



A Revision of *Perdita* (*Xerophasma*) Timberlake (Hymenoptera: Andrenidae)

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Abstract

Three new species of *Perdita* (*Xerophasma*) endemic to the Mojave Desert are described: *P. celadona* Griswold and Miller and *P. vespertina* Griswold and Miller from eastern Clark County, Nevada, and *P. rhondae* Griswold from Death Valley, California. The subgenus is redescribed to accommodate these new species. New distributional records for *P. bequaertiana* and *P. pallida* and a key to the species of the subgenus are provided. A well supported phylogeny suggests evolution toward nocturnal foraging expressed in increasing ocellar size and a trend toward totally pale integument. The apparent origin and center of diversity for the group is the eastern Mojave Desert.

Key words: Apoidea, Andrenidae, *Perdita*, *Camissonia*, *Oenothera*, Mojave Desert, nocturnal bee, key

Introduction

Perdita, despite its restriction to the Nearctic, is one of the most speciose genera of bees. There are 17 subgenera (Michener 2007), 629 described species and an additional 125 subspecies, some of which are expected to be elevated to species rank upon revision. Numerous species remain undescribed. Diversity in *Perdita* is concentrated in the deserts of North America. For example, the Mojave Desert is home to at least 193 taxa, 19 of them undescribed.

Collecting efforts by USDA-ARS Bee Biology and Systematics Laboratory personnel in the Virgin River drainage of Clark County, Nevada in 1973 yielded specimens of the rarely collected subgenus *Perdita* (*Xerophasma*) Cockerell. Originally described as a monotypic genus (Cockerell 1923), *Xerophasma* was redefined as a subgenus (Timberlake 1953) for two crepuscular *Perdita*, *P. bequaertiana* Cockerell and *P. pallida* Timberlake, distinctive in their large size and pale coloration, and subsequently recognized as a subgenus in the phylogenetic analysis of Danforth (1996). P. H. Timberlake recognized the Virgin River specimens as a new species, but his manuscript name was never published. Study of this material and subsequent collections revealed that not one but two new species are present in the Virgin River drainage of southern Nevada. A third undescribed species was recently discovered in Death Valley National Park, California. Here *Xerophasma* is expanded to include these three smaller, darker new species, new distributional records presented for described species, a key to species provided, and phylogenetic relationships explored.

Methods

A total of 416 specimens of *P.* (*Xerophasma*) including holotypes were studied; institutions are referenced by city and listed in the acknowledgements. Descriptions follow the terminology of Michener (2007). Metasomal terga and sterna are abbreviated T1, T2 ... and S1, S2 ... respectively. All locations were georeferenced using GoogleEarth. Maps were constructed in ArcGIS. For the phylogenetic analysis fifