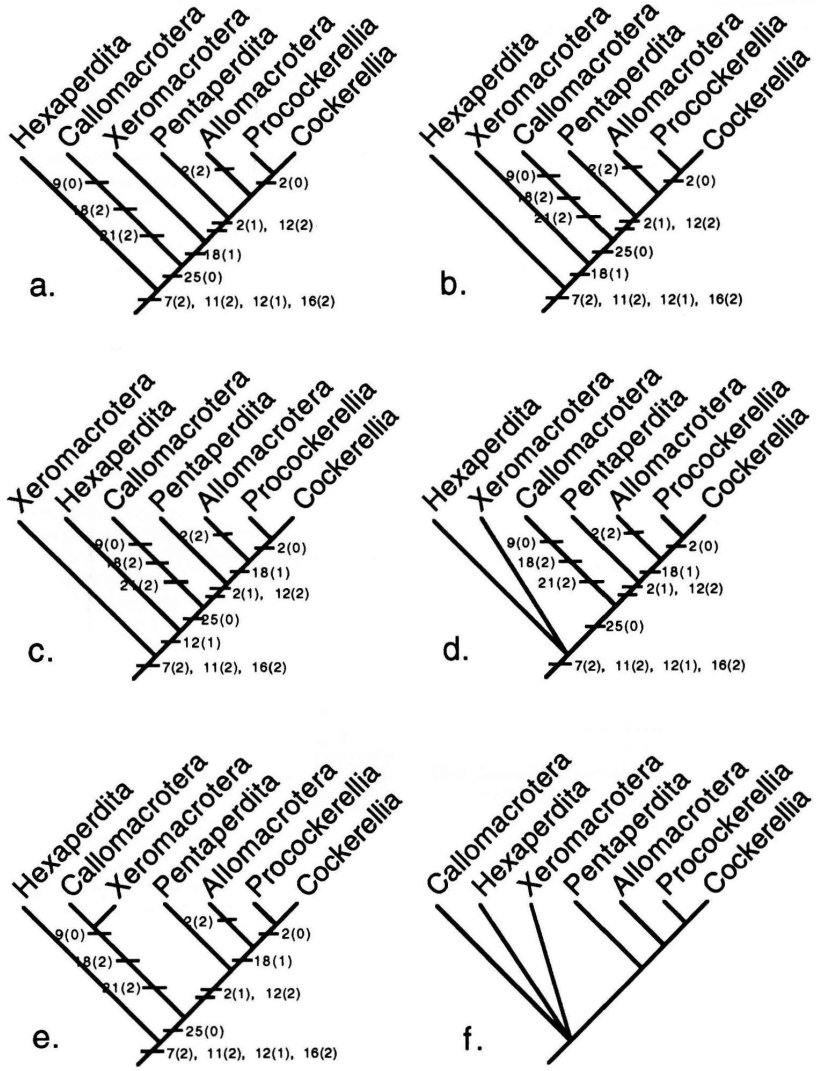

Fig. 22 a-f. Five equally parsimonious placements of the subgenus *Xeromacrotera* **(a-e)**; and the consensus tree of these five trees **(f)**.

agonally across mandible to acetabulum, forming discrete outer mandibular sulcus (present in both sexes).

This character was used in the subgeneric analysis (character 10).

3(0) Pre-episternal groove present and not extending to scrobe or absent; **(1)** Pre-episternal groove plus scrobal groove together forming c-shaped sulcus extending from upper edge of the mesepisternum (below the forewing articulation) to scrobe.

This character was used in the subgeneric analysis (character 5).

4(0) Maxillary palpus relatively long; distal segments (segments 3 to end) subequal to, or slightly shorter than, proximal segments and all segments distinct (Fig. 27); **(1)** Maxillary palpus relatively short due to greatly foreshortened distal segments (Fig. 36a,b).

All non-*Perdita* outgroups possess state 4(0). Within *Perdita* some groups (e.g. *Pentaperdita, Procockerellia* and the *Halictoides* group of *Perdita* sensu strictu) have reduced maxillary palpi, but the distalmost segments are not conspicuously foreshortened relative to the basal segments.

5(0) In females, maxillary palpus 6-segmented (Fig. 27, 36a,c,d);

Table 3. Classification of the basal clade of *Perdita*.

Timberlake (1954-1980)	This paper
Macrotera Smith	*Macrotera*
bicolor Smith (type sp.)	*bicolor* (type sp.)
crassa Timb.	*crassa*
texana texana (Cresson)	*texana* (=*secunda, ablusa*)
texana ablusa Timb.	*sinaloana*
secunda Ckll.	*pipiyolin* Snelling & Danforth
sinaloana Timb.	*nahua* Snelling & Danforth
Macroteropsis Ckll.	*Macroteropsis*
anthracina Timb.	*arcuata*
arcuata arcuata Fox	*echinocacti* (=*tepicensis*)
arcuata dinognatha Ckll.	*latior* (type sp.)
atrella Timb.	*magniceps*
echinocacti Timb.	*portalis*
haplura Ckll.	*haplura*
latior Ckll. (type sp.)	
magniceps Timb.	
parkeri Timb.	*Cockerellula*
peninsularis Timb.	*anthracina*
portalis Timb.	*azteca*
robertsi Timb.	*bidenticauda*
tepicensis Timb.	*knulli*
	laticauda
Cockerellula Strand	*lobata*
azteca Timb.	*opuntiae* (type sp.)
bidenticauda Timb.	*solitaria* (=*atrella, quadridentata*)
knulli Timb.	*peninsularis*
laticauda Timb.	*rubida*
lobata Timb.	*parkeri*
opuntiae Ckll. (type sp.)	*robertsi*
quadridentata Timb.	*seminigra*
rubida Timb.	
seminigra Timb.	
Macroterella Timb.	*Macroterella*
carinata Timb.	*carinata*
mortuaria Timb. (type sp.)	*mortuaria* (type sp.)
mellea Timb.	*opacella*
nigrella Timb.	*tristella*
opacella Timb.	*nigrella*
tristella Timb.	*mellea*
pilonotata Timb.	
solitaria Ckll.	

Table 4. Data Matrix for characters of species in the *Macrotera* group.

Character numbers	00000000011111111112222222223333
	12345678901234567890123456789012 3
PANURGINAE	00000000?000?00?0000000000?000000
PERDITA	10100000?000?00?00?00000000000000
PSEUDOMACR.	00100000000020000000000000000000
AZTECA	01000000010101101000000110111000
BIDENTICAUDA	01000000000101101000000010110000
KNULLI	01000000010101101000000110141000
LATICAUDA	01000000010101101000001010130100
LOBATA	01000000010101101000001010130100
OPUNTIAE	01000000000001101000000110120010
PARKERI	01000000000001101000000110120010
BICOLOR	01000000201000011000000000100000
CRASSA	01000000201000011100000000100000
TEXANA	01000000201000011100000000100000
PIPIYOLIN	01000000201000011000000000100001
NAHUA	01000000201000011000000000100001
CARINATA	01000010000000101011000001000000
MELLEA	01000010000000001000000000000000
MORTUARIA	01000010000000101011000001000000
NIGRELLA	0100000?000000001010000000000000
OPACELLA	01000010000000101011000001000000
SOLITARIA	01000010000001101000000010120010
ARCUATA	0101110100000010?000001010000000
ECHINOCACTI	01010101100000101000000010100000
HAPLURA	01011100000110101000110010100000
LATIOR	01011101100000101000000010100000
MAGNICEPS	01011101000000101000000010100000
PORTALIS	01011100000010101000110010100000
TRISTELLA	01000010010000101010000000000000
RUBIDA	01000000000101101000000010101000
SEMINIGRA	?1000000000?011010??000?101200101

(1) maxillary palpus with less than 6 segments; as few as 3 in some species (Fig. 36b).

All non-*Perdita* outgroups possess state 5(0). However, other groups within *Perdita* show palpal segment reduction. Because these groups appear to be distantly related to the *Macrotera* group, palpal reduction is thought to be convergent and the primitive state for *Perdita* is coded 5(0).

6(0) Second labial palpal segment arising apically on first (Figs. 36c,d); **(1)** second labial palpal segment arising subapically on first (Fig. 36a,b).

Character 6(0) is present in all outgroups except *Callonychium mandibulare,* and is therefore considered plesiomorphic for *Perdita.* Furthermore, the apex of the first segment of the labial palpus in those species of *Perdita* in which the second segment arises subapically is acutely pointed while in *C. mandibulare* it is blunt and quadrate apically. This observation suggests that the subapical placement seen in *Perdita* and *C. mandibulare* are not homologous.

7(0) First labial palpal segment longer than (usually two or more times as long as) remaining segments combined (Figs. 27b,d); **(1)** first labial palpal segment roughly equal to or shorter than remaining segments combined (Figs. 27c, 36d).

All non-*Perdita* outgroups studied except *Panurginus occidentalis* and *Heterosarus illinoensis* have character 7(0), which is considered plesiomorphic for *Perdita.*

8(0) Sclerotized rods on sides of aedeagus lacking setae; **(1)** small patches of stout setae on lateral surfaces of aedeagal sclerotization (penis valves) (Fig. 37d, 38e, 39c).

All outgroups possess 8(0). It is often necessary to pull the aedeagus out of the genital capsule to see this character.

9(0) Male T7 lacking discrete pygidial area apically (Figs. 32c, 33c, 34c); **(1)** male T7 with raised pygidial area apically, separated from surrounding cuticle by parallel, acute carinae (as in *P. echinocacti;* Fig. 38c); **(2)** triangular pygidial area apically (as in *P. bicolor*).

Because this character was variable both in the non-*Perdita* and *Perdita* outgroups it was treated as unpolarized.

10(0) Male S1 unmodified (Fig. 60a,b); **(1)** male S1 with apical margin produced into pucker-like lobe (Fig. 61a).

All outgroups had unmodified male S1.

11(0) Glossa not more than twice length of prementum, in some cases less than length of prementum (Figs. 27a-c); **(1)** glossa two or more, usually three, times length of prementum (Fig. 27d).

Glossa length was measured from the glossal sclerite to the tip of the glossa, and prementum length was measured from the base, at the junction with the postmentum, to the point of attachment of the labial palpi (Fig. 27d). Although the derived state is found in the subgenus *Glossoperdita,* all other outgroups studied have state 0, which is therefore considered the plesiomorphic condition of the *Macrotera* group.

12(0) Female S6 with lateral margin unmodified (Fig. 46b, 48a, 49a); **(1)** female S6 with posteriad directed process from latero-apical corner (Fig. 47a, 51a, 52a).

The unmodified state was present in all outgroups. *P. portalis* may represent an intermediate condition but has been coded 12(0).

13(0) Apical portion of male S8 (portion beyond lateral apodemal arms) about equal in width to the basal portion (as in Fig. 48c); **(1)** apical portion of male S8 much broader than basal portion, S8 appearing spade-shaped, apodemal arms indistinct (Fig. 42e, 44d); **(2)** apical portion of S8 broad and protuberant ventrally (Fig. 116-117; Timberlake, 1954).

Because the overall morphology of the male S8 is highly variable among outgroup taxa I was unable to polarize this character. However, 13(2) is clearly an autapomorphy of *P. turgiceps.*

14(0) Distinct latero-apical projection on gonocoxite lacking; **(1)** latero-apical projection present on gonocoxite (as in Figs. 46f, 47f, 48f, 49d, 51g).

Although variously shaped latero-apical gonocoxal projections are present on some other members of the ingroup (e.g., *P. mellea,* Fig. 28f; *P. turgiceps*) and also in many of the outgroups, the state seen in those taxa coded 14(1) appears not to be homologous to the state seen in any outgroup taxa.

15(0) Anterior margin T7 concave or straight in dorsal view (Fig. 28e, 29e); **(1)** anterior margin T7 convex in dorsal view (Figs. 46e, 47d, 52c).

All outgroups possess the concave or straight condition.

16(0) Forewing length less than or equal to 4.5 mm; **(1)** forewing length greater than 4.5 mm, usually around 5.0 mm.

The polarity of this character is not known because of variability in the outgroups.

17(0) Hind tibia of males with erect, fine setae, not conspicuously branched or thick; **(1)** hind tibia of males with stout, erect, moss-like setae on outer surface.

All outgroups possess state 17(0). Timberlake (1954) used this character in the key to subgenera.

18(0) Male face with yellow maculation; **(1)** male face lacking yellow maculation, though the mandibles may be yellow.

All non-*Perdita* outgroups studied have yellow on the faces of males, so the absence of yellow coloration is considered derived.

19(0) Female mandible with pre-apical pollex; **(1)** female mandible simple, lacking pollex.

All non-*Perdita* outgroups possess simple female mandibles, while in *Perdita* the state is variable.

20(0) Female mesonotum with conspicuous, erect, finely-branched setae; **(1)** female mesonotum with widely scattered, very short, recumbent setae visible only under high magnification (> 60x).

All outgroups possess at least some elongate mesonotal setae.

21(0) Male facial fovea small depression lined with fine setae, as in most andrenids; **(1)** male facial fovea large, slightly protruding, with glandular tissue visible beneath cuticle (Fig. 42b).

Facial foveae in bees and sphecid wasps have been shown to be glandular structures based on histological sections (Duffield et al. 1984; Heselhaus 1922; Nedel 1960; Schönitzer & Schuberth 1993; Schuberth & Schönitzer 1993), but the function of these glands is unknown. All outgroups studied had small inconspicuous male facial foveae, similar to those of females. In *P. portalis* and *P. haplura,* however, the facial foveae are large and convex, with glandular tissue visible through the cuticle. In dissections of male *P. portalis* these structures were pale cream color and were sandwiched between the outer cuticle and an inner layer of thin cuticle.

22(0) Apical margin of male clypeus, where labrum attaches, concave or straight (Fig. 28b, 29b); **(1)** male clypeus overhanging labrum slightly and acutely pointed apically, especially in the larger-headed specimens (Fig. 42b).

All non-*Perdita* outgroups lack the acutely pointed clypeus. Almost all other species of *Perdita* investigated have a concave clypeal margin but in some species of *Perdita* sensu stricto the clypeus is acutely pointed. Nevertheless, 22(0) is considered plesiomorphic for the *Macrotera* group.

23(0) Volsellar cuspus variable in shape but always small and not extending beyond apex of paramere; **(1)** cuspus enlarged, laterally compressed and extending beyond apex of paramere (Fig. 51g, 52d).

All outgroups possess state (0).

24(0) Lateral surfaces of female propodeum with scattered, finely branched setae; **(1)** two patches of dense, short, finely branched setae on lateral surfaces of female propodeum; setae packed so densely as to obscure the cuticle below.

All outgroups possess state (0).

25(0) Male T6 with fine, erect, scattered setae; **(1)** male T6 with single subapical line of few erect, stout, finely branched setae (Fig. 38c, 51c).

Timberlake referred to these as "moss-like" setae (1954:352). All outgroups possess state 25(0).

26(0) Male T7, as in most bees, with lateral margins not meeting ventrally (Figs. 37c, 38d); **(1)** male T7 forming tube due to reflexed lateral margins, which almost touch ventrally (Fig. 32c, 33c, 34c).

All outgroups possess state (0).

27(0) Lateral graduli of male T2 and T3 lacking; **(1)** lateral graduli present on T2 and/or T3 in males (Fig. 1a,b).

Tergal graduli extend completely across the male T2 and T3, ending at the lateral margins of the terga, in most species of *Perdita.* However, in some species (e.g., *P. texana*), near the lateral edges of the terga the graduli turn posteriorly and run parallel to the long axis of the body. These lateral portions of the graduli are referred to as the lateral graduli. In the non-*Perdita* outgroups studied this character varied, with most Calliopsini possessing lateral graduli and the Melitturgini, Panurgini and Protandrenini lacking lateral graduli. I have coded this character as variable (?) for the non-*Perdita* outgroups and (0) for the *Perdita* outgroups.

28(0) Male S2 and S3 unmodified (Fig. 61a); **(1)** male S2 and S3 with broad, obtuse protuberances along posterior margins, strongest in S3 (Fig. 62a); **(2)** male S2 with quadrate protuberance which projects over surface of S3 (Fig. 62b); **(3)** male S3 with discrete, rectangular patch of stout setae (Fig. 62c); **(4)** S2 with paired diverging ridges along posterior margin.

All outgroups possess unmodified male second and third sterna.

29(0) Penis valves variable, but not connected dorsally by slender bars of cuticle; **(1)** penis valves connected dorsally by slender cuticular bars (Fig. 46f, 48f, 49d).

All outgroups have state (0).

30(0) Apical margin of male T7 variable in shape; **(1)** apical margin of male T7 dorso-ventrally flattened, forming a broad horizontal shelf with widely separated, acute corners (Fig. 51e, 52c).

All outgroups possess state (0).

31(0) Penis valves parallel; **(1)** penis valves divergent (Fig. 54f, 55d, 56b, 57f).

All outgroups possess state (0).

32(0) Volsella highly variable in shape, but not as in alternative state; **(1)** volsella chelate, as in a crab claw, with apex of cuspis acute and strongly recurved.

The volsellae are highly variable in shape among species of *Perdita*. *P. nahua* and *P. pipiyolin* are unique in possessing a stout, acutely pointed and apically recurrent cuspis.

33(0) Apical margin of male T7 variable in shape; **(1)** apical margin of male T7 produced at corners into elongate acute prongs, separated by deep emargination (Figs. 55c, 56c,d).

All outgroups possess state (0).

PHYLOGENETIC ANALYSIS

The m*, bb* options of Hennig86 resulted in four equally parsimonious trees of length 46 and consistency index = 82 for the 33 characters and 29 taxa listed in Table 4. Characters were all treated as unordered. The Hennig86 ie (implicit enumeration) command resulted in the same 4 trees. Figure 23 shows the consensus tree, Fig. 24a-d show the 4 equally parsimonious resolutions, and Fig. 25 shows the characters mapped onto the preferred tree. Fig. 26 shows the preferred tree and the limits of the four subgenera.

TREE TOPOLOGY AND RELATIONSHIPS AMONG SPECIES.

The monophyly of the *Macrotera* group of subgenera is supported in the present analysis. Both characters 2(1) and

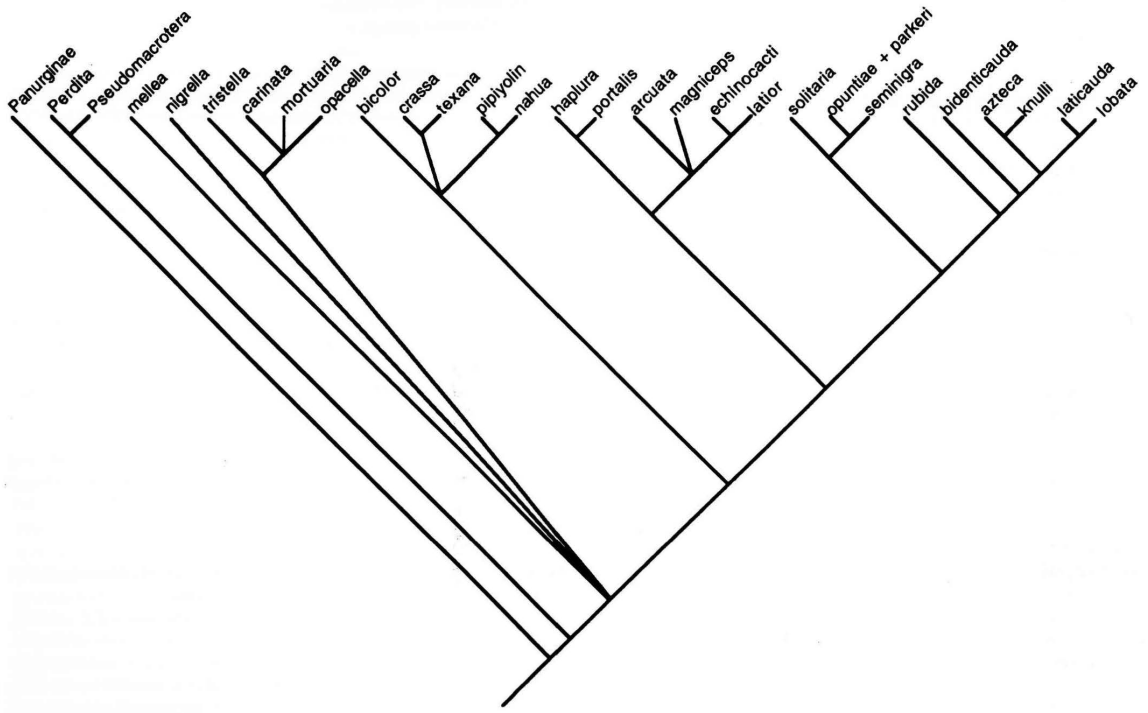

Fig. 23. Consensus tree of species-level analysis. "Panurginae" refers to the panurgine genera used as outgroups in the subgeneric phylogeny. "*Pseudomacrotera*" refers to the monotypic subgenus which includes *P. turgiceps*. While this species does not belong to the groups here treated, it is clearly near the base of the *Perdita* phylogeny, and is useful for character polarization. "*Perdita*" represents all the other species of *Perdita* (referred to in the text as the "higher *Perdita*").

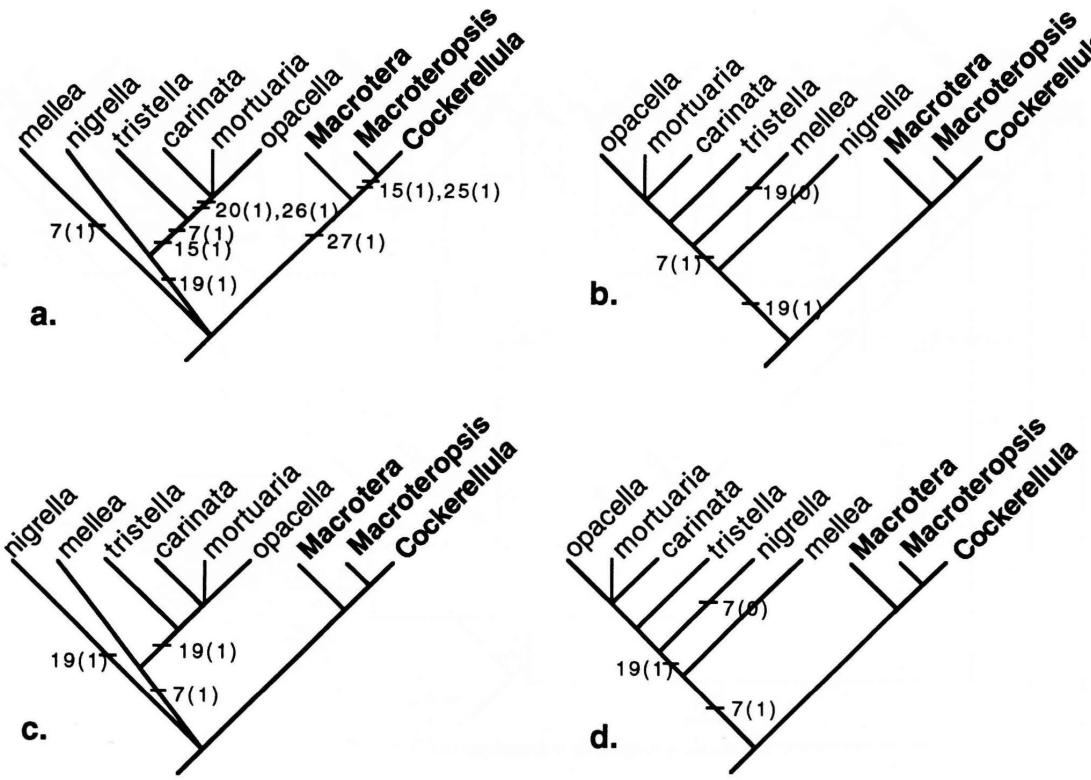

Fig. 24. Four equally parsimonious resolutions of basal polytomy in the consensus tree (Fig. 23).

17(1) unite all four subgenera, excluding the remainder of *Perdita* (Fig. 25).

The primary source of ambiguity in this analysis involves the relationships among the basal species, the members of Timberlake's subgenus *Macroterella* excluding *P. solitaria,* which clearly belongs elsewhere (see below). In two of the four resolutions, *Macroterella* (*P. mellea, P. opacella, P. carinata, P. mortuaria, P. tristella* and *P. nigrella*) appears monophyletic (Fig. 24b,d), while in two others the group is potentially paraphyletic (Fig. 24a,c). The ambiguity arises from the incongruity of characters 7 and 19. I prefer the resolution in which the ci of character 19 is maximized (ci=100, Fig. 24a,d), at the expense of character 7. The tree shown in Fig. 24a seems the most likely, indicating the possibility that *P. mellea* does not belong to a monophyletic *Macroterella.*

On a more positive note, the monophyly of *P. carinata, P. opacella* and *P. mortuaria* is well supported by characters 20(1) and 26(1), and the placement of *P. tristella* as the sister group to these three species is supported by character 15(1), although this character arises in parallel higher up in the tree (Fig. 25). This group of four species all have very similar genital capsules (Figs. 31f, 32d, 33d, 34d).

The monophyly of the subgenera *Macrotera, Macroteropsis* and *Cockerellula* is supported by 27(1), the presence of conspicuous lateral graduli on male T2 and T3.

The monophyly of the subgenus *Macrotera* is supported by the elongate glossa (11[1]), large body size, as measured by forewing length (16[1]), and the distinctly shaped male pygidial plate (9[2]). Although the relationships within this group are not fully resolved, the sister group relationships between *P. crassa* and *P. texana,* and *P. pipiyolin* and *P. nahua* are clear.

The characters uniting the subgenera *Macroteropsis* and *Cockerellula* are the shape of the anterior margin of the male T7 (15[1]) and the presence of a subapical band of erect, coarsely-branched setae on the male T6 (25[1]).

The composition of these two subgenera has been changed somewhat as a result of the present analysis. *Macroteropsis* now refers to a group of 6 species united by characters 4(1), 5(1) and 6(1). Although Timberlake considered reduced maxillary palpi one of the defining characters of *Macroteropsis* (Timberlake, 1954:356), he included several species which did not show such palpal reductions. Other characters listed as diagnostic of the subgenus are common to other groups or are

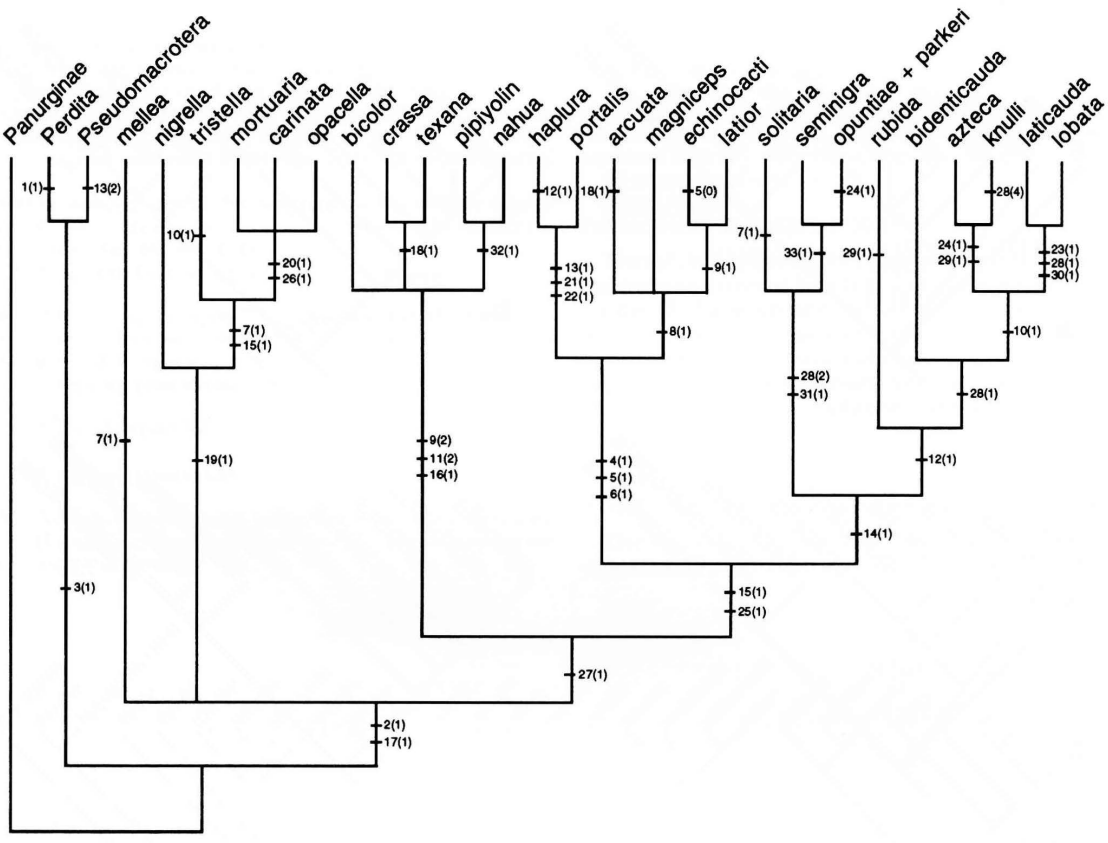

Fig. 25. Preferred tree with characters mapped on. See explanation of outgroup taxa in caption to Fig. 23.

highly variable. He did not mention the maxillary palpal character (6[1]) which I have included.

The monophyletic group united by character 14(1) is an expanded subgenus *Cockerellula*. *P. solitaria* had previously been placed in *Macroterella*, but there is little doubt that it is closely related to *P. opuntiae* and its relatives. Although in the cladogram *Cockerellula* is united by a single male character (14[1]), it was possible to place some species known only from females (e.g., *P. peninsularis, P. anthracina*) with certainty in *Cockerellula* based on female characters included in the analysis (e.g., 12[1]).

CLASSIFICATION

Timberlake's classification of the group and a modified classification, based on the phylogenetic analysis, are shown in Table 3. The subgenus *Macrotera* remains essentially unchanged, except for the addition of two new species and some synonymy. The subgenus *Macroteropsis* has been reduced in size as a result of synonymy (e.g., *P. tepicensis*) and the transfer of some species to *Cockerellula*. *Cockerellula* includes more species than previously.

Timberlake's subgenus *Macroterella* has been changed considerably as a result of this study. *P. pilonotata* clearly belongs to the distantly related subgenus *Heteroperdita*, and, as a result of finding the male of *P. solitaria*, this species has been transfered to *Cockerellula*. Although ambiguity about the relationships among the remaining species of *Macroterella* (*P. mellea, P. nigrella, P. tristella, P. carinata, P. opacella*, and *P. mortuaria*) persists, there is no convincing reason to split this group up further. Although in some of the resolutions (Fig. 24) *Macroterella* is potentially paraphyletic, in others it is monophyletic. One species, *P. mellea*, is highly autapomorphic (see below) and one could, based on phenetic grounds, place this species in its own subgenus in order to call attention to its autapomorphic features, but at present this seems unnecessary.

DIAGNOSIS OF THE *MACROTERA* GROUP OF SUBGENERA

The four subgenera treated below can be recognized by the following characters: (1) mandible with discrete, well impressed sulcus on outer surface running from acetabulum diagonally across base and then along lower, or condylar, mar-

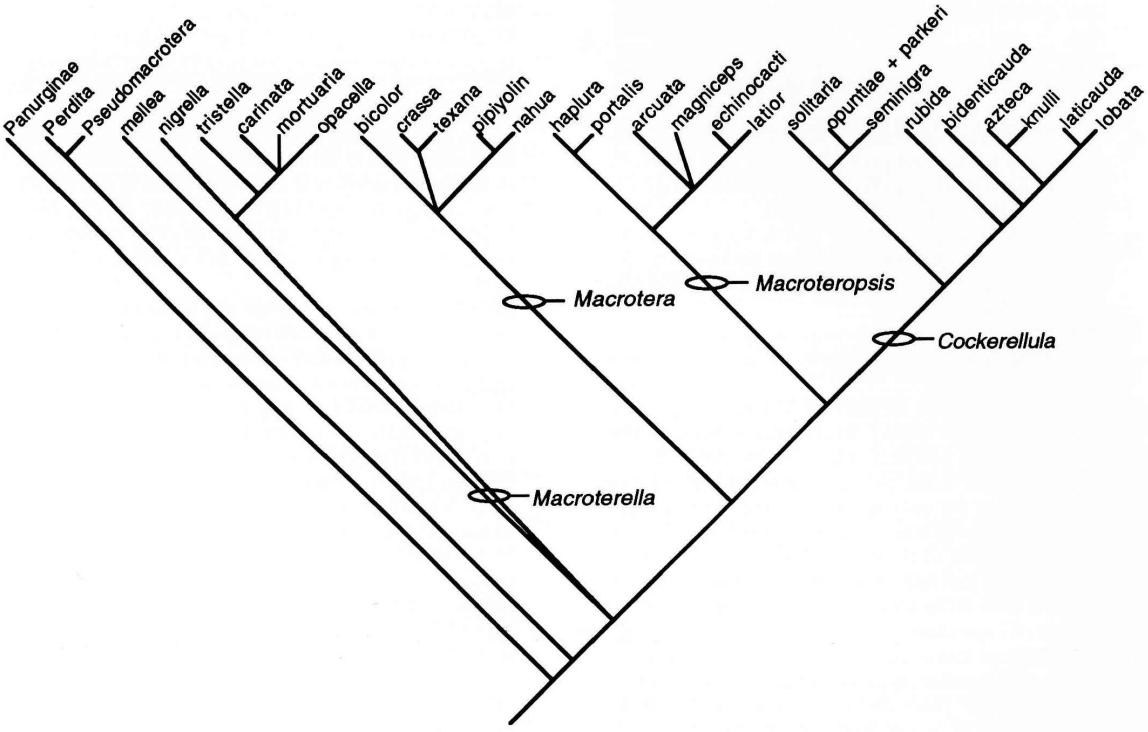

Fig. 26. Preferred tree showing limits of subgenera. See explanation of outgroup taxa in caption to Fig. 23.

gin, (2) paraglossae in females slender basally and expanded into a broad, brushlike apex, (3) scrobal sulcus lacking, (4) male with highly variable head shape due to positive allometry in several aspects of head capsule, but in general head broad and quadrate, (5) yellow maculation usually absent on the meso or metasoma, and (6) male usually with reddish metasoma.

KEY TO THE SPECIES OF THE *MACROTERA* GROUP

1. Large bees (forewing length 4.5 mm or more); glossa 2-3 times length of prementum (*Macrotera*) . . . . . . .see Snelling & Danforth (1992) for a key to species
— Smaller bees (forewing length 4.0 mm or less); glossa no more than 2 times length of prementum and usually about equal to length of prementum 2
2. Second segment of labial palpus arising subapically on first segment, first segment acutely pointed apically; maxillary palpal segments 3 and beyond greatly shortened and sometimes lacking, such that palpi 4 to 6-segmented; head of female broad, width 1.3 times length (*Macroteropsis*) 9
— Second segment of labial palpus arising apically on first segment; maxillary palpus 6-segmented; segments subequal in length; head of female usually rather slender, width 1.1 times length 3
3. Female with extensive yellow maculation on head and mesosoma, metasoma reddish orange; male uniformly reddish orange with yellow maculation on lower part of face; forewing length 1.8-2.3 mm. . . . . .*P. mellea*
— Female head and mesosoma primarily black (yellow on mandible, lower part of frons and foreleg in some species); male head and mesosoma primarily black (except for some yellow on the clypeus and supraclypeal area); forewing length usually greater than 2.5 mm 4
4. Female mandible simple; metasoma black; small bees without conspicuous erect setae; male T6 and T7 lacking mosslike setae; no graduli visible on lateral corners of T2 and T3; S8 not very slender; genital capsule without latero-apical processes (*Macroterella,* in part) 5
— Female mandible with pollex; metasoma usually reddish; some species with dense patches of setae on lateral surfaces of propodeum; larger bees; males with conspicuous moss-like setae on T7 and in a single row across T6; graduli visible on lateral corners of T2 and T3; S8 long and slender; genital capsule with lateroapical processes (*Cockerellula*) 14
5. Male T7 tubelike, lateral portions almost touch ventrally; female lacking erect setae on mesonotum but

with yellow maculation on anterior surface of foretibia 6
— Male T7 not tubelike; females with a few erect setae on mesonotum and no yellow maculation on foretibia 8
6. Male T7 divided medially by slit flanked by two postero-laterally directed prongs; female with relatively broad and obtuse pygidial plate; metallic tinge on frons and vertex distinctly greenish ..... *P. opacella*
— Male T7 not divided medially and lacking prongs; female with relatively slender, acutely pointed pygidial plate; metallic tinge on frons and vertex weak and coppery in coloration 7
7. Male T7 with longitudinal carina at apex ... *P. carinata*
— Male T7 simply tubelike, without apical modifications ..... *P. mortuaria*
8. Female facial fovea slender and deeply impressed (length 5-6 times width); frons more shiny with less greenish tinge; basitibial plate poorly defined, represented by an acute prong on posterior margin of tibia; female S6 only weakly emarginate apically (depth of emargination less than width); male with yellow restricted to clypeus, with very faint yellow on area of frons just lateral to clypeus, between clypeus and eye; male S1 lacking acute prong along posterior margin; S7 spatulate ..... *P. nigrella*
— Female facial foveae broader (length 3 times width); frons more tesselate, greenish tinge more evident; female basitibial plate distinctly raised and well defined all around; female S6 deeply emarginate apically (depth of emargination greater than width), male with more extensive yellow maculation, yellow on face below level of antennal sockets; male with median, acute prong arising from the posterior margin of S1; S7 gradually tapering to acute apex ..... *P. tristella*
9. Maxillary palpi 5- to 6-segmented; wings hyaline with brownish wing veins; facial maculation restricted to below level of antennal sockets in male; aedeagus with small patches of stout setae on each side ..... .10
— Maxillary palpi 4-segmented; wings cloudy whitish with pale brown veins; yellow on face extending up above level of antennal sockets in male, often to vertex, or head entirely orange-ferruginous; aedeagus lacking stout setae ..... .12
10. Male pygidial plate lacking; male mandible simple; S8 of male rather broad apically; clypeus with transverse ridge; female with broad, transparent area on S6 (length 2-3 times width); lateral surfaces of propodeum with erect, white setae ..... *P. arcuata*
— Male pygidial plate formed by two parallel carinae at apex of T7; male mandible bidentate; S8 of male slender and not expanded apically; clypeus flat; female with more slender transparent area on S6 (length 5-6 times width); lateral surface of propodeum with only a few scattered, white setae ..... .11
11. Male with protuberance at midpoint of S2; female with conspicuous bluish tinge; maxillary palpus distinctly 6-segmented ..... *P. echinocacti*
— Male without protuberance at midpoint of S2; female with more greenish tinge; maxillary palpus 6-segmented but segment 5 very difficult to distinguish ..... *P. latior*
12. Male head entirely ferruginous, with yellow maculation below level of antennal sockets; mesosoma and metasoma partly ferruginous; female with dense, closely-appressed white setae over scutum and scutellum; orange-ferruginous maculation over at least lower portion of clypeus, surrounding compound eye and extending medially along vertex to lateral ocellus ..... *P. magniceps*
— Male head yellow or orange ferruginous up to level of ocelli, becoming dark brown across vertex; genal width subequal to width of compound eye; mesosoma and metasoma mostly dark brown ..... .13
13. Male facial fovea large, pale cream colored and seemingly glandular; T7 rather slender apically (apex 0.2 mm in width) and without conspicuous latero-apical prongs; female eyes weakly convergent below (Fig. 42a); female foretibia with yellow maculation; pygidial plate narrow and acute (Fig. 42d) .... *P. portalis*
— Male facial fovea large and black, not noticably glandular; T7 broader, more obtuse apically (apex 0.55 mm in width) and with two small prongs on either side of broad, convex apical margin; female eyes strongly convergent below (Fig. 44a); female foretibia without yellow maculation; pygidial plate broader and obtuse (Fig. 44c) ..... *P. haplura*
14. Females ..... .15
— Males ..... .24
15. Metasoma primarily black or deep brown ..... .16
— Metasoma reddish ..... .19
16. Blue-green metallic tinge to head and mesosoma ..... P. *rubida*
— Very weak, if any, metallic coloration ..... .17
17. Female robust, with long erect white setae over head and mesosoma; wing veins dark brown; pygidial plate gently rounded and obtuse apically ..... *P. anthracina*
— Female more slender and with shorter, less conspicuous white setae; wing veins light brown; pygidial plate acutely pointed and slender ..... .18
18. Labial palpal segments 2-4 elongate and slender, equal in combined length to segment 1; S6 not notched apically; forewing length less than 3.0 mm .. *P. solitaria*
— Labial palpal segments 2-4 shorter, their combined length less than that of segment 1; S6 strongly notched apically; forewing length greater than 3.0 mm ..... *P. peninsularis*
19. Lateral surface of propodeum with discrete patch of stout white setae, which completely obscures the underlying cuticle ..... .20
— Lateral surface of propodeum with more widely spaced white setae, not forming dense patch; cuticle easily visible through setae ..... *P. laticauda, P. bidenticauda,* or *P. lobata* (males needed for definite identification)
20. Large, robust bees with elevated triangular supraclypeal area extending upward between antennal bases;

mid and hind tibial spurs acutely bent at apex and with long teeth, appearing nearly pectinate; facial fovea elongate and slender (0.41-0.54 mm) ..... *P. azteca*
— Bees of various sizes but lacking elevated supraclypeal area; tibial spurs finely serrate; facial fovea slender, shorter 21
21. Anterior face of T1 brownish, rest of metasoma reddish; dorsal, central surface of propodeum with antero-posterior striae converging posteriorly ..... *P. parkeri*
— Anterior surface of T1 reddish like rest of metasoma; dorsal, central surface of propodeum finely alveolate, no obvious linearity to scupturing 22
22. Yellow maculation on lower part of paraoccular area immediately lateral to clypeus, running just above fronto-clypeal suture from outer subantennal sulcus to base of mandible ..... *P. robertsi*
— Face lacking yellow maculation, except for slight yellow on clypeus and mandible 23
23. Large, robust bees (forewing length greater than 3.5 mm) ..... *P. opuntiae* (or *P. seminigra*)
— Smaller bees (forewing length less than 3.0 mm) ..... *P. knulli*
24. S1 of male with median pucker-like fold (Fig. 61a) . . 25
— S1 of male unmodified (Fig. 60a,b) 28
25. S3 of male with median rectangular patch of short, dense setae (Fig. 61c); apex of T7 dorso-ventrally compressed, forming a broad horizontal, roughly quadrate margin 26
— S3 of male without median patch of setae; T7 variable 27
26. Posterior margin of T7 more strongly emarginate medially and lateral corners more pronounced and more strongly bent ventrad (Fig. 52c); papillae on cuspis extend to apex (Fig. 52d) ..... *P. lobata*
— Posterior margin of T7 less strongly emarginate medially and lateral corners more horizontal (Fig. 51f); papillae on cuspis restricted to basal half (Fig. 51g) ..... *P. laticauda*
27. Large, robust bees (forewing length greater than 3.5 mm); mandible simple; bright yellow maculation on mandible, labrum, clypeus and frons below level of antennal sockets; T7 with long, paired, postero-dorsal projections arising subapically ..... *P. azteca*
— Small bees (forewing length less than 3.0 mm); mandible bidentate; creamy white on mandibles, labrum, clypeus and frons below level of antennal sockets; T7 narrowed apically with two small apical prongs ..... *P. knulli*
28. Posterior margin of S2 with median quadrate protuberance extending out of plane of other sterna, over surface of S3, and ending in two sharp points 29
— Margin of S2 with slight thickening or bulge but not extending over surface of S3 32
29. Large bees (forewing length greater than 3.5 mm); apical margin of T7 broadly emarginate with two widely separated, acutely pointed prongs 30
— Small bees (forewing length less than 2.6 mm); T7 quadridentate apically, two median processes directed meso-posteriad, two horizontal processes directed postero-laterad ..... *P. solitaria*
30. Yellow facial maculation extending completely across face below level of antennal sockets (on clypeus, supraclypeal and paraoccular areas); prongs of T7 more widely separated (>0.56 mm) and emargination between prongs u-shaped 31
— Yellow to white facial maculation restricted to paraoccular area, no yellow maculation on clypeus; prongs on T7 less widely separated (<0.48 mm), and emargination between prongs v-shaped ..... *P. seminigra*
31. Mesoscutum shiny with small, widely scattered, but distinct, punctures; head and thorax brownish ... . *P. opuntiae*
— Mesoscutum dull, infuscate, with barely discernible punctures; head and thorax black ..... *P. parkeri*
32. S3 with broad, transverse bulge along posterior margin; S2 with similar, but less prominant bulge; facial maculation creamy white, on lower part of face reaching to upper margin of antennal sockets .... *P. bidenticauda*
— S2 and S3 unmodified; yellow facial maculation on clypeus, supraclypeal and paraoccular areas, extending upward along inner margins of eyes to facial foveae ..... *P. rubida*

SPECIES DIAGNOSES

Although Timberlake published complete descriptions of most of the species in this group, I have included diagnoses for each species, listing the most useful characters for species-level recognition. Many of these features were not mentioned by Timberlake. Brief descriptions of the geographic distributions and floral host associations are also given. I have included complete descriptions of species which were not adequately described originally and a description of a newly discovered species from Mexico.

In the lists of plant records I have given the plant associations according to plant genus, and included specific names, if given, in parentheses. I have also included the numbers of males and females collected on each plant genus, for those specimens with plant records.

Subgenus *Macroterella* Timberlake

Macroterella Timberlake, 1954:360 [description]; 1954:361 [key to species]; 1956:324 [additional species]; 1960:125 [new records]; 1968:7 [additional keys]; 1980:6 [additional species, new records].
Type species – *Perdita mortuaria* Timberlake, by original designation.

Diagnosis – Members of this subgenus are some of the smallest species in the *Macrotera* group. Features which serve to distinguish this subgenus from all other *Perdita* include: (1) greatly shortened mouthparts, with glossa length usually equal to or less than length of prementum, (2) first labial palpal segment equal in length to remaining segments combined, (3) female mandible simple and acutely pointed (except *P. mellea*).

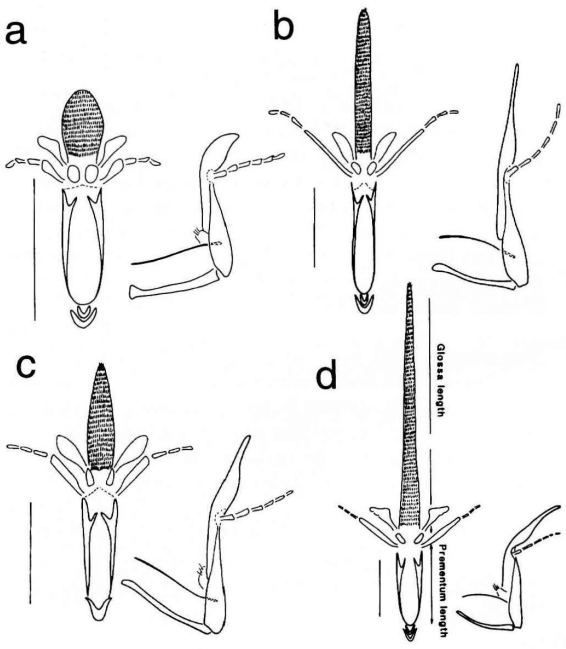

Fig. 27. Mouthpart morphology, females. **(a)** *P. mellea,* **(b)** *P. nigrella,* **(c)** *P. opacella,* **(d)** *P. bicolor* (Scale bar = 0.5 mm, except in *P. bicolor,* in which it equals 1.0 mm).

Perdita (*Macroterella*) *mellea* Timberlake

(Figs. 27a, 28, 30)

Perdita (*Macroterella*) *mellea* Timberlake, 1954:364 [description]; 1954:361 :[key]; 1960:125 [additional material]; 1968:7 [key].

Type material – The holotype male and allotype are located in the CAS (Type No. 14606). Both specimens were collected at Picacho Pass, Pima Co., Arizona, August 7, 1940, on *Euphorbia* (Timberlake, coll.).

Diagnosis – Forewing length 1.8 - 2.3 mm. This species is very distinctive. The male is entirely ferruginous, with erect, white setae over the mesonotum, metanotum, pleura and lateral surfaces of the propodeum, and with yellow maculation on the face up to the level of the antennae. The head is broad with blue-grey eyes (in the normal male morph collected on flowers, see below) and the mandibles are simple. The distinctive male genitalia and apical sterna further distinguish this species. The head and mesosoma of females is black with extensive yellow maculations on the medial and lateral areas of the clypeus, along the midline of the frons from the frontoclypeal suture to the anterior ocellus, from the paraocular areas upward along the inner margins of the eyes to the vertex, and on the scutellum the metanotum and the upper, horizontal surface of the propodeum. The fore and mid legs are yellow beyond the apices of the femora. Females also possess a distinctive type of sculpturing over the mesopleura: although imbricate-punctate, with erect white setae on the lower portion of the mesopleuron, the cuticle is deeply and minutely alveolate on the upper portion. The metasoma is reddish. The mouthparts of *P. mellea* are the shortest of all the species in the *Macrotera* group. The glossa is scarcely longer than wide and considerably shorter than the length of the prementum. The galea and the labial palpi are greatly shortened. The maxillary palpi are six-segmented but also very short.

Like *P. portalis,* males of *P. mellea* are dimorphic (Rozen, pers. comm.). The typical, flight-capable male is described in the diagnosis given above. As there is no published description of the macrocephalic male morph, I present a description of this form below, based on two specimens provided by Dr. Jerome G. Rozen, Jr., AMNH.

Description – MACROCEPHALIC MALE MORPH – Head: (43) greatly expanded compared with flight-capable morph, width 3.2 mm; (44) quadrate, 1.42 times broader than long; head width increases from top to bottom, so that greatest head width is at level of mandibles; (45) clypeus compressed and elongate, ventral projections on either side of labrum enclose labrum as in small-headed male; (46) frons, supraclypeal and paraocular areas shiny with abundant, closely-spaced punctures and fine, white recumbent setae; (47) vertex and entire region above ocelli shiny and without punctation; (48) gena greatly expanded behind eye (maximum width 0.51 mm); glabrous and impunctate down to level of upper margin of eye; below upper margin of eye surface shiny but with numerous, minute punctures; (49) head coloration more or less as in small-headed male, honey yellow over most of head, with yellow to white maculation on face below level of antennae; (50) head, except impunctate regions, clothed in fine white setae; (51) eyes greatly reduced (0.34 mm in length) in comparison to small-headed male, weakly convex and roughly coplanar with surrounding head capsule; eyes black (in pinned specimens); (52) median and lateral ocelli separated by more than one ocellar width; ocelli greatly reduced in size (1/2 size of ocelli in large-headed male) and hardly convex above level of surrounding cuticle; (53) facial fovea very weak, appearing as faint dimples at about level of upper eye margin; (54) scape light yellow as on lower part of face, pedicel and flagella darker yellow, concolorous with head above level of antennae.

Mouthparts: (55) labrum rectangular and pale yellow; glabrous medially with small, weak punctures and fine white setae laterally; (56) mandible stout, and tapering to an acute apex; no preapical tooth; yellow, with reddish tips; (57) glossa short, 1/5 length of prementum and barely longer than wide; (58) paraglossa slender and acutely pointed, roughly equal to glossa in length; (59) labial palpus 4-segmented, first segment shorter than remaining segments combined; (60) galeal comb absent or at least very difficult to see; (61) maxillary palpus 6-segmented, segments short but all distinct, maxillary palpi extend beyond apex of galea. The mouthparts of large-headed males are similar to those of small-headed males but differ from females in that females have broad, brush-like paraglossae.

Mesosoma: (62) pronotum longer (length = 0.32 mm along midline in dorsal view) and far more robust than in small-headed male; dorsal surface divided by transverse groove and lateral surface rather deeply impressed giving rise to distinct dorso-lateral lobes of pronotum; pronotal lobes clothed in white setae; (63) mesoscutum paler and reduced in size relative to small-headed male; dorsal surface essentially flat (far more convex in small-headed male); surface weakly imbricate with scattered erect white setae; (64) mesoscutellum and metanotum in comparison to small-headed male reduced in size and flattened; (65) mesopleuron as in small-headed male, with dense white setae; (66) metapleuron weakly alveolate, lacking setae; (67) propodeum more abruptly declivous than in small-headed male, with same erect white setae separating dorsal and lateral surfaces and similar alveolate sculpturing; (68) intertegular distance 0.51 mm; (69) wings reduced in size;

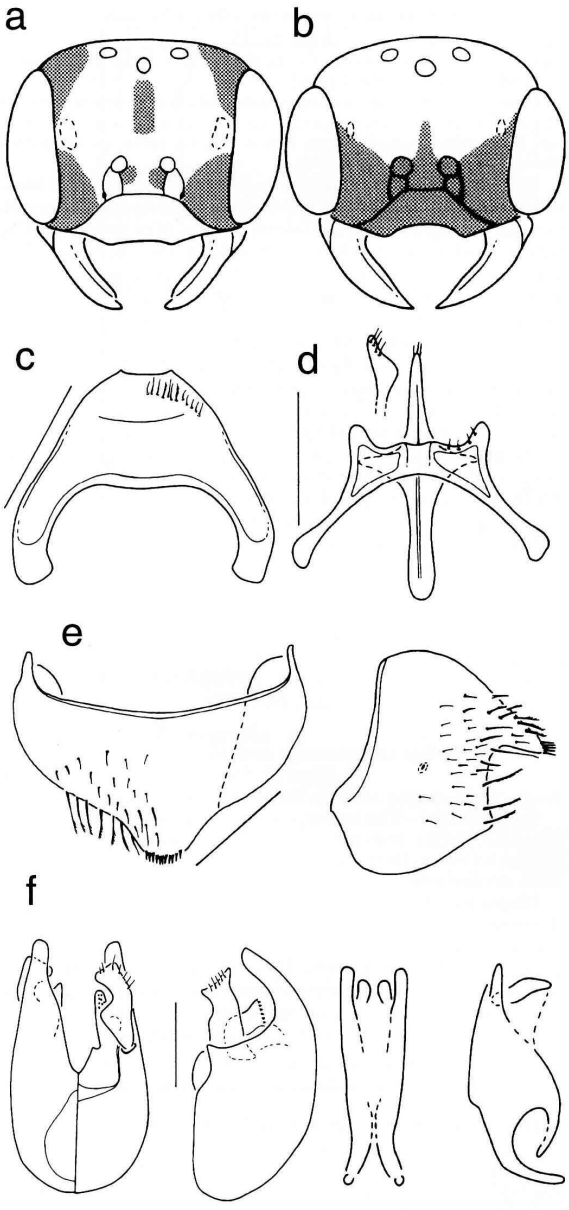

Fig. 28. *Perdita mellea.* **(a)** female head, **(b)** male head, **(c),** female S6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view). In this figure and the following figures, the scale bar lengths are as follows (unless specified differently on the figure): female S6, 0.25 mm; female T6, 0.5 mm; male T6, 0.5 mm; male S7 and S8, male T7, genital capsules, 0.25 mm.

forewing length 1.56 mm (forewing length usually reaches 2.0 mm in small-headed males); (70) legs concolorous with rest of mesosoma except for apices of femora and bases of tibiae, which are pale yellow; (71) basitibial plate slightly smaller than in small-headed male but well-defined; (72) outer surface of hind tibia with erect, finely branched setae; (73) midtibial spur minutely serrate; (74) hind tibial spurs subequal in length and finely serrate; (75) tarsal claws all bifid.

Metasoma: (76) terga concolorous with mesosoma; metasoma overall broader and more dorso-ventally flattened than in small-headed male; (77) T1-T6 clothed in minute, unbranched, appressed setae; (78) T6 with more elongate, erect, but unbranched setae; (79) fovea on T2 present but shallow and weakly developed; (80) pygidial plate lacking on T7, but band of long, erect setae present apically; (81) graduli present on T2-T6 but do not extend far enough laterally and posteriorly to be visible in dorsal view; (82) sterna similar in color to terga; (83) S1-S6 similar in color and vestiture to terga; (84) sternal graduli only present on S1, lacking on all other sterna; (85) S7 and S8 as in small-headed male (Fig. 28d); (86-89) genital capsule as in small-headed male (Figs. 28f).

Distribution – Desertic parts of San Bernardino, Riverside counties, California; Cochise, Pima, Pinal and Yuma counties, Arizona; Hidalgo Co., New Mexico; Presidio Co., Texas; states of Sonora, Baja California Norte and Baja California Sur, Mexico (Fig. 30). Additional specimens are recorded from Chihuahua, Mexico by the Programa Cooperativo sobre la Apifauna Mexicana (PCAM) (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – July through October.

Floral associations – The vast majority of specimens were collected on *Euphorbia* (*polycarpa, polycarpa* var. *hirtella, albomarginata hirtella*) (89 females/32 males) with some specimens on *Eriogonum inflatum* (2 females/0 males).

Perdita (Macroterella) nigrella Timberlake

(Figs. 27b, 29, 30)

Perdita (*Macroterella*) *nigrella* Timberlake, 1954:362 [description]; 1954:361 :[key]; 1968:7 [key].

Type material – The holotype male is located in the CAS (Type No. 14631). The holotype and allotype were collected along Artist Drive, West side of Death Valley, Inyo Co., California, April 7, 1939, on *Phacelia* (E.G. Linsley, coll.).

Diagnosis – Forewing length 2.6 to 3.0 mm. This species, like the following one, can be distinguished from other members of the subgenus by the presence of scattered, erect setae on the scutum of both males and females. Females are mostly black with a slight greenish metallic hue on the head and scutum and yellowish mandibles, becoming fuscous apically. There is no yellow coloration on the foretibia. In females, the facial foveae are slender and the basitibial plate is unusual in that it does not have a clearly defined rim separating it on all sides from the remainder of the tibia. Rather, the basitibial plate forms an acute projection off the posterior margin of the tibia. Females of this species are further distinguished by the shape of S6. Males have large, quadrate, mostly black heads with yellow restricted to the clypeus and the paraocular areas, below the upper margin of the clypeus. The mesosoma is entirely black and minutely imbricate, with scattered erect, white setae on the scutum, scutellum and pleura. The metasoma is entirely fuscous. Additional diagnostic features of males include the spatulate S8, and an unusual genital capsule. In lateral view the apex of the gonocoxite bears three prongs: one prong extends from the dorsal surface, and a pair of prongs extend from the ventral surface.

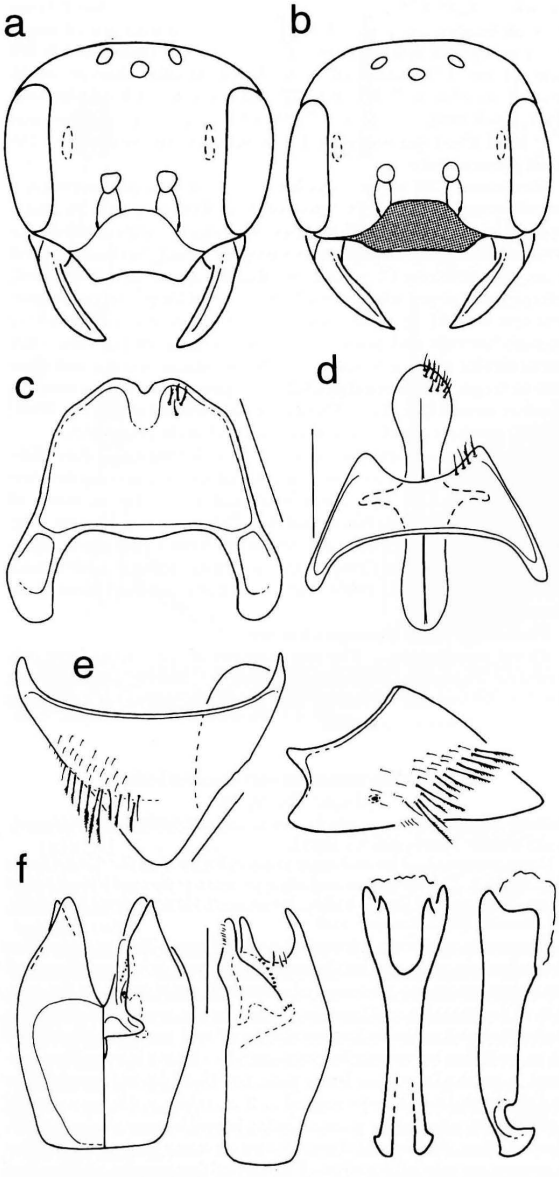

Fig. 29. *Perdita nigrella.* **(a)** female head, **(b)** male head, **(c)** female S6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Distribution – Arid regions of Inyo county near Death Valley and Panamint Mountains, and desertic portions of Riverside county, California (Fig. 30).

Phenology – April to May.

Floral associations – *Phacelia* (*crenulata*) (7 females/3 males)

Perdita (*Macroterella*) *tristella* Timberlake

(Figs. 31, 35)

Perdita (*Macroterella*) *tristella* Timberlake, 1954: 363 [description]; 1954:361 [key]; 1968:7 [key].

Type material – The holotype male and allotype are in the CAS (Type No. 14741). Both specimens were collected at The Gavilan, Riverside Co., California, May 8 and 12, 1950, on *Eriogonum fasciculatum,* (Timberlake, coll.).

Diagnosis – Forewing length 2.4 - 2.6 mm. Females are all black with scattered erect white setae over the frons, mesoscutum, scutellum, pleura, metanotum and lateral surfaces of propodeum. The female head is 1.1 times broader than long, the frons has a blue-green, metallic tinge, and the facial foveae are large and broad, and lined with minute setae. The basitibial plates are very clearly defined on all sides (more so than in any other black *Macroterella*), triangular, and covered with a few short, recumbent finely branched setae. The female is unique in the shape of S6: the apicial margin has a slender slit flanked on either side by erect, finely branched setae. This feature can be seen without dissecting the apical segments. The male is similar to *P. nigrella* but can be distinguished by the shape of the S7, the genital capsule, and a modified S1: the posterior margin is reflexed medially into an acute protuberance which projects above the plane of S2 (this feature is not considered homologous to the modified S1 seen in some *Cockerellula*).

Distribution – Cismontane regions of Riverside Co., California (Fig. 35).

Phenology – April through June.

Floral associations – Although collected on *Eriastrum virgata* (1 female), *Calochortus splendens* (1 female), and *Sphaeralcea ambigua* (1 female), *Eriogonum* (*fasciculatum*) (1 female/5 males) appears to be the source of pollen, based on inspection of pollen in the scopa of females (Timberlake, 1954:363).

Perdita (*Macroterella*) *carinata* Timberlake

(Figs. 32, 35)

Perdita (*Macroterella*) *carinata* Timberlake, 1968:9 [description]

Type material – The holotype male and allotype are in the CAS (Type No. 14453). Both specimens were collected at the Boyd Desert Research Center, Deep Canyon, Riverside Co., California, May 10, 1963, on *Eschscholtzia* (E.I. Schlinger, coll.).

Diagnosis – Forewing length 2.3 - 2.7 mm. Females are predominantly black with yellow on the anterior surface of the foretibia and mandibles. The head and thorax are minutely imbricate, giving the surface of the body a tesselate appearance. Males are lighter colored than females; the head is brownish ferruginous to black with yellow on the mandibles, labrum, clypeus and supraclypeal area. The pronotum is light brown and the rest of the mesosoma darker brown. The metasoma is ferruginous and the male T7 is tubular and bears a distinct median, longitudinal carina on the apical margin.

Distribution – Collected most frequently in the vicinity of Deep Canyon, Riverside county, but also occurrs in the arid parts of San Bernardino and Imperial counties, California; Pima, Pinal counties, Arizona; Baja California Sur, Mexico (Fig. 35).

Phenology – April through May; August through October.

Floral associations – Collected most commonly on *Eschscholtzia* (7 females/12 males) and *Euphorbia* (*hirtella*) (6 females/7 males) but also on *Ferrocactus* (*acanthodes*) (2 females/3 males), *Eriogonum* (1 female), *Echinocactus* (2 males) and *Opuntia* (1 male).

Perdita carinata and the next two species (*P. mortuaria* and *P. opacella*) are similar to each other, sharing the following characters: (1) male T7 tubular, lateral margins nearly touching ventrally, (2) genital capsules similar in shape, (3) scutum and scutellum minutely imbricate, lacking erect setae and seemingly impunctate,

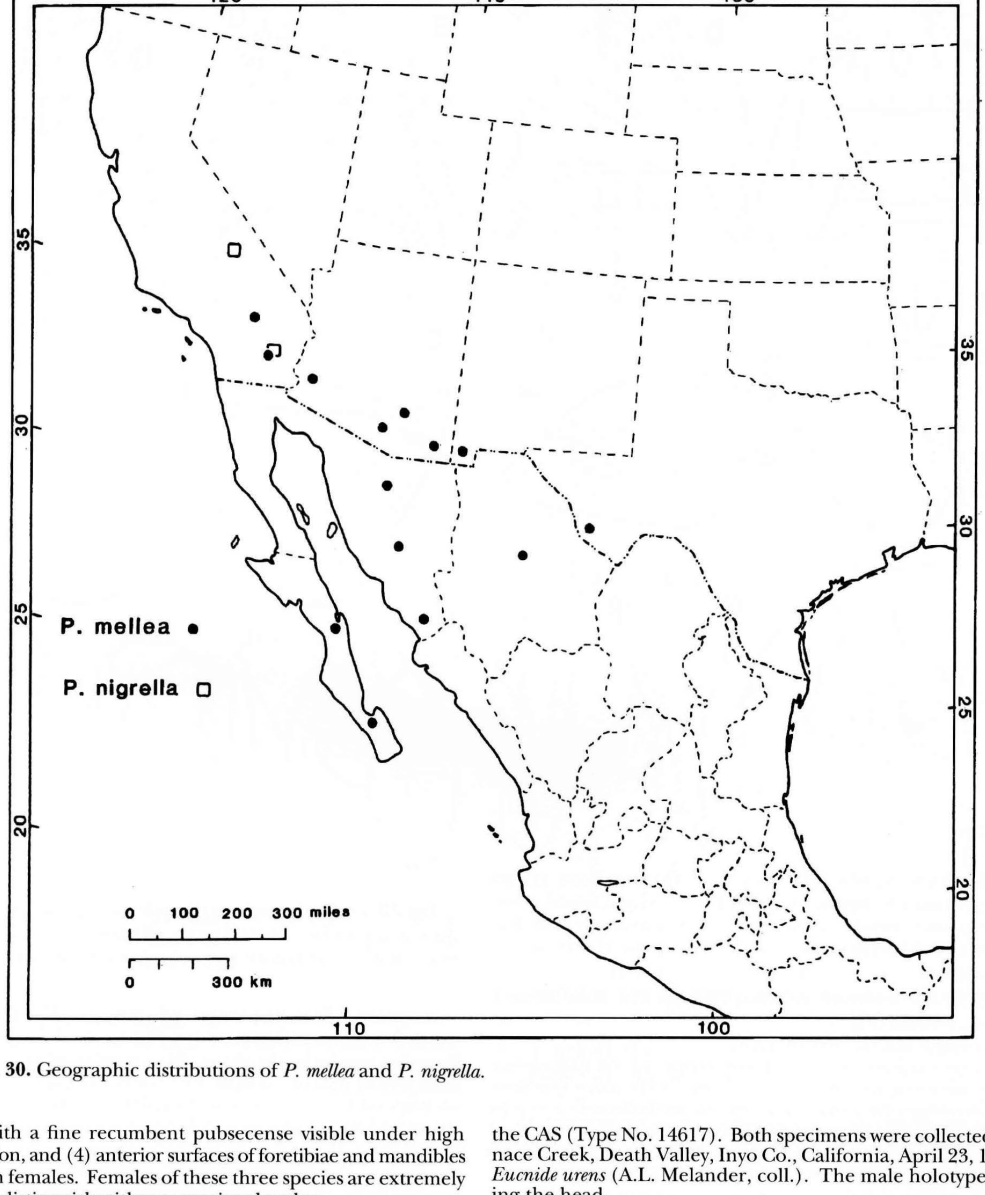

Fig. 30. Geographic distributions of *P. mellea* and *P. nigrella.*

however with a fine recumbent pubsecense visible under high magnification, and (4) anterior surfaces of foretibiae and mandibles yellowish in females. Females of these three species are extremely difficult to distinguish without associated males.

Perdita (*Macroterella*) *mortuaria* Timberlake

(Figs. 33, 35)

Perdita (*Macroterella*) *mortuaria* Timberlake, 1954:362 [description]; 1954:361 [key]; 1956:324 [additional material]; 1960:126 [additional material]; 1968:7-8 [key]; 1968:10 [additional material]; 1980:7 [new records].

Type material – The male holotype and allotype are located in the CAS (Type No. 14617). Both specimens were collected at Furnace Creek, Death Valley, Inyo Co., California, April 23, 1935, on *Eucnide urens* (A.L. Melander, coll.). The male holotype is missing the head.

Diagnosis – Forewing length 2.4-2.7 mm. The female is similar to *P. carinata,* but facial foveae are longer and parallel the eye margin (Timberlake, 1968:7). The male is similar to *P. carinata* in coloration and cuticular sculpturing. However, in *P. mortuaria,* although the male T7 is tubular, it lacks the longitudinal carina at the apex.

Distribution – Desertic and arid montane regions of Riverside, Inyo, Imperial counties, California; Maricopa, Yuma, Mojave, Co-

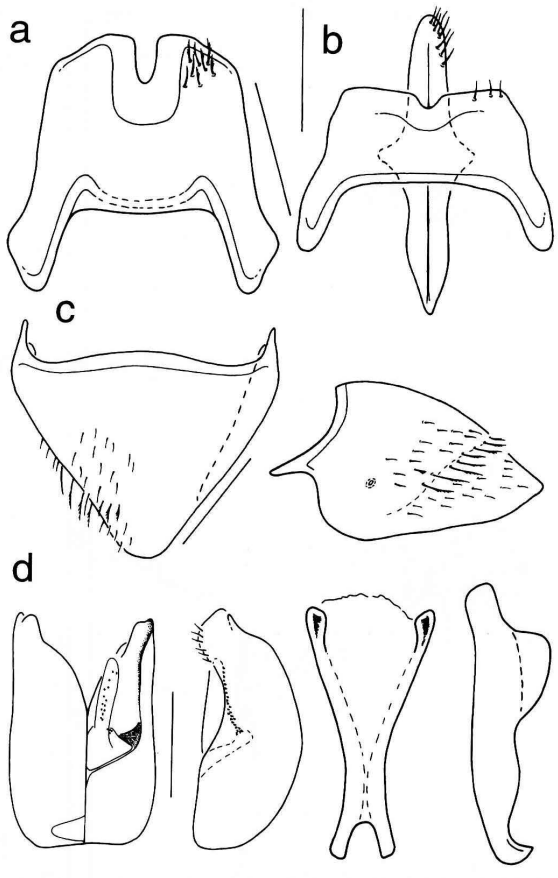

Fig. 31. *Perdita tristella.* **(a)** female head, **(b)** male head, **(c),** female S6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

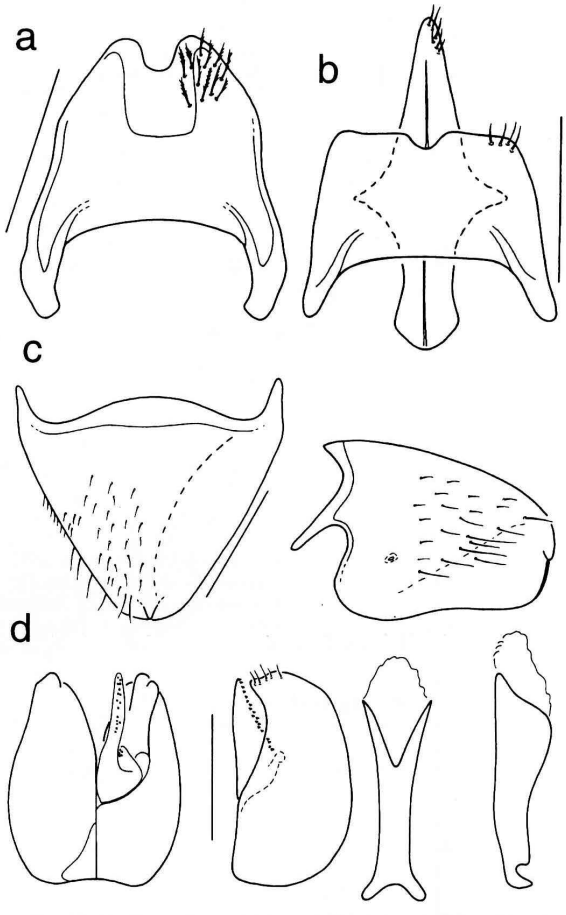

Fig. 32. *Perdita carinata.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

conino, Cochise counties, Arizona; Hidalgo Co., New Mexico; Clark Co., Nevada (Fig. 35).

Phenology – March through June.

Floral associations – Collected most frequently on *Eschscholtzia* (*parishii, mexicana, darwinensis, minutiflora*) (10 females/6 males), which is seemingly the source of pollen, but also collected on *Prosopis* (4 females/1 male), *Eriogonum* (*inflatum, abertianum*) (2 females/1 male), *Eucnide urens* (5 males), *Larrea divaricata* (1 male), *Phacelia calthifolia* (1 female), *Echinocereus engelmanni* (1 female).

Perdita (*Macroterella*) *opacella* Timberlake

(Figs. 27c, 34, 35)

Perdita (*Macroterella*) *opacella* Timberlake, 1956:324 [description of female]; 1968:7,8 [key]; 1968:8 [description of male].

Type material – The female holotype is located in the CAS (Type No. 14644). This specimen was collected at Marble Canyon, near Lee's Ferry, Grand Canyon, Coconino Co., Arizona, June 5 1953, on *Stanleya* (G.D. Butler, coll.).

Diagnosis – Forewing length 2.5 - 2.8 mm. The female is similar to *P. carinata* and *P. mortuaria,* but can be distinguished from these two species by the shape of the pygidial plate (broader and more obtuse apically) and by the presence of faint metallic greenish tinge on the frons (Timberlake, 1968:8). Males are similar to the preceding two species in coloration and punctation; however, with more creamy-white facial maculation, which extends up to the level of the antennal sockets. Males are most easily distinguished from all other members of *Macroterella* by the shape of T7: dorsoapically it bears two lateroposteriorly directed protuberances which are separated along the posterior margin of the tergum by a deep median slit. As in the other two species, the lateral margins of T7 meet ventrally to form a tube through which the genitalia project, in some specimens. The genital capsule is distinctive as well.

Distribution – Desertic regions of Coconino and Cochise counties, Arizona; San Juan Co., Utah (Fig. 35).

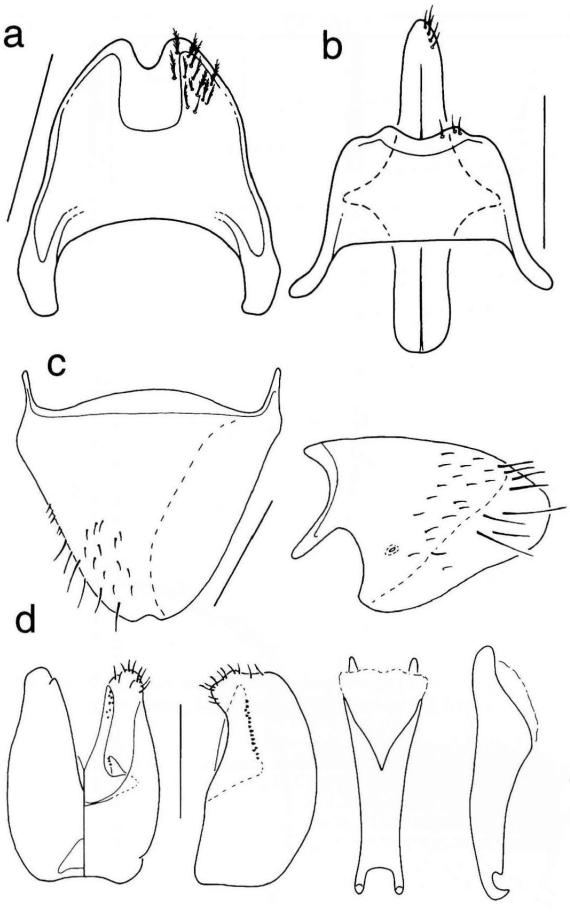

Fig. 33. *Perdita mortuaria.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

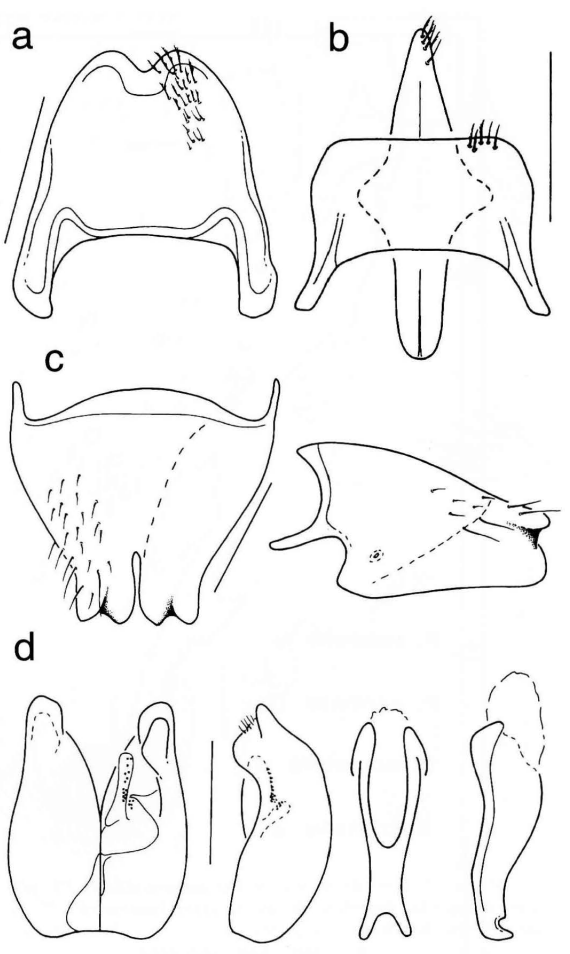

Fig. 34. *Perdita opacella.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Phenology – June and August.

Floral associations– *Cleome lutea* (7 females/11 males) is almost certainly the primary source of pollen for this species, although females have been collected on *Stanleya* (1 female) and *Eriogonum abertianum neomexicanum* (1 female).

Subgenus *Macrotera* Smith

Macrotera Smith, 1853:130 [description]; Cresson, 1878:70-71 [additional species]; Cockerell, 1904 [additional species]; Cockerell, 1905; Timberlake, 1954:352 [diagnosis and key to species]; 1958:375-378 [additional species and key to species]; Snelling & Danforth, 1992 [additional species, keys to species].

Type species – *Perdita bicolor* Smith, monobasic.

Diagnosis – The species in this subgenus are distinguished by: (1) large body size (forewing length usually exceeding 4.5 mm and often approaching 5.0 mm); (2) glossa two or more, usually three, times length of prementum (Fig. 27d); (3) male with pygidial plate on T7; (4) second maxillary palpal segment longer than first, or any other segments.

All the species in this subgenus are oligolectic on *Opuntia.* Females of this subgenus are very hard to identify to species without associated males. The female S6 is the most useful structure for distinguishing females of this group. The subgenus ranges from Oklahoma and northern Texas (*P. crassa* and *P. texana*) to southern Mexico (*P. bicolor*).

Snelling and Danforth (1992) published taxonomic notes, keys, and illustrations of *Macrotera.*

Subgenus *Macroteropsis* Ashmead

Macroteropsis Ashmead, 1899:85; Cockerell & Porter, 1899:417 [de-

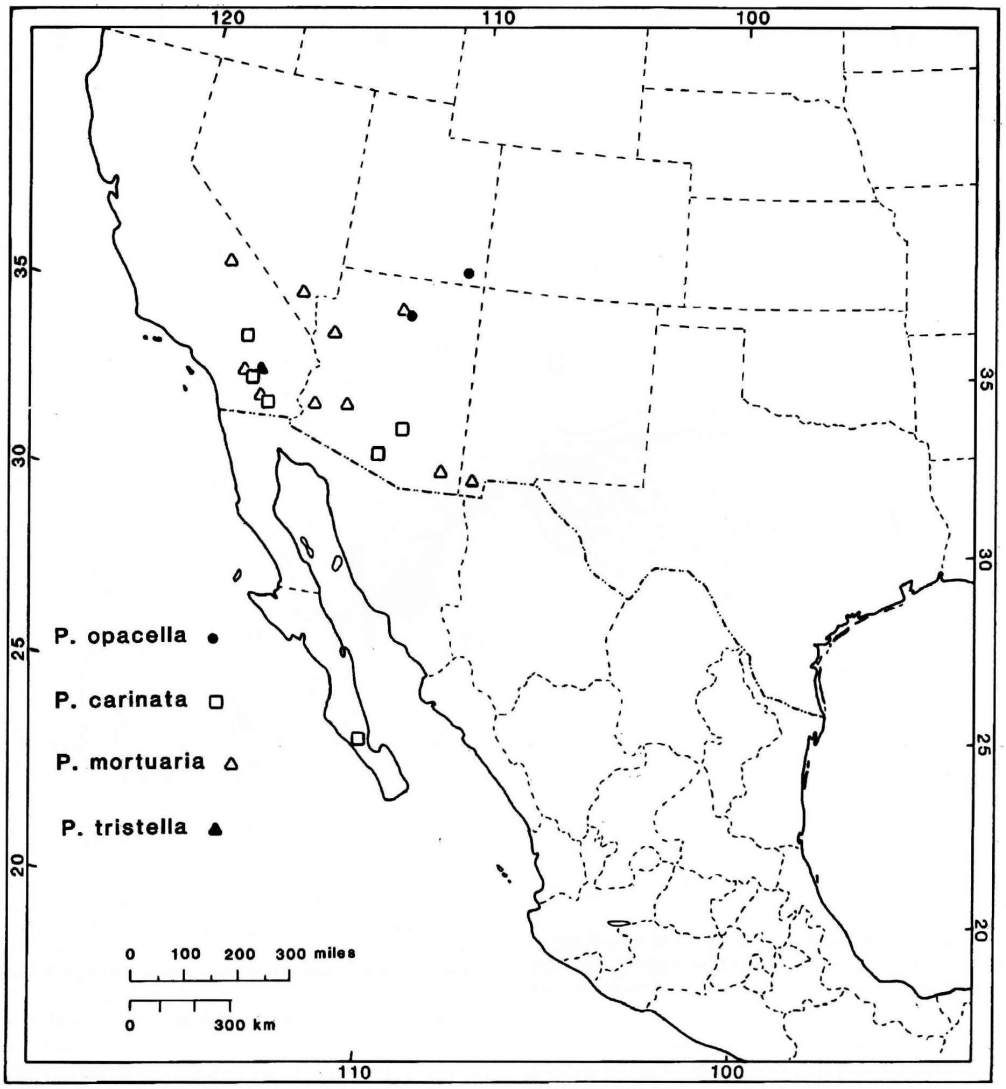

Fig. 35. Geographic distributions of *P. opacella, P. carinata, P. mortuaria, P. tristella.*

scription]; Timberlake 1954:356-360 [description, key to species]; 1956:323 [additional material; 1960:124 [additional material]; 1962:87-89 [key to males, additional material]; 1968:4-7 [additional species]; 1980:2-5 [key to females, additional species].
Type species – *Perdita latior* Cockerell, by original designation.

Diagnosis – This subgenus is easily recognized based on the following characters: (1) second labial palpus arising subapically on first, and first tapering to an acute point (Fig. 36 a,b), (2) maxillary palpal segments, especially distal segments, reduced in length and obscure or totally absent (in most species the number of maxillary palpal segments is reduced from 6 to 5 or 4), (3) head of female relatively broad (maximum width roughly 1.3 times the length from vertex to clypeal margin), and eyes protuberant, (4) females with dense, erect, finely branched white setae over head and mesonotum, (5) female metasoma dark brown to black, usually lacking any reddish coloration, (6) metallic sheen on frons and mesosoma.

Perdita (*Macroteropsis*) *arcuata* Fox

(Figs. 37, 41)

Perdita arcuata Fox, 1893:18 [description of male]; Cockerell, 1896:54.
Perdita dinognatha Cockerell 1922a:19 [description of male].

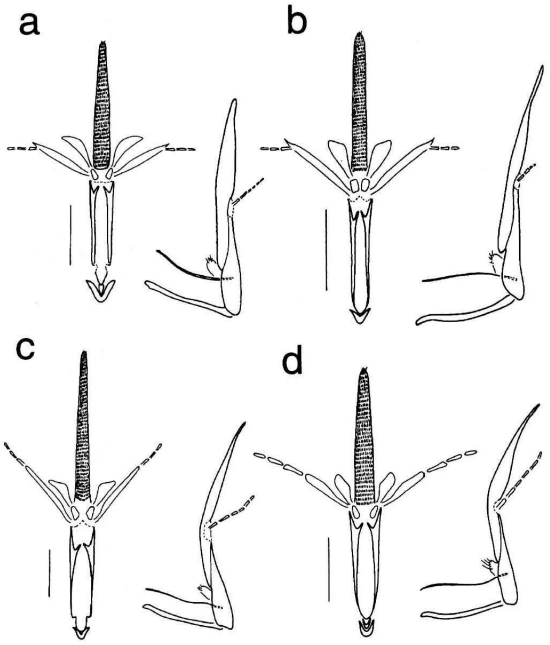

Fig. 36. Mouthpart morphology, females. **(a)** *P. echinocacti,* **(b)** *P. portalis,* **(c)** *P. azteca,* **(d)** *P. solitaria* (Scale bar = 0.5 mm).

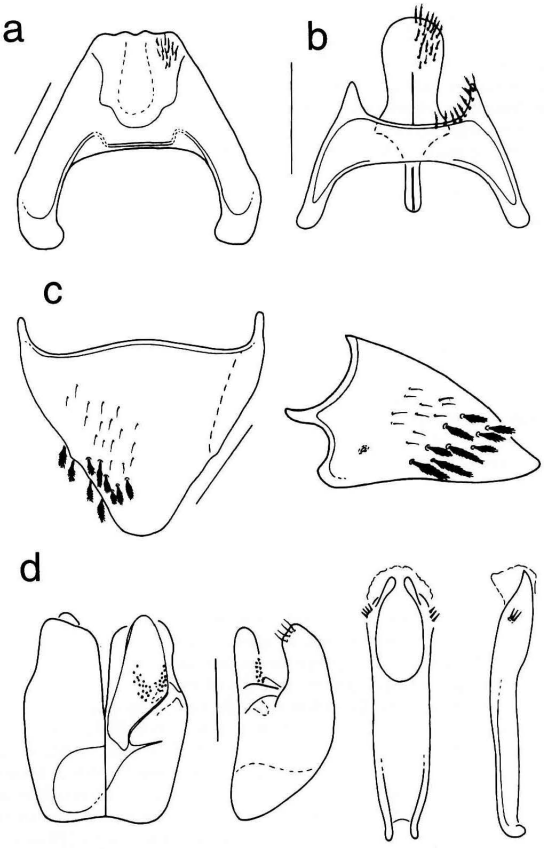

Fig. 37. *Perdita arcuata.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Perdita (*Macroteropsis*) *arcuata arcuata:* Timberlake, 1953:968; 1954:358 [new localities]; 1954:357 [key]; 1962:87 [key]; 1968:4 [additional material and comments on distribution]; 1980:3 [key]. *Perdita* (*Macropteropsis*) *arcuata dinognatha:* Timberlake 1953:968 [additional material]; Timberlake, 1954:359 [description of female and additional material]; 1980:3 [key].

Type material – The male lectotype (Type No. 275) and the allotype (Type No. 276) are located in the CAS. The lectotype was collected at Calmalli Mines, Baja California Norte, Mexico (Fox, coll.). The male holotype of *P. dinognatha* is located in the NMNH (Cat. No. 24895) and was collected at San Diego Co., California, April (Coquillett, coll.).

Diagnosis – Forewing length 3.0 - 4.0 mm. Males of this species can be distinguished from all other species of *Macroteropsis* by the simple mandibles, lacking a pollex, and by the quadrate labrum with a transverse ridge across the middle (all other species have a round or ovoid labrum lacking a transverse ridge). Females have a uniquely-shaped S6 with the central pale area broad (length only 2-3 times width) while in *P. echinocacti* and *P. latior* the central pale area is very slender (length 5-6 times width). This is the best character for positively identifying females.

The two previously recognized subspecies of *P. arcuata* are not recognized here because no consistent suite of congruent characters could be found to delineate them. The two characters on which the distinction was based were the presence/absence of yellow maculation on the male clypeus and the number of maxillary palpal segments (5 or 6). The majority of the male specimens from Baja California lack yellow maculation on the clypeus (Timberlake, 1953:968) and most (10/12; 7 males, 5 females) of the specimens I dissected had 6-segmented maxillary palpi. In constrast, all 22 (16 males, 6 females) of the specimens from the states of Arizona and California had 5-segmented palpi and most of these males had yellow maculation on the clypeus. However, the specimens from San Benito Co., California, present somewhat of a problem. They possess both the derived traits of lacking yellow maculation and of reduced maxillary palpi. Timberlake (1968:4) considered them to belong to the subspecies *arcuata* because of the former character, and concluded that the true range of *P.* (*a.*) *arcuata* was coastal California from San Benito Co. to Baja California Sur. However, 5-segmented maxillary palpi suggest that this population is more closely related to the other California (and Arizona) populations than to those in Baja California.

Description – FEMALE – Head: (1) width 1.52-1.88 mm (x = 1.69 ± 0.05; n=6); (2) 1.3-1.4 times broader than long (as measured from the vertex to the lower margin of the clypeus); (3) clypeus weakly imbricate-punctate; (4) frons granulate with small punctures and with linear depression along midline; (5) vertex imbricate-punctate; (6) gena imbricate with scattered punctures; (7) head coloration dark brown with metallic blue or green sheen, strongest on the frons; (8) whole head clothed in white, finely-branched setae, recumbent and shorter on clypeus and frons, erect and longest

on vertex and genae; (9) inner margins of eyes diverging very slightly above; eyes brownish; (10) posterior ocelli at level of upper margin of compound eye; (11) facial foveae deeply impressed, elongate and broadened slightly dorsally; (12) scape of antenna equal in length to flagellar segments 1-6, first flagellar segment slightly longer than second.

Mouthparts: (13) labrum with central depressed area, clothed with erect, finely-branched setae, and central transverse ridge; (14) mandible rufous, bidentate, with sulcus originating at mandibular acetabulum and extending diagonally across base of mandible; (15) glossa elongate, roughly 1.25 times longer than prementum; (16) paraglossa slender basally but expanding distally into broad, brushlike apex; (17) labial palpus 4-segmented, first segment longer than remaining segments combined and second segment inserted subapically on first; (18) galeal comb absent or present and very small; (19) maxillary palpus 5-6 segmented, distal segments (3 to end) greatly shortened so that overall length of palpus short.

Mesosoma: (20) pronotum brownish with transverse sulcus dorsally and fringe of erect setae on leading edge; dorsal surface glabrous and with scattered punctures becoming imbricate laterally; pronotal lobe with coarsely branched setae; (21) mesoscutum black with metallic blue sheen; surface minutely imbricate-punctate with two types of setae: small recumbent setae and more widely scattered elongate erect setae; notauli (weak), parapsidal lines and central longitudinal sulcus present; (22) mesoscutellum and metanotum brownish with similar sculpturing and setae; (23) mesopleuron brown with faint metallic blue or green sheen; sculpturing imbricate-punctate anterior to scrobe, reticulate posterior to scrobe; scrobal sulcus absent; (24) metapleuron reticulate, lacking setae; (25) propodeum reticulate dorsally, becoming glabrous posteriorly; paired patches of erect setae flank central glabrous area; laterally, below spiracle, cuticle imbricate; (26) intertegular distance 1.12 - 1.18 mm ($x = 1.16 \pm 0.01$; n=6); (27) forewing length 3.16 - 4.00 mm ($x = 3.75 \pm 0.12$; n=6); wings slightly opaque with brownish tinge, veins brown; (28) legs brown; forecoxa with long, erect, unbranched, posterior-directed setae; (29) basitibial plate distinct, the cental portion clothed in recumbent setae; (30) scopal hairs on anterior surface of tibia simple, becoming finely branched along outer edge of tibia; (31) midtibial spur finely serrate and gently hooked at apex; (32) hind tibial spurs subequal in length (inner slightly longer than outer) and finely serrate; (33) tarsal claws all bifid.

Metasoma: (34) terga dark brown, with paler transparent apical margin; (35) terga 1-5 minutely imbricate-punctate with small posteriorly-directed, recumbent setae; on cleared terga pale membranous slits extend from leading edge to spiracle; (36) deeply impressed fovea on lateral edge of T2; (37) T5 with long, erect, plumose setae along posterior margin; (38) graduli on T2-T4; (39) T6 with raised, acutely pointed pygidial plate flanked by dense, plumose setae; central portion of pygidial plate colliculate; (40) sterna slightly paler than terga; sterna 1-5 similar in sculpturing and vestiture to terga; (41) S6 as in Fig. 37a; (42) sternal graduli lacking on all segments except S1, where they are present only laterally.

MALE – Head: (43) width 1.20 - 1.96 mm ($x = 1.57 \pm 0.08$; n=8); (44) quadrate, 1.4 - 1.6 times broader than long; (45) clypeus broad and dorso-ventrally compressed, surface weakly imbricate-punctate; (46) frons granulate with many small punctures and with median linear depression above level of antennal sockets; (47) vertex imbricate-punctate; (48) gena imbricate-punctate; (49) head deep brown, becoming paler at clypeus which may be yellow in specimens from California (except San Benito Co.), Arizona and Nevada; blue or olive metallic sheen becoming strongest on frons; (50) head clothed in finely-branched setae, recumbent on clypeus and supraclypeal area, erect and longer on upper part of frons, vertex and genae; (51) inner margins of eyes subparallel; (52) posterior ocelli just above level of upper margin of compound eyes; (53) facial fovea weakly impressed, oval or teardrop shaped; (54) antennae brown.

Mouthparts: (55) labrum pale brown to yellow, rectangular, broader than long, with transverse ridge and scattered, finely-branched setae; (56) mandible yellow, with reddish tips; no subapical tooth and with outer sulcus (as in female); (57-61) male mouthparts as in female except paraglossae slender and acutely pointed, not broad and brushlike.

Mesosoma: (62-67) coloration and sculpturing of mesosoma as in female; (68) intertegular distance 0.92 - 1.24 ($x = 1.08 \pm 0.04$, n=8); (69) forewing length 2.84 - 3.72 ($x = 3.33 \pm 0.12$; n=8); wings as in female except for veins forming the posterior and distal margins of second medial cell (veins Cu1a and 2m-cu), which are distinctly weaker than other veins; (70) legs brown, or in some specimens, with yellow maculation on inner surface of fore-tibia; (71) basitibial plate concave and well defined around entire margin; surface of plate with a few apressed setae; (72) outer surface of hind tibia imbricate with stout moss-like setae; (73-75) tibial spurs and tarsal claws as in female.

Metasoma: (76) terga brown to reddish brown; (77) terga 1-6 minutely punctate with small, recumbent, white setae; (78) single row of stout moss-like setae across T6; (79) faint longitudinal fovea on lateral edge of T2; (80) T7 with paired patches of moss-like setae apically; lacking pygidial plate; anterior edge convex in dorsal view; (81) graduli present on terga 2-6; weak lateral extensions of graduli on T2 and T3; (82) sterna similar in coloration to terga; (83) sterna 1-6 similar in vestiture and coloration to terga 1-6; (84) sternal graduli present laterally on S1 and complete on S2-S5; (85) S7 and S8 as in Fig. 37b; (86) genital capsule with broad, horizontal gonocoxites clothed apically with setae; (87) volsellar cuspis large with papillae located dorsally sometimes restricted to base of cuspis and sometimes extending to the apex; (88) digitus with papillae; (89) penis valves with two patches of stout setae laterally (Fig. 37d).

Distribution – Throughout desertic and montane regions of Riverside, San Bernardino, Inyo, San Diego, Imperial, San Benito counties, California; Mojave, Yavapai, Coconino, Yuma, Pima, Maricopa counties, Arizona; Clark Co., Nevada; Washington, San Juan counties, Utah; Baja California Norte and Sur, Mexico (Fig. 41).

Phenology – April through July, and October (in Baja California).

Floral associations – Collected primarily on *Sphaeralcea* (*ambigua, rosacea*) (224 females/340 males); but also collected on *Hibiscus denudatus* (1 female), *Malva* (2 males), *Eriogonum polyfolium* (1 female), *Eriodictyon trichocalyx* (1 male), *Echinocactus acanthodes* (1 female), *Eschscholtzia californica* (1 male), *Malacothamnus orbiculatus* (1 male), *Encelia frutescens* (1 male/1 female), *Hemizonia lobbii* (1 male).

Perdita (*Macroteropsis*) *echinocacti* Timberlake

(Figs. 36a, 38, 41)

Perdita (*Macroteropsis*) *echinocacti* Timberlake, 1954:360 [description]; 1954:357 [key]; 1960:125 [additional material]; 1962:87 [key]; 1980:3 [key]; Simpson & Neff, 1987:426 [biology].

Perdita tepicensis Timberlake, 1968:5 [description of male] NEW SYNONYMY.

Type material – The holotype male and allotype are in the CAS (Type No. 14499). The type specimens were collected 4 1/2 miles

above Pepper Sauce Canyon, Santa Catalina Mts., Pima Co., Arizona, August 14, 1940, on *Echinocactus* (Timberlake, coll.). The holotype male of *P. tepicensis* is at KU, and was collected west of Tepic, Nayarit, Mexico, 1600 ft., Aug. 19, 1961 (C.F. Bennett, coll.).

Diagnosis – Forewing length 3.0 - 3.7 mm. Males have yellow maculation on the labrum, clypeus and supraclypeal area up to the level of the antennal sockets, and have a bluish metallic sheen on the frons and mesonotum. Unlike males of the other members of *Macroteropsis* (except *P. latior*), males of this species have a pygidial plate on T7 formed by two parallel carinae. The presence of a median, posteriorly-directed prong on male S2 will distinguish this species from all other *Macroteropsis*. In both males and females the maxillary palpi are distinctly 6-segmented; segments 1 and 2 are subequal and relatively long; segments 3-6 are much shorter. Females can be distinguished from other *Macroteropsis* (except *P. latior*) by the shape of S6 (central clear area 5-6 times longer than wide), by the maxillary palpi, and by the distinctly bluish tinge to the frons and mesonotum.

I see no reason to consider the holotype of *P. tepicensis* distinct from *P. echinocacti*. According to Timberlake this species differs from the former in the sculpturing of the mesonotum. However, the seemingly unique cuticular sculpturing of the *P. tepicensis* holotype results from dirt caked on the specimen.

Distribution – Pinal, Pima, Santa Cruz, Cochise counties, Arizona; states of Sonora, Sinaloa and south to Nayarit (the type locality of *P. tepicensis*), Mexico (Fig. 41). Additional specimens are recorded from Chihuahua, Mexico by PCAM (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – August through September.

Floral associations – *Kallstroemia* (*grandiflora*) (44 females/54 males), *Echinocactus* (*wislezeni* [sic]) (12 females/36 males), *Convolvulus* (6 females/16 males), *Antigonum* (3 females), *Boerhaavia* (1 female/1 male), *Ferocactus* (1 female/2 males). Although this species is commonly thought to be a cactus oligolege, the frequency of females on *Kallstroemia* suggests this as a possible pollen source as well.

Perdita (*Macroteropsis*) *latior* Cockerell

(Figs. 39, 41)

Perdita latior Cockerell, 1896:53 [description]; Cockerell, 1897a:354 [flower record].

Macroteropsis latior: Cockerell and Porter, 1899:417.

Perdita (*Macroteropsis*) *latior:* Timberlake, 1953:968 [additional material]; Timberlake, 1954:359 [localities and flower records]; 1954:357 [key]; 1962:87 [key]; 1980:3 [key].

Type material – One female co-type is located in the USNM (Type No. 3365). This specimen was collected at Las Cruces, Dona Ana Co., New Mexico, August 1895, on *Sphaeralcea angustifolia* (Cockerell, coll.). Two additional co-types are located at the Academy of Natural Sciences of Philadelphia. Both specimens were collected at the same locality as the co-type in the USNM. Along with the locality and host plant labels, the male bears the label "Ckll. 4815" and the female bears the label "Ckll. 4822." I designate the male at the Academy of Natural Sciences the lectotype.

Diagnosis – Forewing length 2.9 - 4.0 mm. *P. latior* is very similar to *P. echinocacti*. The males can be distinguished from *P. echinocacti* because they lack the prong on the apical margin of S2. The yellow facial maculation is less extensive on the face of *P. latior,* scarcely reaching the upper margin of the clypeus laterally, whereas in *P. echinocacti* the yellow extends upward along the inner margins of the eyes to above the level of the antennal sockets. Maxillary palpi are 6-segmented, as in *P. echinocacti,* but segment 5 is often indistinct. Females of these two species are difficult to distinguish (Timberlake, 1954:360) and it is best to rely on associated males. However, in the absence of males, this species may be distinguished from *P. echinocacti* by (1) the more bluish tinge on frons and mesoscutum in *P. echinocacti,* and (2) the more elongate and slender central pale area on the female S6 in *P. latior,* as compared to *P. echinocacti.*

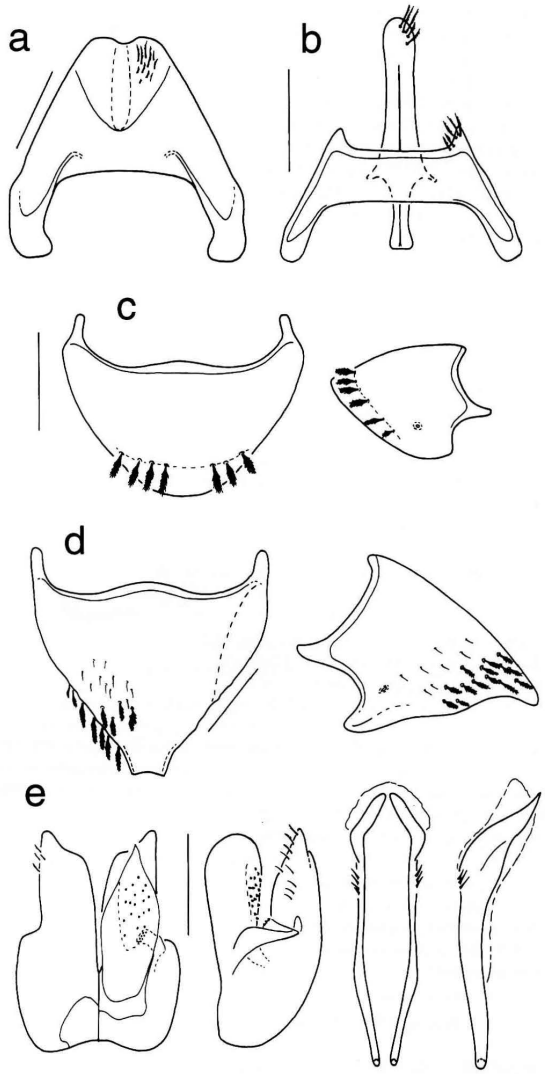

Fig. 38. *Perdita echinocacti.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T6, dorsal and lateral views showing moss-like setae along posterior margin, **(d)** male T7, dorsal and lateral views, **(e)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Distribution – Desertic regions of Cochise, Yavapai, Coconino, Apache, Navajo, Gila, Mojave, Pima, Pinal counties Arizona; Dona Ana, Sandoval, Santa Fe, Hidalgo, Grant, Valencia, McKinley, Lin-

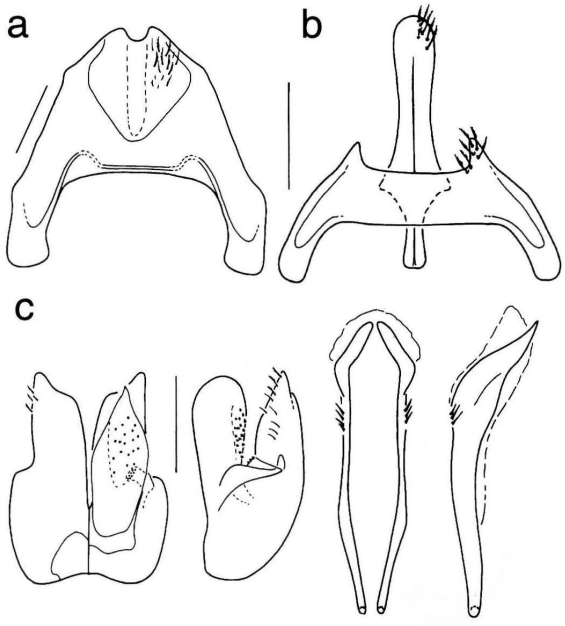

Fig. 39. *Perdita latior.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

coln counties New Mexico; Robertson Co., Texas; Clark Co., Nevada; Sonora, Mexico (Fig. 41). Additional specimens are recorded from Chihuahua, Mexico by PCAM (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – May through October.

Floral associations – The vast majority of specimens were collected on *Sphaeralcea* (*angustifolia*) (115 females/108 males) and this is apparently the sole pollen source, but specimens have also been collected on *Heterotheca subaxillaris* (5 females), *Malva* (1 male), *Sida heteracea* [sic] (1 female), *Tidestromia lanuginosa* (1 male), *Helenium hoopesi* (1 female) and *Lygodesmia juncea* (1 female).

Perdita (*Macroteropsis*) *magniceps* Timberlake

(Figs. 40, 41)

Perdita (*Macroteropsis*) *magniceps* Timberlake, 1960:124 [description of male].

Type material – The male holotype is located in the CAS (Type No. 14597). The holotype was collected 17 miles east of Deming, Luna Co., New Mexico, September 13, 1957, on *Kallstroemia* (Timberlake, coll.).

Diagnosis – Forewing length 3.2 - 3.8 mm. At the time Timberlake described this species there was only a single, rather large-headed, male specimen available. Since his original description was written, a long series of both male and female specimens have been collected at several additional localities and a more complete description of male variation can be given along with a description of the female (see below). The male of this species is clearly distinct from all other species of the subgenus *Macroteropsis*. In all specimens the head is orange-ferruginous with small, black facial foveae. In the largest specimens (head width = 1.6 mm) the head is almost entirely glabrous except for sparsely distributed, small, appressed hairs over the frons and genae and a band of erect setae running across the vertex posterior to the ocelli. In lateral view, the gena of the largest males is expanded to 1.9 times the width of the compound eye, while the smallest specimens show almost no genal enlargement. Unlike in all other members of *Macroteropsis* there can be extensive orange-ferruginous maculation over the mesosoma. The extent of the maculation covaries with overall body size. In the smallest specimens orange-ferruginus maculations are restricted to the pronotum and a small central spot on the scutellum. In the largest specimens orange maculation covers the pronotum, the lateral portions of the mesopleuron, metapleuron and the entire propodeum, although the dorsal and posterior surfaces of the propodeum appear brownish. Dorsally, small lateral portions of the scutum, immediately above the forewing bases, the central parts of the scutellum and the mesono-

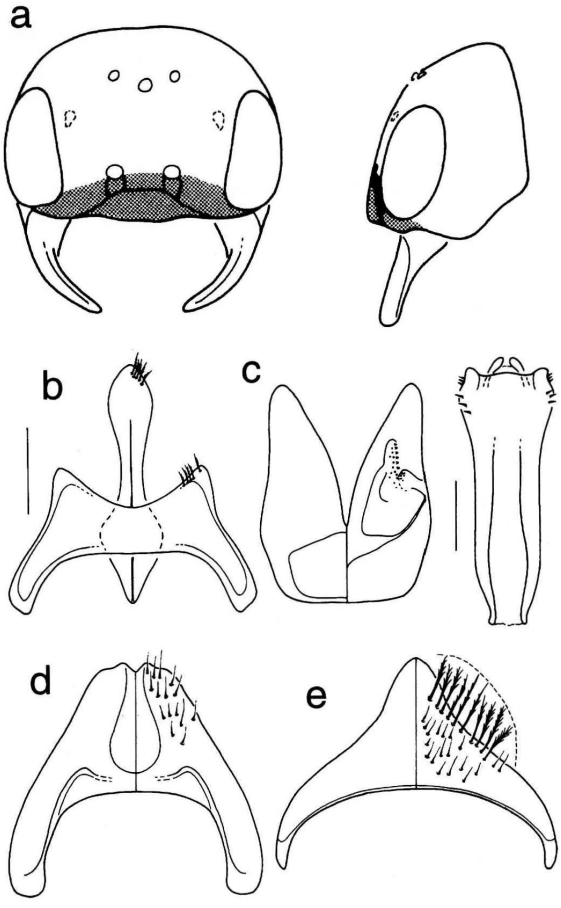

Fig. 40. *Perdita magniceps.* **(a)** male head, frontal and lateral views, **(b)** male S7 and S8, **(c)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view), **(d)** female S6, **(e)** female T6.

tum are orange-ferruginous. The maxillary palpi are four-segmented, but unlike those of *P. haplura* and *P. portalis,* the mandibles are simple. The genital capsule, S7 and S8 slide mounted by Timberlake (slide no. 887) agree in all respects with the new material of this species, and serve to further distinguish this species from all other *Macroteropsis.*

Females are distinctive in showing similarly colored, although much less extensively distributed, orange-ferruginous maculation on the head and, in some specimens, the lateral lobes of the pronotum. Orange-ferruginous maculation is present on the mandibles, labrum, and clypeus, and extends upward as two thin bands on either side of the eye which meet dorsally and form a broad band along the vertex. The orange band extends medially from the eye and reaches the lateral ocellus in all specimens. The presence of orange-ferruginous bands on the vertex will separate this species from all others treated herein.

One of the most distinctive feature of this species, in both the males and females, is the extensive development of dense, closely appressed setae clothing the mesoscutum, scutellum and lateral portions of the mesopleura. These setae gives the females in particular a frosted appearance.

This species is united with *P. latior, P. echinocacti* and *P. arcuata* by the setae on the lateral surfaces of the penis valves.

Description – FEMALE – Head: (1) width 1.35 - 1.60 mm (x = 1.51 ± 0.20; n=10); (2) 1.30 - 1.40 (x = 1.34 ± 0.01; n=10) times broader than long (as measured from the vertex to the lower margin of the clypeus); (3) clypeus distinctly and densely punctate, with weakly imbricate regions between the punctation; (4) frons imbricate with small punctures and with linear depression along midline; (5) vertex imbricate with scattered punctations; (6) gena imbricate with scattered punctures; (7) head coloration primarily black with coppery sheen on frons and orange-ferruginous maculation with the following distribution: clypeus (along lower margin or extending upward to cover entire surface), in some specimens, small medial area between the antennal bases, thin band surrounding compound eyes and extending medially from upper margins of the compound eyes along vertex to lateral ocellus (never meeting to form continuous band across vertex); (8) entire face up to level of compound eyes clothed in closely appressed thick white setae in unworn specimens; more elongate, erect setae along vertex, lateral, and posterior portions of head; (9) inner margins of eyes diverging above; eyes brownish (in pinned specimens); (10) posterior ocelli at level of upper margin of compound eye; (11) facial foveae weakly impressed, slender (0.32 mm in length); difficult to see through hairs on unworn specimens; (12) scape of antenna equal in length to flagellar segments 1-5, first flagellar segment slightly longer than second.

Mouthparts: (13) labrum with central depressed area, clothed with erect, finely-branched setae, and central transverse ridge; (14) mandible yellow, becoming reddish apically; bidentate, with sulcus originating at mandibular acetabulum and extending diagonally across base of mandible; (15) glossa elongate and slender, roughly equal to prementum in length; (16) paraglossa slender basally but expanding distally into broad, brushlike apex; (17) labial palpus 4-segmented, first segment longer than remaining segments combined and second segment inserted subapically on first; (18) galeal comb absent or present and very small; (19) maxillary palpus 4-5 segmented at most, distal segments (3 to end) greatly shortened so that overall length of palpus short.

Mesosoma: (20) pronotum blackish with orange-ferruginous maculation weakly developed on lateral lobes and dorsal surface; dorsal and lateral surfaces imbricate and hairless; (21) mesoscutum black with metallic green or coppery sheen; surface coarsely imbricate-punctate with extremely dense clothing of white recument setae and more widely scattered longer, erect setae; notauli (weak), parapsidal lines and central longitudinal sulcus present; (22) mesoscutellum and metanotum dark brownish with similar sculpturing and setae but with more erect than recumbent setae; (23) mesopleuron weakly metallic; sculpturing reticulate-punctate dorsally becoming imbricate-punctate ventrally; setae on lateral portions of mesopleuron erect, white, and finely branched; setae on ventral portion of mesopleuron simple, distinct from ones on lateral portion; scrobal sulcus absent; (24) metapleuron reticulate, lacking setae; (25) propodeum imbricate to reticulate laterally; posterior surface glabrous; dorsal surface (propodeal triangle) with metallic bluish sheen and weakly imbricate; lateral and posterior surfaces separated by dense row of erect, white setae similar to those on metanotum and scutellum; (26) intertegular distance 1.12 - 1.28 mm (x = 1.18 ± 0.017; n=10); (27) forewing length 3.20 - 3.80 mm (x = 3.46 ± 0.04; n=10); wings milky white with pale yellowish to whitish wing veins; (28) legs mostly brown but apices of forefemur, most of foretibia, apices of mesofemur, base of mesotibia and apex of metafemur orange to fuscous; (29) basitibial plate quadrate and well-developed, with a few recumbent setae on its concave surface; (30) scopal hairs on anterior surface of tibia simple, becoming finely branched along outer edge of tibia; (31) midtibial spur finely serrate and very slightly hooked at apex; (32) hind tibial spurs finely serrate; subequal in length; (33) tarsal claws all bifid.

Metasoma: (34) most terga dark brown, with paler transparent apical margin; sometimes with weakly-defined light brown areas on anterior and dorsal surface of T1 and dorsal surface of T2; (35) terga 1-5 minutely imbricate-punctate with small posteriorly-directed, recumbent setae; pale membranous slits extending from leading edge to spiracle visible in cleared terga; (36) deeply impressed fovea on lateral edge of T2; (37) T5 with long, erect, plumose setae along posterior margin; (38) graduli on T2-T4; (39) T6 with raised, acutely pointed pygidial plate flanked by dense, plumose setae; central portion of pygidial plate colliculate; (40) sterna dark brown like terga; S1-S5 similar in sculpturing and vestiture to terga; (41) S6 as in *P. arcuata* (Fig. 40d); (42) sternal graduli lacking on all segments except S1, where they are present only laterally.

Distribution – Luna and Socorro counties, New Mexico; northern part of Chihuahua, Mexico (Fig. 41). This species seems to be restricted to mostly sandy soils as compared to other members of *Macroteropsis* since most collecting sites were located within large dune formations, such as the Samalayuca sand dunes south of El Paso, Texas, and a dune system running northward from Deming to Hatch, New Mexico (Brown & Lowe 1980).

Phenology – August and September.

Floral associations – The male holotype was collected on *Kallstroemia,* but all of the other 94 specimens were collected on *Sphaeralcea* sp., in particular, *S. incana. P. magniceps* is clearly a *Sphaeralcea* oligolege since pollen-laden females carry *Sphaeralcea* pollen in their scopae. *S. incana* is a distinctive species of *Sphaeralcea* that grows up to two meters in height. Like *P. magniceps, S. incana* is restricted to very dry, sandy localities in New Mexico and northern Mexico (Martin & Hutchins 1981), suggesting that these two species form a close association.

Perdita (*Macroteropsis*) *portalis* Timberlake

(Plates I and II; Figs. 36b, 42, 43, 45)

Perdita (*Macroteropsis*) *portalis* Timberlake, 1954:357 [description and key]; 1956:323 [additional material]; 1960:125 [additional material]; 1962:27 [key]; 1968:4 [new record]; 1980:5 [description of macrocephalic male]; 1980:3 [key].

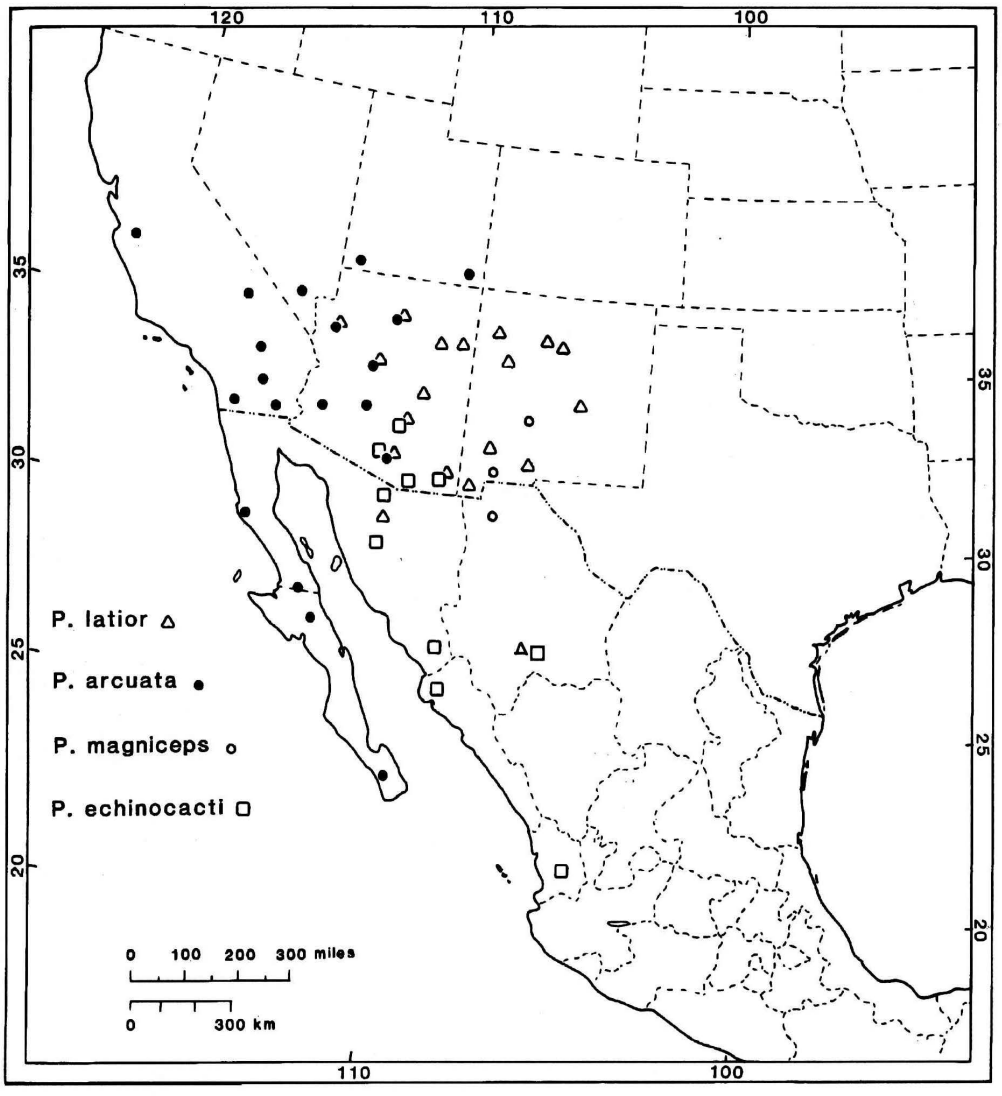

Fig. 41. Geographic distributions of species in the subgenus *Macroteropsis,* in part.

Type material – The male holotype and allotype are located in the CAS (Type No. 14670). The types were collected at Portal, Cochise Co., Arizona, August 12, 1940, on *Sphaeralcea,* (Timberlake, coll.).

Diagnosis – Forewing length 2.7 - 3.4 mm. This species and *P. haplura* are the smallest in *Macroteropsis.* Males of these two species are similar in having greatly enlarged, apparently glandular, facial foveae (black in *P. haplura* and cream colored in *P. portalis*), strongly protuberant, grey-blue eyes which are convergent below, elongate, thick, white erect setae over the vertex, meso- and metanotum (as well as the usual fine, recumbent pilosity), an acutely pointed clypeus which hangs over the base of the labrum (in the smallest specimens this feature can be weakly developed) and a broad, spade-like S8 (Fig. 42e). Furthermore, males have a conspicuous, acute inner tooth at the apex of the mandibles. Males of these two species can be distinguished based on the color of the facial foveae (see above), size (*P. portalis* smaller than *P. haplura*), the shape of T7 (apex more slender in *P. portalis* [Fig. 42g] than in *P. haplura* [Fig. 44e]) and the genital capsule (cuspis expanded in *P. haplura* and with extensive papillae over upper surface). Female *P. portalis,* like *P. haplura,* have a black head and mesosoma covered with scattered, erect, finely-branched, white setae and a fuscous metasoma. *P. portalis* can be distinguished from *P. haplura* by the presence of yellow maculation on the fore-

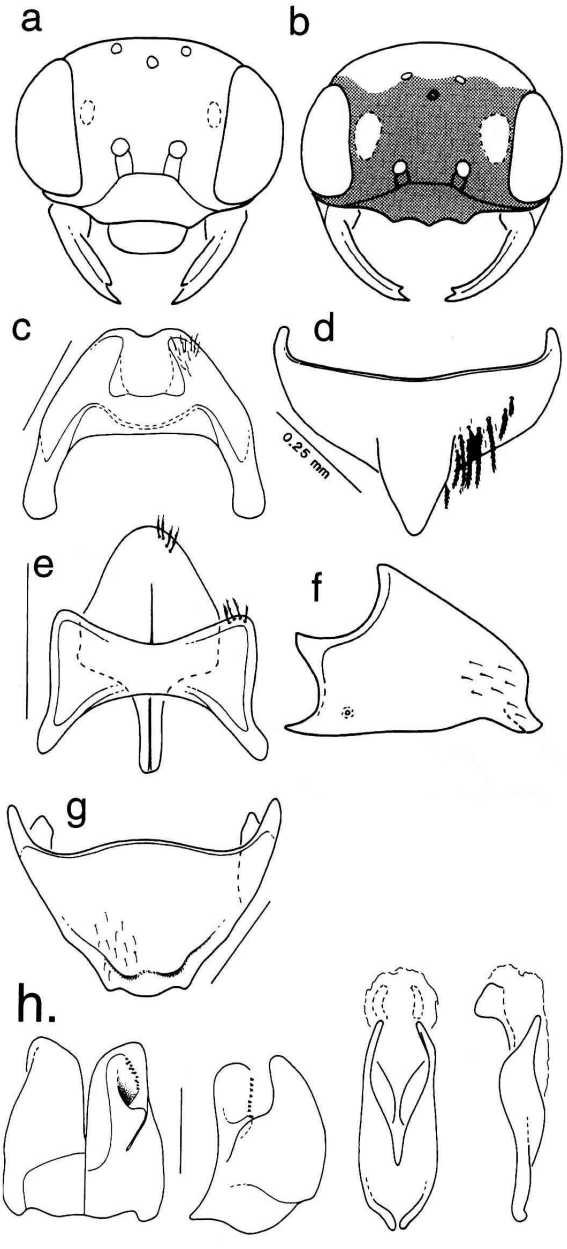

Fig. 42. *Perdita portalis.* **(a)** female head, **(b)** male head, **(c)** female S6, **(d)** female T6, **(e)** male S7 and S8, **(f)** male T7, lateral view, **(g)** male T7, dorsal view, **(h)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

tibia, by the weaker convergence of the eyes ventrally, by the shape of S6 and by the more slender, acutely pointed pygidial plate.

A pair of male specimens, collected at Gray mountain, Coconino Co., Arizona, July 26, 1952 by M. Cazier and R. Schrammel, differ from the majority of the *P. portalis* specimens in the structure of the genital capsule and T7. The apex of the genital capsule is more quadrate and the mesal margins of the volsellae are obtusely produced (Fig. 43a). The apex of the male T7, which possesses a broad, blunt protuberance in typical *P. portalis,* bears an acute, horizontal shelf (Fig. 43b). One of these males was seen by Timberlake (1956:323). In the absence of more material from this locality I see no reason to consider these specimens a different species from *P. portalis;* more likely they simply represent the extreme of the morphological variation in this species.

P. portalis, like *P. mellea,* has dimorphic males. The male referred to in the diagnosis is the typical flight-capable male most common in collections (Plate I). However, in 1970, J.G. Rozen, Jr., discovered in nests a flightless, macrocephalic male morph (described by Timberlake, 1980:5-6) (Plate II). The behavior and morphology of this bizarre and highly derived male morph is described elsewhere (Danforth, 1991b).

Distribution – Semidesert/grassland regions of Cochise, Graham, Coconino counties, Arizona; Luna, Hidalgo, Socorro, Otero, Chaves, Eddy, Quay counties, New Mexico; Hudspeth Co., Texas; Zacatecas and Coahuila states, Mexico (Fig. 45). Additional specimens are recorded from Chihuahua and Durango, Mexico by PCAM (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – July through September.

Floral associations – The majority of specimens were collected on *Sphaeralcea* (*angustifolia, laxa*), (79 females/29 males) and this is clearly the predominant pollen source for this species, but some specimens have been collected on *Aplopappus* (2 males) and *Tidestromia lanuginosa* (1 female).

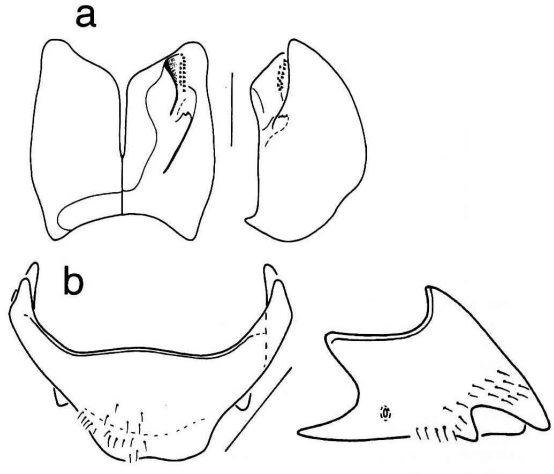

Fig. 43. *Perdita portalis* (variant form). **(a)** male genital capsule (dorsal, ventral and lateral views), **(b)** male T7, dorsal and lateral views.

Perdita (*Macroteropsis*) *haplura* Cockerell

(Figs. 44, 45)

Perdita haplura Cockerell, 1922a:19 [description of female].
Perdita (*Macroteropsis*) *haplura:* Timberlake, 1954:357; 1960:124 [redescription of female]; 1962:87 [description of male]; 1968:4 [additional material]; 1980:3 [key].

Type material – The holotype female is in the NMNH (Type No. 24896). The type was collected at Sanderson, Terrell Co., Texas, May 9, 1912 (J.D. Mitchell, coll.).

Diagnosis – Forewing length 3.2 - 4.0 mm. Males of *P. haplura* and *P. portalis* share greatly enlarged, apparently glandular, facial foveae (black in *P. haplura* and cream colored in *P. portalis*), strongly protuberant, grey-blue eyes (in pinned specimens) which are convergent below, elongate, thick, white, erect setae over the vertex, meso- and metanotum (as well as the usual fine, recumbent pilosity), an acutely-pointed clypeus which hangs over the base of the labrum (in the smallest specimens this feature can be weakly developed), a broad, spade-like S8 (Fig. 44d) and elongate, bifid mandibles. These two species can be distinguished based on the features given above (in the diagnosis of *P. portalis*). Female *P. haplura*, like *P. portalis*, have a black head and mesosoma with scattered, erect, finely branched setae and a fuscous metasoma. The density of the white mesosomal setae will distinguish these two species from all other members of *Macroteropsis*. *P. haplura* can be distinguished from *P. portalis* by the lack of yellow maculation on the foretibiae, by the stronger convergence of the eyes ventrally (Fig. 44a), by the shape of S6, and by the broader, less acutely pointed pygidial plate.

Distribution – Desert/grassland habitats of Lincoln and Dona Ana counties, New Mexico; Terrell, Pecos, Val Verde counties, Texas (Fig. 45).

Phenology – April through May and September.

Floral associations – Collected primarily on *Sphaeralcea* (*angustifolia* var. *cuspidata*) (5 females/4 males), but also on *Fallugia paradoxa* (1 female).

Subgenus *Cockerellula* Strand

Lutziella Cockerell, 1922c:1.
Cockerellula Strand 1932:196; Timberlake 1953:963-968 [key to species, additional species]; 1954:354 [description, key to species]; 1956:323 [additional species]; 1960:122-123 [key to males; additional species]; 1968:2-4 [key to males, additional species]; 1980:1-2 [additional species].

Type species – *Perdita opuntiae* Cockerell, by original designation for *Lutziella* and autobasic for *Cockerellula*.

Diagnosis – This subgenus can be distinguished from the other subgenera treated here by the following combination of characters: (1) un-segmented, latero-apical projection on side of gonocoxite, (2) extremely slender S7, (3) modifications of male S1-S3 (in some species), (4) female metasoma reddish, (5) 6-segmented maxillary palpus, (6) second labial palpal segment arising apically on first, and (7) apodemes of the penis valves curving dorsad.

Perdita (*Cockerellula*) *azteca* Timberlake

(Figs. 36c, 46, 50)

Perdita (*Cockerellula*) *azteca* Timberlake, 1954:355 [description]; 1954:354 [key]; 1960:122 [key]; 1968:2 [key].

Type material – Holotype male and allotype are in the CAS (Type No. 14438). They were collected at Zimapan, Hidalgo, Mexico, June 11, 1951 (P.D. Hurd, coll.).

Diagnosis – Forewing length 3.6 - 4.0 mm. With *P. opuntiae* this is the largest species of *Cockerellula*, with forewing lengths reaching 4.0 mm. Males are easily distinguished from all other close relatives by the uniquely-shaped seventh tergum, with paired blunt prongs extending dorso-posteriorly from the posterior margin (Fig. 46d), by the hind tibial spurs, which have particularly long teeth on the inner surface, which gives them a pectinate appearance, and by the male genital capsule (Fig. 46f). In addition, males have a unique combination of sternal modifications: the first sternum is produced medially into a pucker-like fold, and S2 and S3 have obtuse transverse protuberances along their posterior margins (strongest on S3) (Fig. 62a). Females can be recognized by the presence of a raised triangular area between the antennal

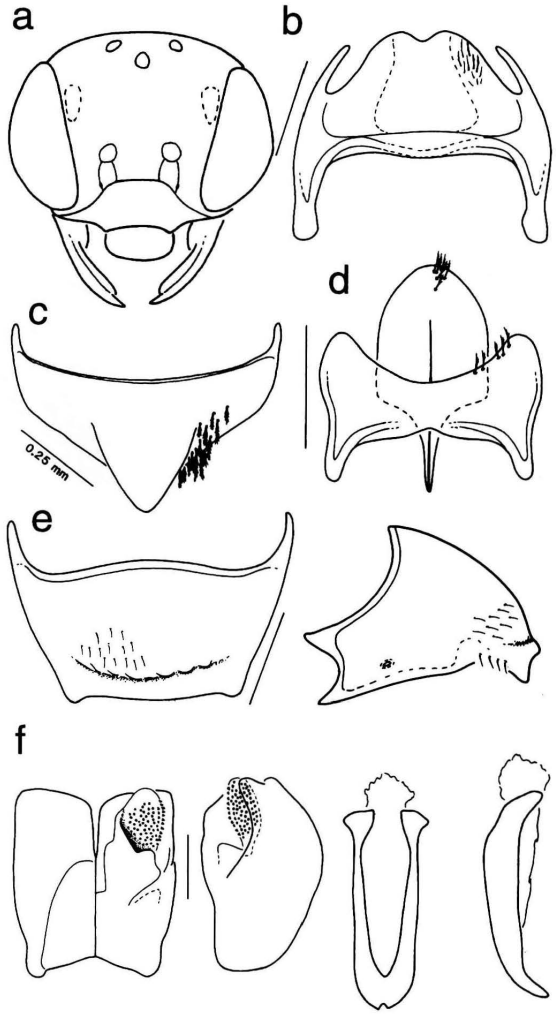

Fig. 44. *Perdita haplura.* **(a)** female head, **(b)** female S6, **(c)** female T6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

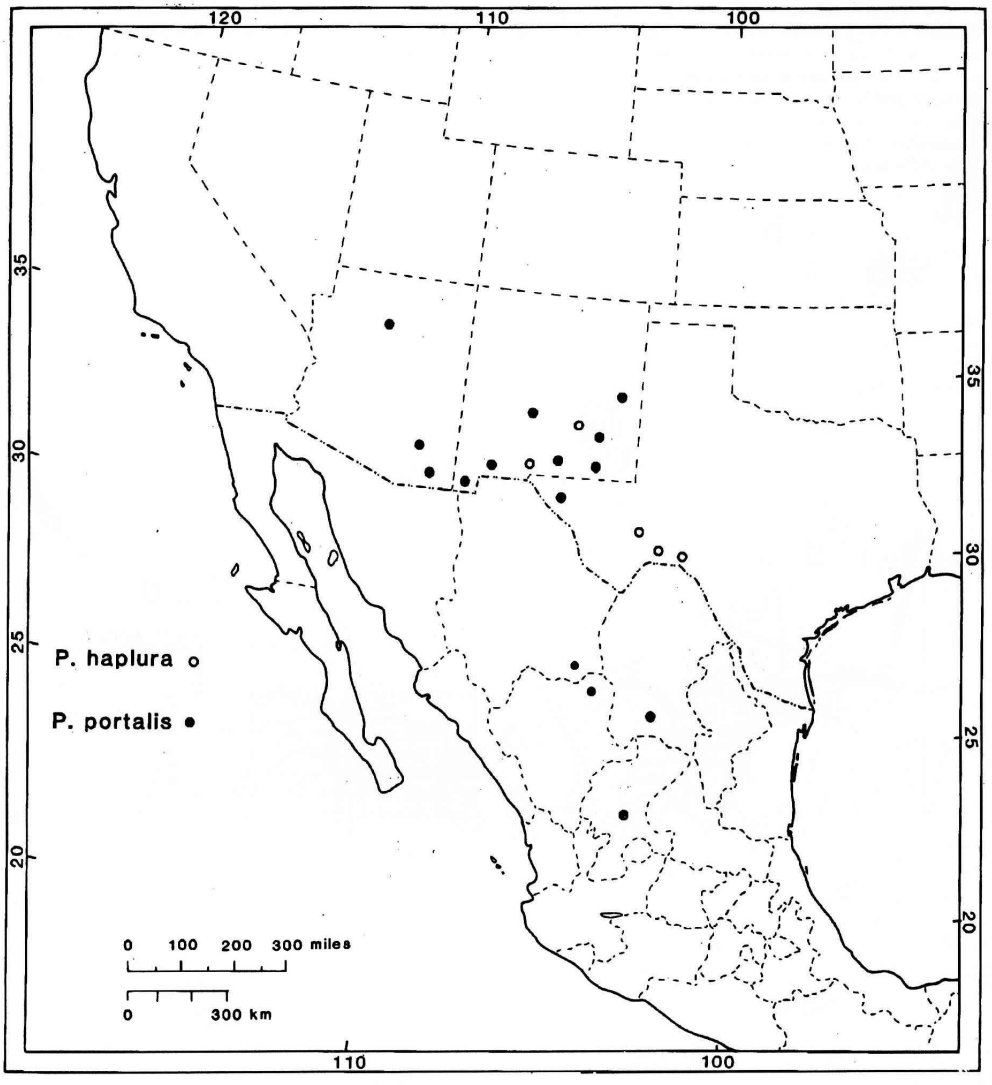

Fig. 45. Geographic distributions of species in the subgenus *Macroteropsis,* in part.

sockets which extends down to the lateral corners of the clypeus. On the postero-lateral surfaces of the propodeum there are patches of dense, finely-branched, white setae, which are present in only a few other species, and the female mandibles are particularly bright yellow. The pygidial plate is especially broad and blunt in *P. azteca* (e.g., in comparison to *P. knulli* and *P. bidenticauda* (Fig. 46b), and S6 is uniquely shaped also (Fig. 46a).

Distribution – States of Hidalgo, San Louis Potosí, Jalisco, Puebla and Oaxaca, Mexico; up to 8100 ft. in elevation (Fig. 50).

Phenology – March through July, and rarely into September.

Floral associations – Collected exclusively on Cactaceae: *Opuntia* (25 females/16 males), *Eysenhardtia polystachya* (7 females), *Echinocactus* (2 females) and *Ferrocactus* (1 male).

Perdita (*Cockerellula*) *bidenticauda* Timberlake

(Figs. 47, 50)

Perdita (*Cockerellula*) *bidenticauda* Timberlake, 1953:965 [description]; 1953:964 [key]; 1954:356; 1954:354 [key]; 1960:122 [key]; 1968:2 [key].

Type material – The male holotype is at KU. The holotype was collected at Cooper's Store, Big Bend National Park, Brewster Co., Texas, April 11, 1947, on *Opuntia* (Michener and Beamer, coll.).

Diagnosis – Forewing length 2.8 - 3.2 mm. Males of this species can be recognized by the T7 shape, which has paired, postero-apical processes, as in *P. azteca,* however much less well developed. The presence of obtuse transverse protuberances along the posterior margin of S2 and S3 (more pronounced on S3) and the *lack* of a pucker like fold on S1 will further distinguish this species. In the key to *Cockerellula,* Timberlake states that *P. bidenticauda* and *P. laticauda* are indistinguishable in the female sex (1954:355). I have found no characters which allow one to distinguish them. These two species may be distinguished from all others by the shape of the female S6, with the elongate central fused area and the deeply divided lateral portions (Fig. 47a).

Distribution – This species is known only from the type locality (Fig. 50).

Phenology – April.

Floral associations – All paratype and the holotype specimens (2 females/6 males) were collected on *Opuntia* flowers.

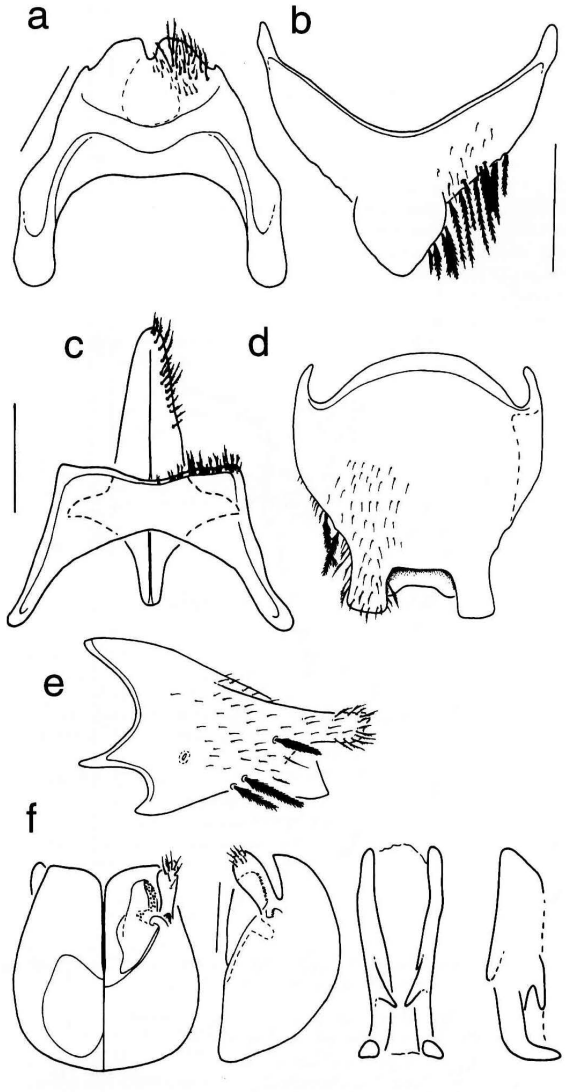

Fig. 46. *Perdita azteca.* **(a)** female S6, **(b)** female T6, **(c)** male S7 and S8, **(d)** male T7, dorsal view, **(e)** male T7, lateral view, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

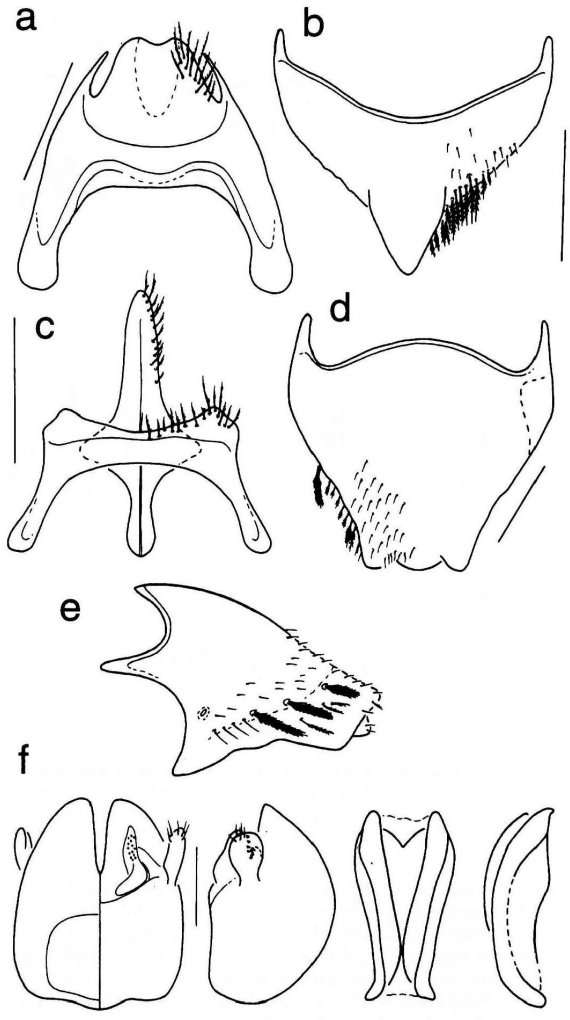

Fig. 47. *Perdita bidenticauda.* **(a)** female S6, **(b)** female T6, **(c)** male S7 and S8, **(d)** male T7, dorsal view, **(e)** male T7, lateral view, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

***Perdita* (*Cockerellula*) *knulli* Timberlake**

(Figs. 48, 50)

Perdita (*Cockerellula*) *knulli* Timberlake, 1960:123 [description]; 1960:122 [key]; 1968:2 [key].

Type material – The male holotype and allotype are located at OhS. Both were collected in the Davis Mts., Jeff Davis Co., Texas, June 21, 1949 (D.J. and J.N. Knull, colls.).
The female allotype bears similar labels.

Diagnosis – Forewing length 2.6 - 3.0 mm. Males can be distinguished by the narrowly bidentate apex of T7. S1 is produced medially into a pucker-like lobe (which will distinguish this species from *P. bidenticauda*) and S2 has paired diverging ridges which end at the posterior margin of the sternum in minute prongs or points. These are similar to the structures on the second sternum in *P. opuntiae,* but are less strongly protuberant. Female *P. knulli* can be recognized by the unique combination of very small size (wing length < 3.0 mm), reddish metasoma, and thick, dense erect setae on lateral surface of propodeum. The head and thorax are entirely dark, and have a distinct greenish sheen.

Distribution – Jeff Davis, Brewster and Pecos, Texas; Luna Co., New Mexico. Additional specimens from Mexico were collected by Terry Griswold and others at two localities (Ojinaga and Mapimi) in the states of Chihuahua and Durango; up to 4700' (Fig. 50).

Phenology – April to June and August to November (in the southern-most locality).

Floral associations – *Opuntia* (1 female/1 male) and *Acacia* (2 males); in Mexico, *Argemone turneri* (7 females/10 males) and *Opuntia imbricata* (3 females/2 males).

***Perdita* (*Cockerellula*) *rubida* Timberlake**

(Figs. 49, 50)

Perdita (*Cockerellula*) *rubida* Timberlake, 1968:2 [description of male]; 1968:2 [key].

Type material – The male holotype is reported to have been deposited in the CAS, but there is no record of this species in their type catalog or in the collection, nor is this specimen in the UCR collection. The holotype male was collected at 9 miles south of San Juan del Rio, Durango, Mexico, Aug. 21, 1960 (Arnaud, Ross, Rentz, colls.).

Diagnosis – Forewing length is 2.6-2.8 mm. This is the smallest *Cockerellula* species. Males can be easily recognized based on the paired, dorso-ventrally directed prongs arising preapically on the seventh terga. These are similar to prongs seen in *P. azteca* but more slender and acutely pointed. Metasomal sterna lack modifications seen in other members of this group. Yellow maculation on the face of males reaches the antennal sockets medially, but unlike all other close relatives, maculation extends above the antennal sockets along the inner margins of the eyes laterally. The background coloration of the head and metasoma is black with a metallic blue sheen. Females are entirely black with a metallic blue tinge to the head and mesosoma. The female S6 is similar to that of *P. azteca.* Timberlake did not have any female specimens of this species when he described it.

Although I have not seen the male holotype, nor any other specimens identified by Timberlake, I have two specimens, a male and a female, found in the undetermined *Perdita* collection of the AMNH, which appear to belong to this species. The male specimen agrees in all respects to Timberlake's description, except the AMNH specimen lacks any small fold along the posterior margin of S1, a feature Timberlake noted for the holotype. The shape of the S1 could easily vary depending on the condition of the specimen, and so I do not consider this discrepancy reason for describing the AMNH specimens as a new species.

Description – FEMALE – Head: (1) width 1.32 mm; (2) 1.1 times broader than long (as measured from the vertex to the lower margin of the clypeus); (3) clypeus weakly imbricate, shiny, with distinct punctation; (4) frons imbricate to granulate with distinct, widely scattered punctures and with linear depression along midline; (5) vertex imbricate-punctate; (6) gena imbricate with scattered punctures; (7) head except clypeus and central, raised triangular area between antennae distinctly bluish-green; (8) whole head clothed in fine, white, minutely branched setae, especially dense on genae, vertex and paraoccular areas; (9) inner margins of eyes subparallel, diverging slightly below; eyes brownish; (10) posterior ocelli slightly above upper margin of com-

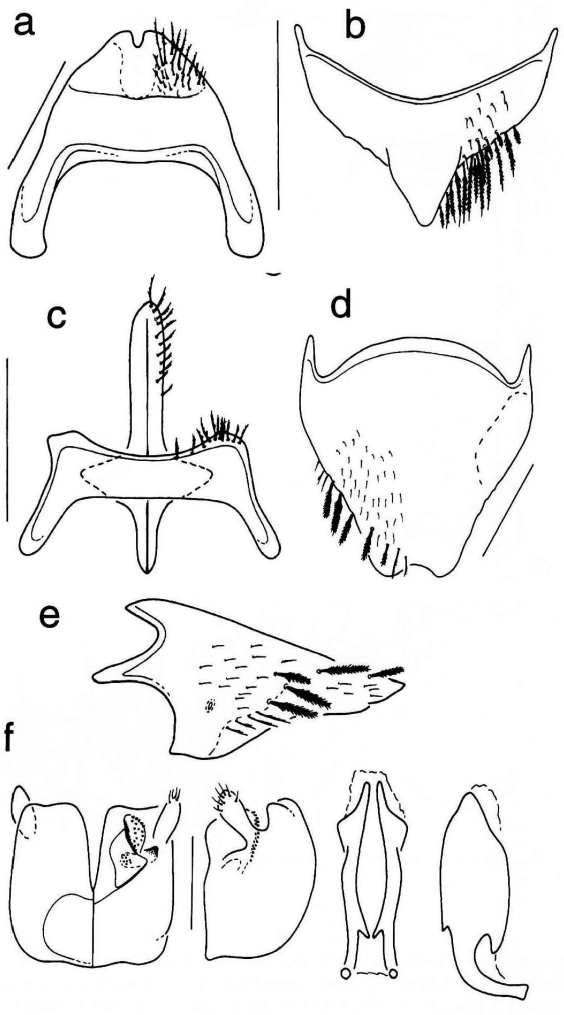

Fig. 48. *Perdita knulli.* **(a)** female S6, **(b)** female T6, **(c)** male S7 and S8, **(d)** male T7, dorsal view, **(e)** male T7, lateral view, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

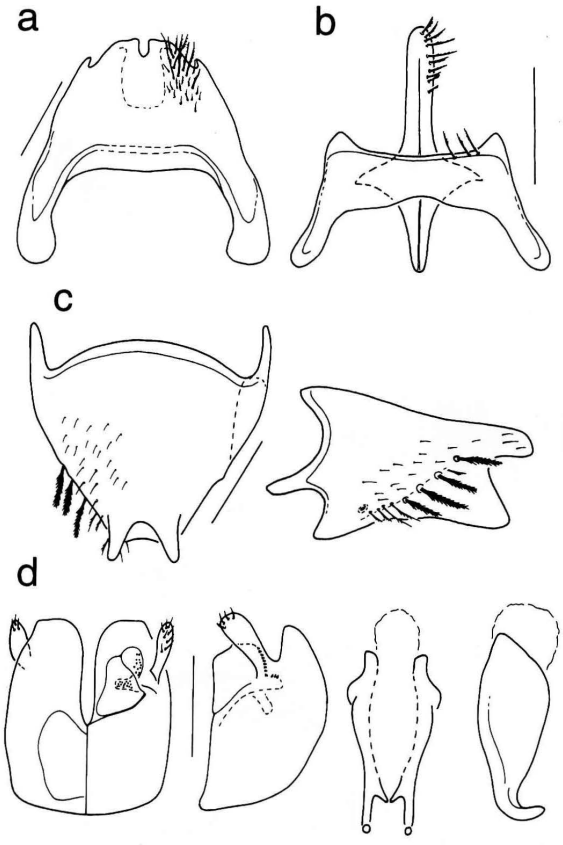

Fig. 49. *Perdita rubida.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

pound eye; lateral ocelli one ocellar width from central ocellus; (11) facial foveae distinct; 0.6 mm in length and slightly expanded above; (12) scape of antenna equal in length to flagellar segments 1-5, first and second flagellar segments equal in length.

Mouthparts: (13) labrum with central depressed area flanked by erect, finely branched setae and distal transverse ridge; apical margin with long, simple setae (14) mandible brown, becoming rufous apically; with distinct pre-apical tooth and sulcus originating at mandibular acetabulum and extending diagonally across base of mandible; (15) glossa elongate, roughly 1.2 times longer than prementum; (16) paraglossa slender basally but expanding distally into broad, brushlike apex; (17) labial palpus 4-segmented, first segment twice length of remaining segments combined and second segment inserted apically on first; (18) galeal comb short, consisting of only 6-7 small setae at proximal end of galea; (19) maxillary palpus 6-segmented, all segments distinct and well developed; palpus almost equal in length to distal part of galea.

Mesosoma: (20) pronotum brownish with faint bluish tinge dorsally; coriarious-imbricate dorsally, with weak punctures, becoming more distinctly coriarious laterally; (21) mesoscutum with distinct metallic blue-green sheen; surface finely imbricate and appearing dull, with weak punctures and mixture of erect, white, finely branched setae and smaller, silver, recumbent setae; notauli weakly developed, parapsidal lines and central longitudinal sulcus present; (22) mesoscutellum and metanotum similar in coloration, sculpturing and setae; (23) mesopleuron distinctly bluish; sculpturing finely alveolate dorsally, gradually changing to imbricate laterally; scrobal sulcus absent; (24) metapleuron imbricate; (25) propodeum distinctly and deeply alveolate dorsally, with weak rugae at propodeal-metanotal suture, becoming imbricate laterally; with small patches of erect, white setae separating the dorsal and lateral surfaces, as in other *Cockerellula;* entire propodeum bluish; (26) intertegular distance 0.92 mm; (27) forewing length 2.80 mm; wings translucent; veins brown; (28) legs brown, no yellow maculation evident; (29) basitibial plate distinct, quadrate apically, with a few stout recumbent setae on its concave surface; (30) scopal hairs on anterior surface of tibia simple, becoming finely branched along outer edge of tibia; (31) midtibial spur finely serrate and gradually curving to apex; (32) inner hind tibial spur distinctly longer than outer; both finely serrate; (33) tarsal claws all bifid.

Metasoma: (34) terga dark brown (35) terga 1-5 minutely imbricate with small posteriorly-directed, recumbent setae and a very few long, erect, finely branched setae laterally; (36) deeply impressed fovea on lateral edge of T2; (37) T5 with long, erect, plumose setae arising on distal 1/2 of tergum and small, median patch of finely branched setae on distal margin of tergum; (38) graduli on terga 2-4; lateral portions of graduli visible on T2 and T3; (39) T6 with raised, acutely pointed pygidial plate flanked by dense, plumose setae; central portion of pygidial plate colliculate; (40) sterna light brown; S1-5 similar in sculpturing and vestiture to terga except with a few long, finely branched setae ventrally; (41) S6 with apical slender notch and small lateral emarginations giving rise to two apico-lateral prongs (Fig. 49a); (42) sternal graduli lacking on all segments except S1, where they are present only laterally.

Distribution – Grant Co., New Mexico (AMNH specimens) and Durango, Mexico (holotype male) (Fig. 50). Additional specimens are recorded from Sonora, Mexico by PCAM (Ayala, et al., 1996), but I have not examined these specimens myself.

Phenology – August; up to 2100 m. elevation.

Floral associations – unknown.

Perdita (*Cockerellula*) *laticauda* Timberlake

(Figs. 51, 53)

Perdita (*Cockerellula*) *laticauda* Timberlake, 1953:967 [description]; 1953:964 [key]; 1954:356 [additional material]; 1960:122 [key].

Type material – The male holotype and allotype are at KU, and were collected 15 miles southeast of Dryden, Terrell Co., Texas, April, 13 1949, on *Gilia acerosa* (Michener and Beamer, colls.).

Diagnosis – Wing length 3.0 - 3.2 mm. This species is the sister species to *P. lobata.* Males of both of these species can be recognized based on the unique combination of a protuberant S1 (produced into a pucker like fold) and a rectangular patch of setae along the posterior margin of S3 (Fig. 62c). In both species the posterior margin of T7 is dorso-ventrally compressed, with sharp apico-lateral corners, and concave ventrally. This species can be distinguished from *P. lobata* based on the coloration of the head and mesosoma and posterior margin of the male T7. Male *P. lobata* have paler, more reddish head and mesosoma coloration, while in *P. laticauda* the background coloration of the head and mesosoma is dark brown with bluish metallic sheen. Furthermore, in *P. lobata* the posterior margin of T7 is more strongly emarginate

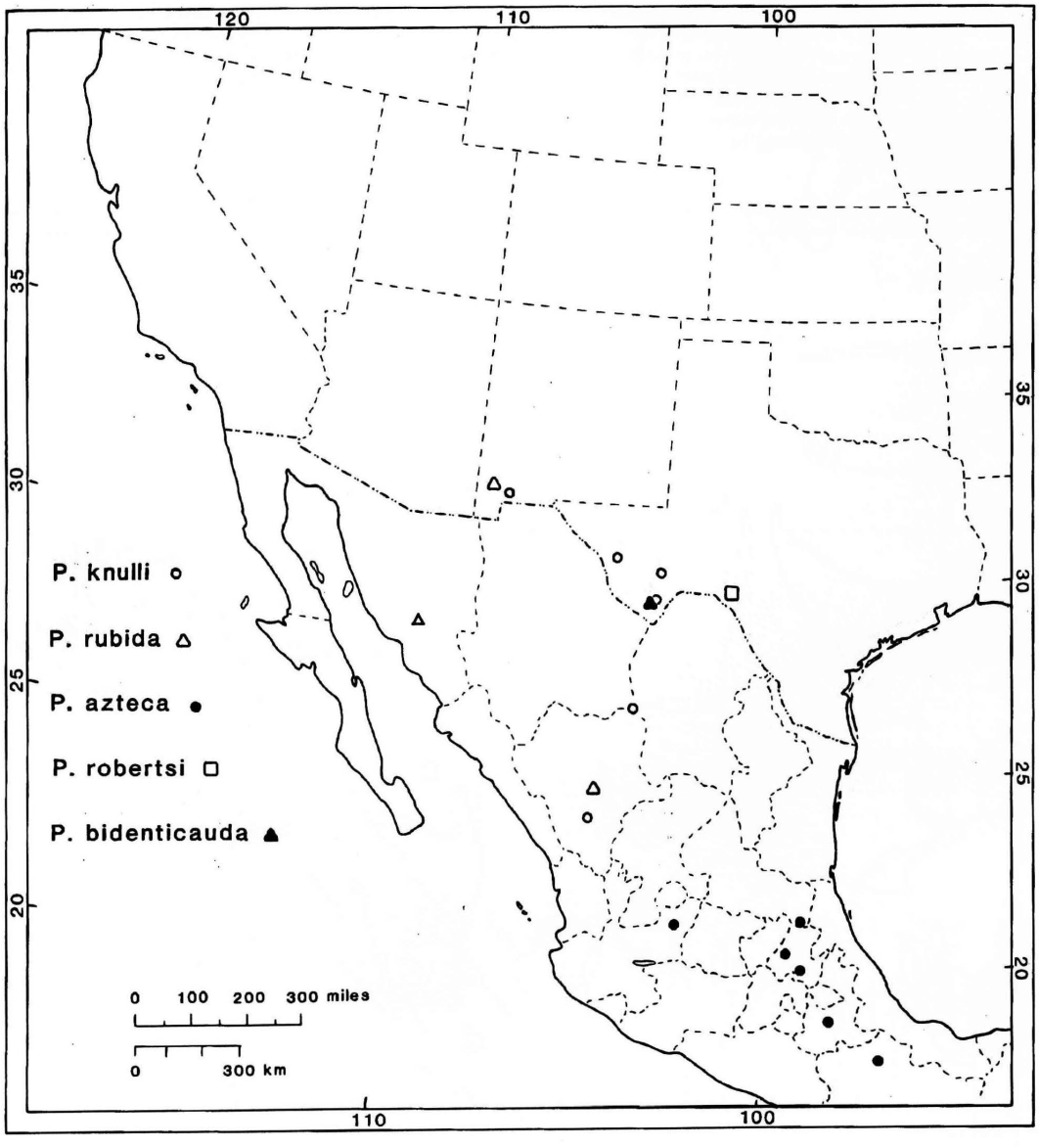

Fig. 50. Geographic distributions of species in the subgenus *Cockerellula,* in part.

medially and the lateral corners are bent further ventrally. The genital capsule of these two species is very similar, but in *P. lobata* the apical margin of the gonocoxites are produced medially, in ventral view, while in *P. laticauda* the apical margin is more or less straight. Finally, in *P. lobata* the papillae extend almost all the way to the apex of the cuspis, while in *P. laticauda* the papillae are further removed from the apex of the cuspis, restricted to the basal 1/2, in dorsal view. Female *P. laticauda, P. lobata* and *P. bidenticauda* are very difficult to distinguish, and one must rely on associations with males collected at the same locality.

Distribution – Terrell and Webb counties, Texas; Coahuila, Mexico (Fig. 53).

Phenology – April in Texas and August in Mexico.

Floral associations – *Gilia acerosa* (9 females/11 males), *Chamaesaracha conioides* (6 females/2 males), *Opuntia* (1 male) and *Gaillardia* (1 female).

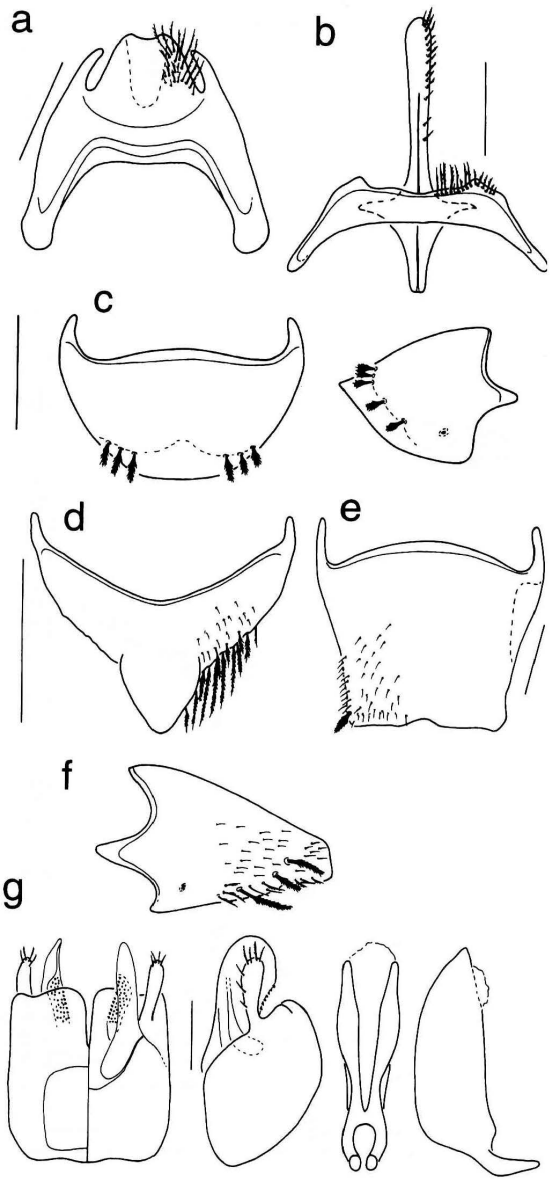

Fig. 51. *Perdita laticauda.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T6, dorsal and lateral views showing erect, moss-like setae, **(d)** female T6, dorsal view, **(e)** male T7 dorsal view, **(f)** male T7, lateral view, **(g)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

***Perdita* (*Cockerellula*) *lobata* Timberlake**

(Figs. 52, 53)

Perdita (*Cockerellula*) *lobata* Timberlake, 1953:967 [description, male]; 1953:964 [key]; 1954:356; 1954:354 [key]; 1960:122 [additional material, including female specimens, but no description of female].

Type material – The male holotype is located at KU, and was collected 15 miles northwest of Mission, Hidalgo Co., Texas, March 30, 1946, on *Opuntia* (C.D. Michener, coll.).

Diagnosis – Forewing length 3.0-3.2 mm. This species is very similar to *P. laticauda.* See above for features which allow them to be distinguished.

Distribution – Starr and Hidalgo counties, Texas (Fig. 53).

Phenology – March.

Floral associations – *Opuntia* (2 males).

***Perdita* (*Cockerellula*) *opuntiae* Cockerell**

(Figs. 54, 58)

Perdita (*Lutziella*) *opuntiae* Cockerell, 1922c:2 [description]; Custer, 1928:67-84; 1929a:50-51; 1929b:294-295 [biology].

Perdita (*Cockerellula*) *opuntiae:* Timberlake, 1953:964 [key]; 1954:355

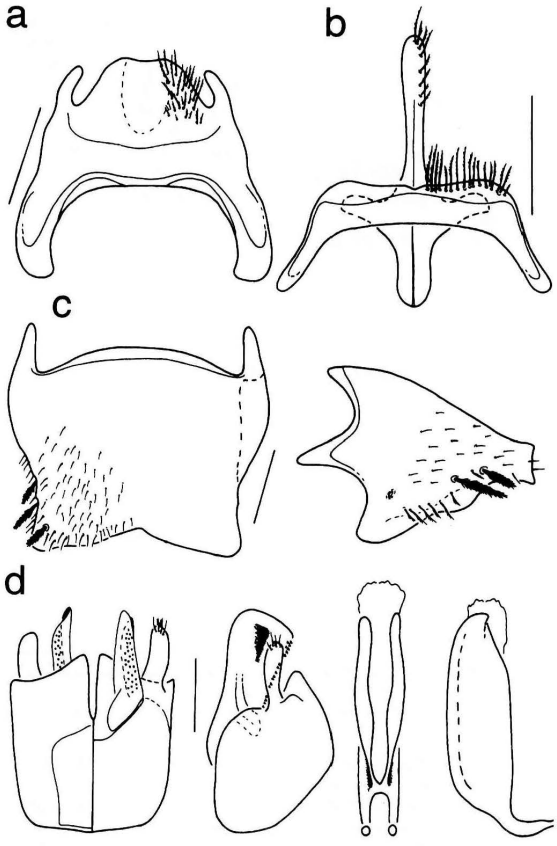

Fig. 52. *Perdita lobata.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

[additional material]; 1954:354 [key]; 1960:122 [key]; Bennett & Breed, 1985:185-194 [biology].

Type material – The male holotype is located in the CAS (Type No. 15443). The holotype was collected at White Rocks, Boulder, Boulder Co., Colorado, June 13, on *Opuntia* (W.P. Cockerell, coll.).

Diagnosis – This species, along with *P. azteca* and *P. seminigra,* are the largest species of *Cockerellula* (forewing length = 3.6 - 4.0 mm). Males are easily recognized by the shape of T7, with two latero-apical prongs separated by a wide emargination, and the presence of a broad, quadrate protuberance on the posterior margin of the S2. The female head and mesosoma are much lighter in coloration than in the similarly-sized *P. azteca,* and possess dense patches of yellowish-white setae on the postero-lateral surface of the propodeum. Scopal hairs are longer and denser than in *P.*

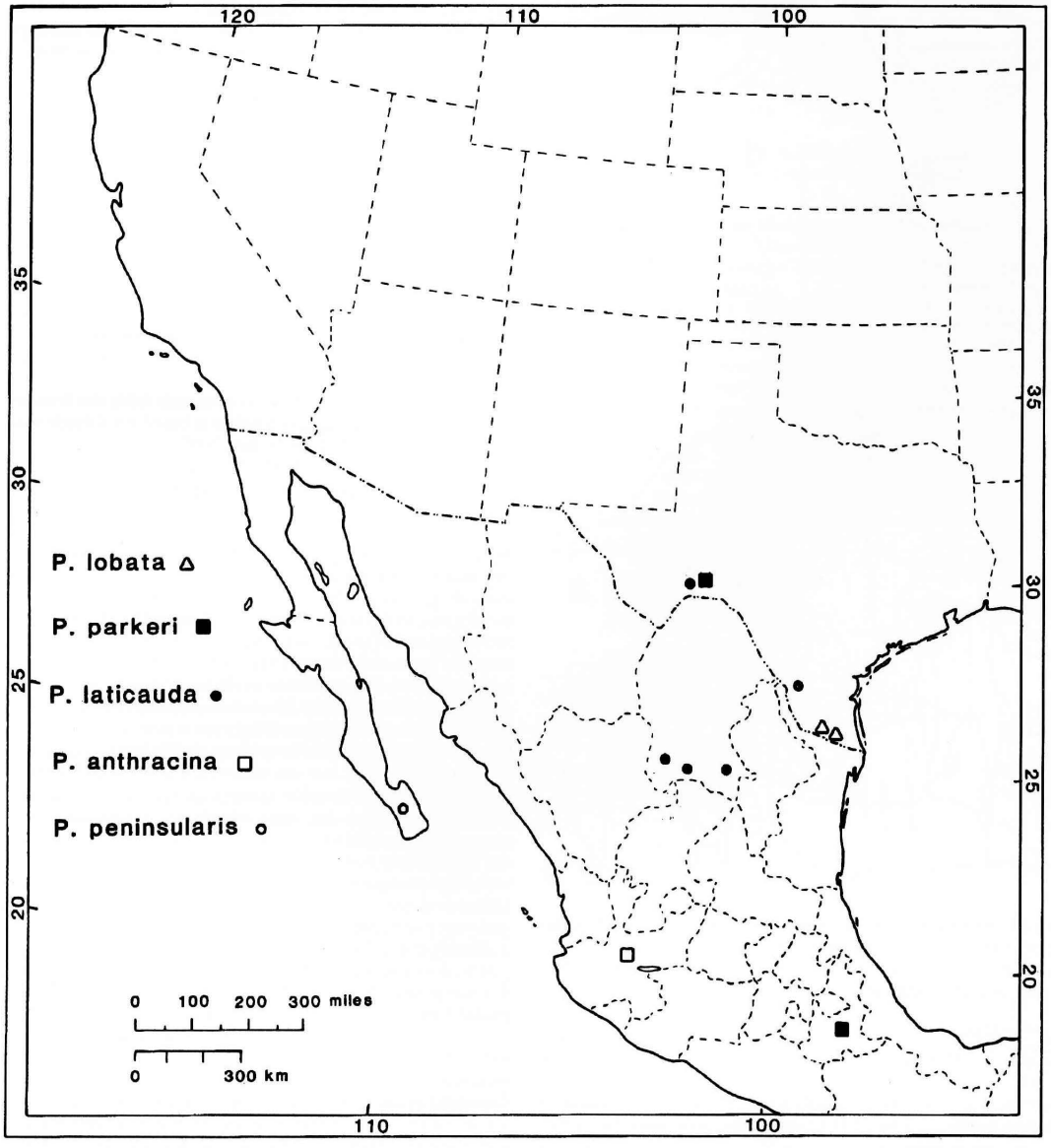

Fig. 53. Geographic distributions of species in the subgenus *Cockerellula,* in part.

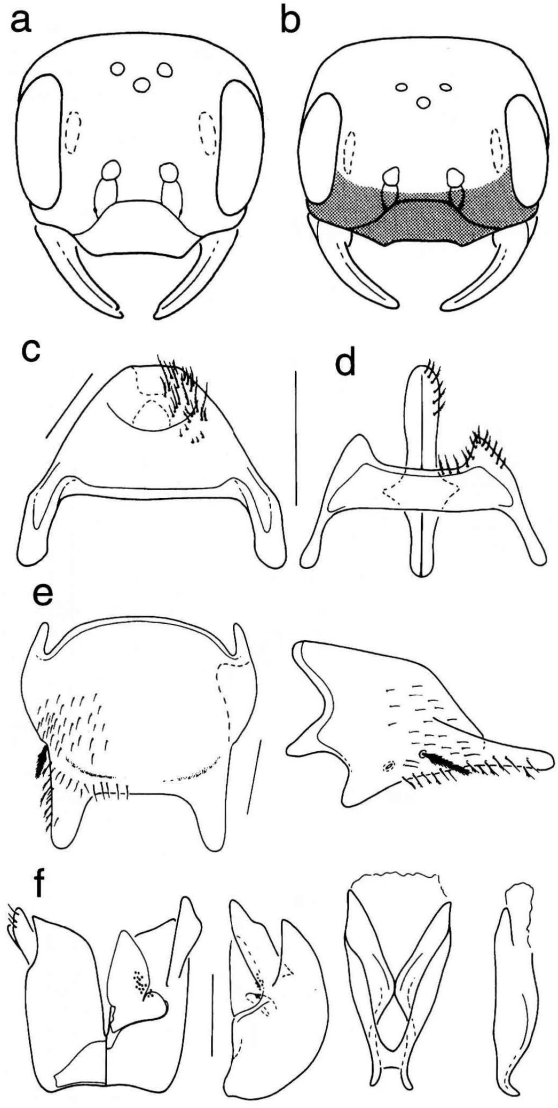

Fig. 54. *Perdita opuntiae.* **(a)** female head, **(b)** male head, **(c)** female S6, **(d)** male S7 and S8, **(e)** male T7, dorsal and lateral views, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

azteca. The shape of the female S6 should serve for positive identification: the transparent area is divided in two in *P. opuntiae* (Fig. 54c).

Distribution – Known primarily from White Rocks, a Laramie sandstone formation located 11 km northeast of Boulder, Colorado, although one male was collected in Shannon Co., South Dakota [Timberlake, 1954:355] (Fig. 58).

Phenology – June through July.

Floral associations – Pollen collection is restricted to *Opuntia compressa* and *O. polycantha* (Bennett and Breed, 1985).

Perdita (*Cockerellula*) *parkeri* Timberlake

(Figs. 53, 55)

Perdita (*Macroteropsis*) *parkeri* Timberlake, 1980:4 [description of female]; 1980:3 [key].

Type material – The female holotype is located in the CAS (Type No. 14656), and was collected at Cacaloapan, Puebla, Mexico, April 26, 1962 (F.D. Parker, coll.).

Diagnosis – This species is known only from the holotype and two additional specimens collected by Jack Neff in Blanco Co., Texas. The male is very similar to *P. opuntiae* except that the mesonotum and mesopleura are more dull (they are shining in *P. opuntiae*), and the head and thorax are black (they are light brown in *P. opuntiae*). The female of this species shows a number of characteristics that indicate it is more closely related to members of *Cockerellula* than to species of *Macroteropsis:* the head is only 1.1 times wider than long (rather than 1.3 times in *Macroteropsis*), the lateral surfaces of the propodeum have dense patches of setae, as in female *P. azteca* and *P. opuntiae,* the maxillary palpi are six-segmented and the segments are all much longer than wide, and the second labial palpal segment inserts apically on the first. Females of this species differ from all others in *Cockerellula* in the the striate (or lineolate; Timberlake, 1980) sculpturing of the dorsal surface of the propodeum, in the shape of S6 (Fig. 55a), and in the dark coloration of T1.

This species was heretofore known only from the female. The description of the male given below is based on a single male collected along with a female by Jack Neff.

Description – MALE – Head: (43) width 1.84 mm; (44) 1.35 times broader than long; (45) clypeus broad, imbricate and weakly punctate; (46) frons coarsely granulate, unusually dull, with shallow punctures; (47) vertex similar but more distinctly punctate; (48) gena imbricate-punctate; (49) head black with creamy white maculation on clypeus, subantennal plates and paraoccular area extending upward along inner margin of eye to between eye and facial fovea; sharp border between yellow and black areas; very weak reddish metallic sheen on frons; (50) head nearly bare; few, short setae on frons and vertex; (51) inner margins of eyes strongly divergent below; (52) posterior ocelli separated from occipital margin by 0.4 mm; (53) facial fovea distinctly impressed, slender, 0.30 mm in length; (54) antennae light brown; scape equal in lenth to first six flagellar segments.

Mouthparts: (55) labrum yellow, 2.4 times broader than long; shallow, concave depression along proximal margin; (56) mandible yellow with reddish tip; apex simple, no sub-apical tooth; (57) glossa normal, equal to prementum in length; (58) paraglossae slender and acutely pointed; (59) labial palpus normal, 4-segmented, with the first segment longer than remaining segments combined; (60) galeal comb absent; (61) maxillary palpus 6-segmented, second segment elongate, as in other members of the *Macrotera* group.

Mesosoma: (62) pronotum brown, imbricate; thick white setae across dorsum, extending to pronotal lobes; (63) mesoscutum densely granulate with large, shallow punctures as on head; parapsidal lines distinct, unusually deeply impressed, 0.32 mm in length; notauli absent; (64) sculpturing of mesoscutellum and metanotum similar to mesoscutum; metanotum with erect white setae laterally and along posterior margin; (65) mesopleuron with distinctly imbricate, scale-like sculpturing; scrobe deeply impressed; scroal sulcus lacking; erect, widely-scattered setae over surface; (66) metapleuron similar but without setae; (67) lateral surface of propodeum alveolate; lateral and dorsal or posterior surface sep-

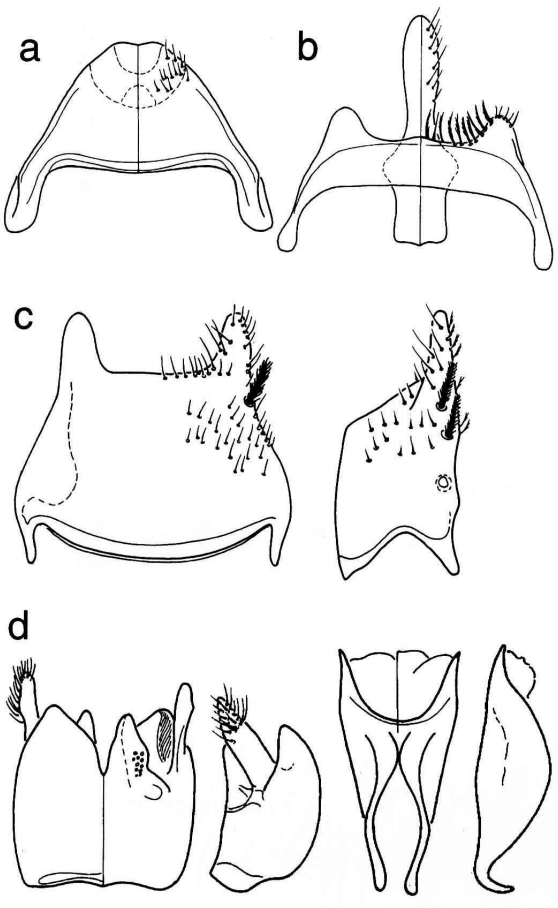

Fig. 55. *Perdita parkeri.* **(a)** female S6, **(b)** male S7 and S8, **(c)** male T7, dorsal and lateral views, **(d)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

arated by row of setae that are erect and widely separated dorsally, becoming shorter and much more closely-spaced ventrally (toward junction of metanotum) to form a discrete patch of setae; dorsal surface of propodeum of propodeal triangle deeply alveolate; lateral alveoli roughly quadrate while those along midline are laterally compressed giving the propodeum a slightly lineolate or striate appearance, as in female; (68) intertegular distance 1.16 mm; (69) forewing length 3.64 mm; wing veins light brown; stigma dark brown; venation pattern roughly as in female except veins Cu1a and 2m-cu slightly weaker than others; (70) legs dark brown except for apex of forefemur and anterior surface of foretibia, which are light brown/yellowish; (71) basitibial plate distinct; surface imbricate with 6-8 punctures; no setae covering surface; (72) outer surface of hind tibia with erect, moss-like setae intermixed with slender, white setae; (73-74) mid- and hindtibial spurs finely serrate and hooked at apex; (75) tarsal claws all bifid.

Metasoma: (76) terga all bright red; (77) T1-T7 smooth with minute punctation and inconspicuous, recumbent white setae; (78) single row of stout setae across T6; (79) longitudinal fovea on lateral surface of T2; (80) T7 divided apically into paired prongs separated by 0.45 mm (similar to *P. opuntiae*); (81) graduli present on T2-T6; graduli on T2 and T3 especially well-developed with lateral portions visible; (82-83) sterna similar in coloration, punctation and vestiture to terga; (84) S2 with paired acute projections from posterior surface extending out of plane of sternum; (85) S7 elongate and slender, S8 narrow (as in Fig. 55b); (86) genital capsule quadrate in dorsal view, with ventro-lateral projections (Fig. 55d) as in other *Cockerellula;* (87) volsellar cuspis compressed laterally; (88) papillae along dorsal surface of cuspis; (89) penis valves diverging apically, as in *P. seminigra* and *P. opuntiae* (Fig. 55d).

Distribution – Blanco Co., Texas south to Puebla, Mexico (Fig. 53). The specimens collected by Jack Neff greatly expand the known range of this species.

Phenology – April.

Floral associations – The holotype bears no flower record but the specimens collected in Texas were on *Opuntia.*

Perdita (Cockerellula) seminigra Timberlake

(Figs. 56, 58)

Perdita (Cockerellula) seminigra Timberlake, 1956:323 [description of male]; 1960:122 [key].

Type material – The male holotype is in the CAS (Type No. 14705), and was collected 34 miles south Acatlan, Puebla, Mexico, 6000', July 10, 1952 (E.E. Gilbert and C.D. MacNeill, colls.).

Diagnosis – This species is known only from the holotype specimen. Forewing length 3.6 mm. The male of this species is very similar to that of *P. opuntiae.* Both species are large (forewing length > 3.6 mm) and have brownish heads and mesosomas, and fuscous metasomas. The facial maculation in *P. seminigra,* however, is whiter than in *P. opuntiae* and is restricted to the paraocular areas, between the outer subantennal sulcus and the compound eye up to the level of the antennal sockets. In both

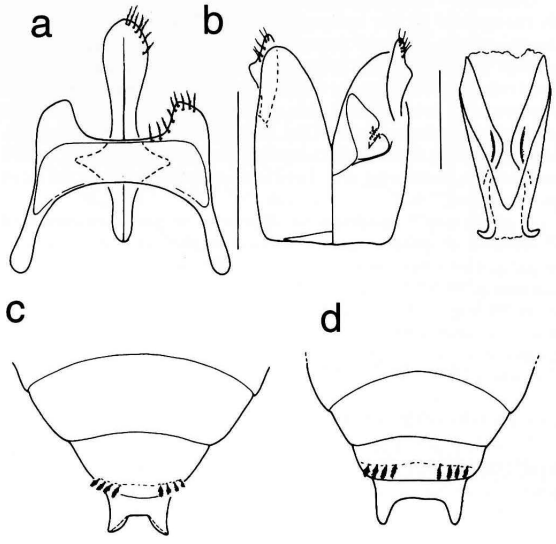

Fig. 56. *Perdita seminigra.* **(a)** male S7 and S8, **(b)** male genital capsule (dorsal and ventral views), aedeagus (dorsal view), **(c)** apex of male metasoma in *P. seminigra* as compared to **(d)** *P. opuntiae.*

species, the male S2 has a broad, quadrate protuberance (broader in *P. opuntiae* [width = 0.5 mm] than in *P. seminigra* [width = 0.32 mm]) and the male T7 has two, large, latero-apical prongs along the posterior margin which are separated by a wide, concave emargination. The prongs are more widely separated in *P. opuntiae* (distance between apices of two prongs roughly 0.56 mm) than in *P. seminigra* (0.48 mm), and in *P. seminigra* there is a distinct flange on the inner margin of each prong (Fig. 56c). The setae over the metanotum and lateral surface of the propodeum are shorter and less dense in *P. seminigra.* The penis valves and genital capsules of *P. opuntiae* and *P. seminigra* are also very similar.

Distribution – Known only from the type locality (Fig. 58).

Phenology – July.

Floral associations – unknown.

Perdita (*Cockerellula*) *solitaria* Cockerell

(Figs. 36d, 57, 58)

Perdita solitaria Cockerell, 1897b:152 [description of female]; Cockerell, 1922b:1 [new locality].

Perdita (*Macroteropsis*) *solitaria:* Timberlake, 1954:365; 1954:361 [key]; 1968:7 [key].

Perdita (*Cockerellula*) *quadridentata* Timberlake 1980:1 [description of male] NEW SYNONYMY.

Perdita (*Macroteropsis*) *atrella* Timberlake 1968:4 [description of female]; 1980:3 [key] NEW SYNONYMY.

Type material – The female holotype is located in the NMNH (Type No. 3384). The holotype was collected at Soledad Canon, Organ Mountains, Dona Ana Co., New Mexico, August 15 (C.H.T. Townesend, coll.). The male holotype and allotype of *P. quadridentata* are in the CAS (Type No. 14680), and were collected 5 miles east of Nogales, Santa Cruz Co., Arizona, September 1, 1970, on *Baccharis* (G.E and R.M. Bohart, colls.). The female holotype of *P. atrella* is in the CAS (Type No. 14434) and was collected 20 miles south Estacion Llano, Sonora, Mexico, August 18, 1964 (M.E. Irwin, coll.).

Diagnosis – Forewing length 2.4 - 2.6 mm. Males are most easily recognized by the uniquely-shaped T7, with two converging dorso-apically directed prongs and two diverging latero-apical prongs (Fig. 57). Both males and females can be distinguished from other close relatives by the unusually proportioned labial palpi: segments 2-4 are long and thin and their total combined length is equal to the first segment (Fig. 36d). Females are entirely dark, lacking reddish metasomal coloration, the body is sparsely clothed in elongate, erect setae and there is no metallic sheen to the head or mesosoma.

P. atrella and *P. quadridentata* appear to be junior synonyms of *P. solitaria. P. quadridentata* was based on the male of *P. solitaria,* as judged by a male specimen collected along with females of *P. solitaria* at Sycamore Canyon, Santa Catalina Mts., Pima Co., Arizona, 20 August, 1916. Timberlake (1954:365) was unaware of this male specimen when he treated *P. solitaria* as a species known only from the female. Cockerell (1922b:1) does not mention this male specimen, although he did report having seen two females from the same locality and date. The female allotype of *P. quadridentata* is indistinguishable from females of *P. solitaria.*

P. atrella is also a junior synonym of *P. solitaria;* the type agrees in all respects with *P. solitaria.* Because Timberlake (1968:4) compared the holotype specimen of *P. atrella* to species of *Macroteropsis* rather than *Macroterella* (which contained *P. solitaria*), he was lead to the incorrect conclusion that it was a new species.

Distribution – Pima, Cochise and Santa Cruz counties, Arizona; Dona Ana Co., New Mexico and Sonora, Mexico (Fig. 58); collected up to 3800 ft. (in Santa Catalina Mts.)

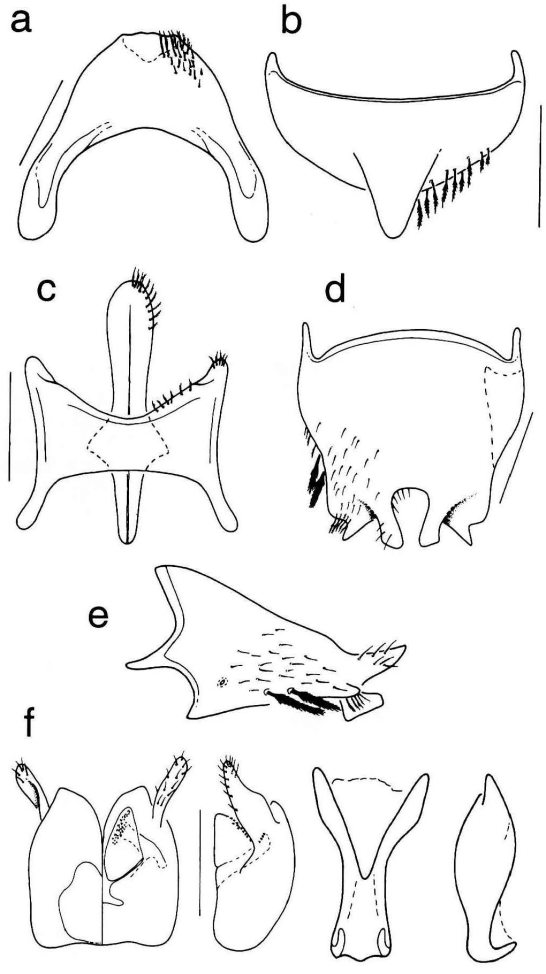

Fig. 57. *Perdita solitaria.* **(a)** female S6, **(b)** female T6, **(c)** male S7 and S8, **(d)** male T7, dorsal view, **(e)** male T7, lateral view, **(f)** male genital capsule (dorsal, ventral and lateral views), aedeagus (dorsal and lateral view).

Phenology – August to September.

Floral associations – Collected on *Baccharis* (holotype male and allotype) and on *Eriogonum abertianum neomexicanum* (1 female).

Perdita (*Cockerellula*) *anthracina* Timberlake

(Figs. 53, 59)

Perdita (*Macroteropsis*) *anthracina* Timberlake, 1980:3 [description of female and key].

Type material – The female holotype is in the CAS (Type No. 14422), and was collected 10 miles north of Guadalajara, Jalisco, Mexico, October 16, 1968 (G.E. Bohart, coll.).

Diagnosis – This species is known only from the holotype fe-

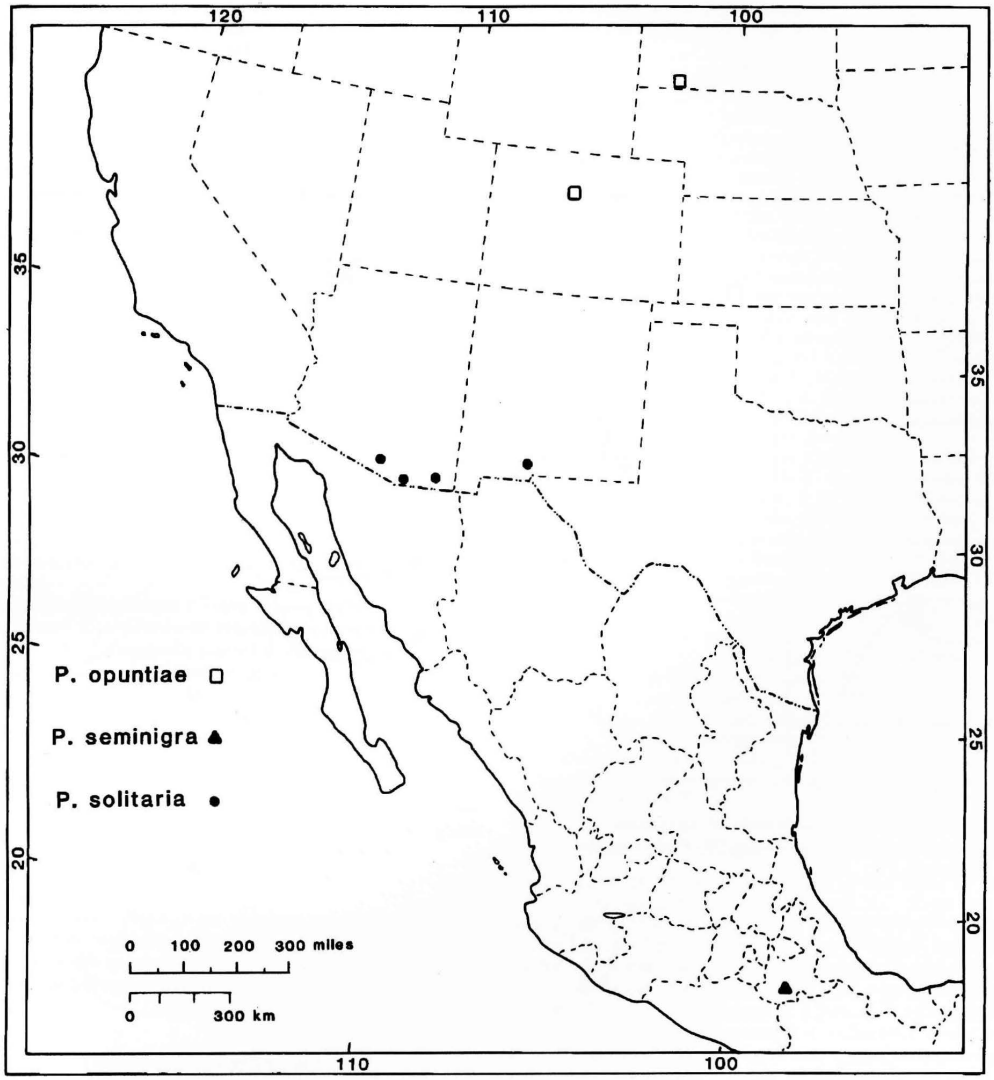

Fig. 58. Geographic distributions of species in the subgenus *Cockerellula,* in part.

male. Forewing length 3.4 mm. The body is entirely black with a faint coppery sheen on the head and mesosoma; and scattered, long, erect setae. Wing veins are brown. The female is superficially similar to female *Macroteropsis,* but lacks the mouthpart characters of that group. The holotype female lacks dense patches of setae on the lateral surface of the propodeum.

Distribution – Jalisco, Mexico (Fig. 53).

Phenology – May.

Floral Associations – unknown.

***Perdita* (*Cockerellula*) *peninsularis* Timberlake**

(Figs. 53, 59)

Perdita (*Cockerellula*) *peninsularis* Timberlake, 1968:3 [description of female].

Perdita (*Macroteropsis*) *peninsularis:* 1980:2; 1980:3 [key].

Type material – The holotype female is located in the CAS (Type No. 12993), and was collected at Triunfo, Baja California Sur, Mexico, July 7, 1938 (Michelbacher and Ross, coll.).

Diagnosis – Forewing length 3.4 mm. This species is known from only two female specimens collected at the type locality on 7 and 13 July, 1938. Timberlake originally placed it in the subgenus *Cockerellula* but in 1980 (p.2), he transferred it to the subgenus

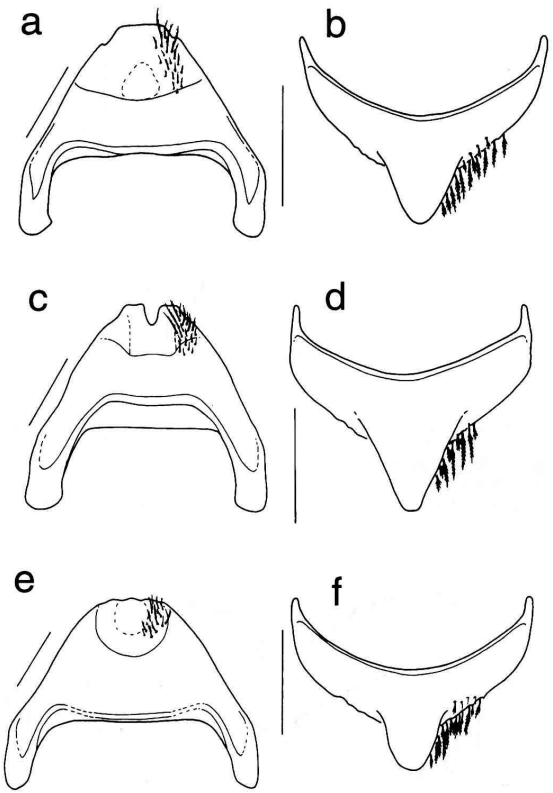

Fig. 59. *Perdita anthracina.* **(a)** female S6, **(b)** female T6. *Perdita penninsularis.* **(c)** female S6, **(d)** female T6. *Perdita robertsi.* **(e)** female S6, **(f)** female T6

Macroteropsis, without giving any explanation for this change. I have since seen all of Timberlake's material from the CAS, and in this material were one male and one female, collected 6 mi. NW El Rosario, near Consuelo, Baja California, Mexico on 18 May, 1965 by D.Q. Cavagnaro, C.E. and E.S. Ross and V.L. Vesterby, which were identified by Timberlake as *P. peninsularis.* Based on dissections of these specimens it is clear that they are really *P. arcuata.* In fact, in the CAS *P. arcuata* material is another female specimen with the same locality data which he had identified as *P. arcuata.* I believe that by mistaking these specimens of *P. arcuata* as *P. peninsularis* he made the incorrect decision to transfer *P. peninsularis* to *Macroteropsis.*

Based on the two female *P. peninsularis,* this species clearly belongs in *Cockerellula.* Females have relatively long faces (width only 1.1 times length), elongate, well-developed maxillary palpi, and the second labial palpus arises apically on the first. The body is entirely black, with fine imbricate-punctate sculpturing over much of the head and metasoma and scattered, erect white setae. Wing veins are brown. The propodeal triangle is finely areolate and the lateral surfaces of the propodeum bear erect, plumose, white setae, similar to the setae on the propodea of *P. opuntiae* or *P. azteca,* but less dense. This species can be most easily distinguished from the other *Cockerellula* by the conspicuously concave basitibial plate, the shape of the female S6 (deeply divided apically), and pygidial plate (elongate and slender with narrowly quadrate apex; Fig. 59d).

Distribution – Baja California Sur, Mexico (Fig. 53).

Phenology – July.

Floral associations – unknown.

Perdita (*Cockerellula*) *robertsi* Timberlake

(Figs. 50, 59)

Perdita (*Macroteropsis*) *robertsi* Timberlake, 1968:6 [description of female]; 1980:3 [key].

Type material – The female holotype is in the CAS (Type No.

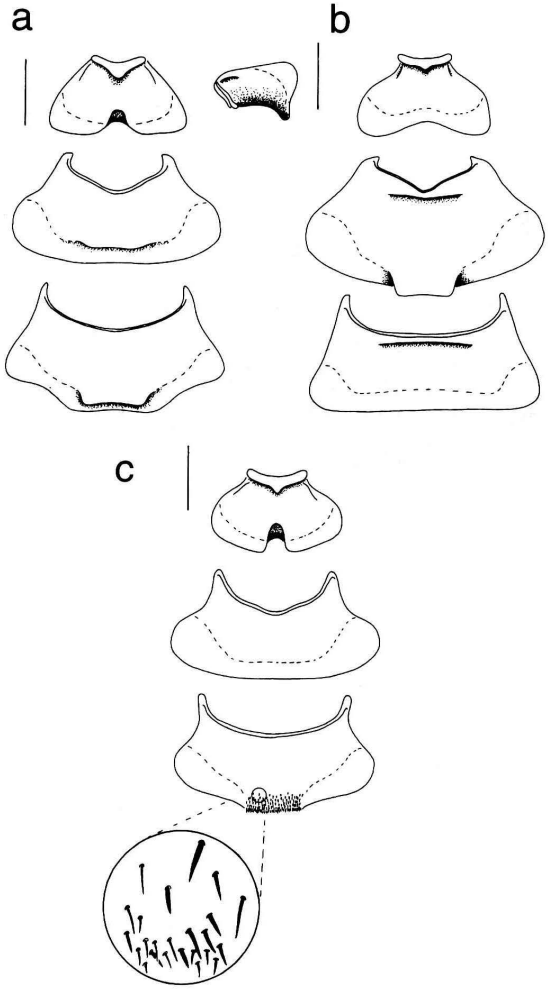

Fig. 60. Male sterna 1 through 3. **(a)** *Perdita texana,* **(b)** *Perdita echinocacti.*

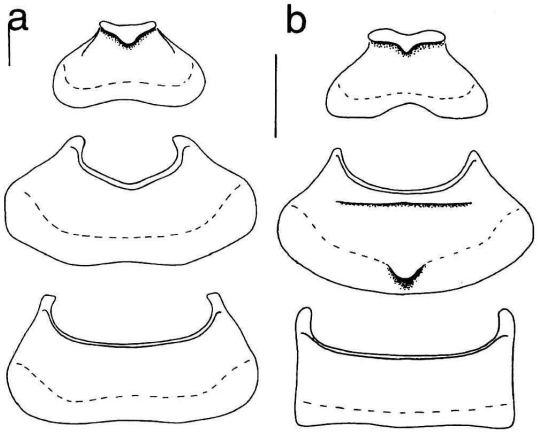

Fig. 61. Male sterna 1 through 3. **(a)** *Perdita azteca,* **(b)** *Perdita opuntiae,* **(c)** *Perdita lobata.*

14687). This specimen was collected at Pecos River Canyon, 38 miles north west Del Rio, Val Verde Co., Texas, 13 April 1963 (R.B. Roberts, coll.).

Diagnosis – Forewing length 3.7 mm. This species is known from the holotype and four additional female specimens collected by John Neff. Although originally placed in *Macroteropsis,* this specimen lacks the characters of that group and possesses a number of features of the subgenus *Cockerellula:* the head is scarcely longer than wide, the maxillary palpi are well developed and six-segmented, the second labial palpal segment arises apically on the first, the metasoma is reddish and there are two dense patches of thick, white setae on the lateral surfaces of the propodeum, as in *P. azteca.* The yellow maculation on the paraocular areas, immediately above the mandibular bases, and S6 shape will distinguish females of this species from all others in the subgenus.

Distribution – Val Verde Co., Texas (Fig. 50).

Phenology – April.

Floral associations – Although the holotype lacks a flower record, Timberlake (1968) suggested that it was most likely collected on *Opuntia.* John Neff's specimens were collected in Val Verde Co., Texas (as was the holotype) on *Opuntia engelmannii* and *Echinocereus enneacanthus.*

Heteroperdita Timberlake

Perdita (*Heteroperdita*) *pilonotata* Timberlake

Perdita (*Macroterella*) *pilonotata* Timberlake, 1980:6 [description].

Type material – I was unable to locate the holotype female.

Diagnosis – Forewing length 2.0 mm. This species clearly belongs in the subgenus *Heteroperdita* and is thus not part of the *Macrotera* complex. The characters which unite *P. pilonotata* with other species in *Heteroperdita* include: (1) hypostomal region of female, on either side of proboscidial fossa, with elongate, posteriorly directed setae, (2) although lacking yellow maculation present in other members of this group, female with short, appressed white setae on the frons, the scuto-scutellar suture and the metanotum, (3) portion of male S8 beyond apodemes (disc of the male S8) quadrate and blunt apically and male genital capsule resembling other species of *Heteroperdita.*

Distribution – NEW MEXICO: Otero Co., 3900 ft., 21 Aug., 1962; Catron Co., 16 mi. S. Datil, 16 June, 1956; Valencia Co., Correo, 15 June, 1956 (Timberlake, 1980:7).

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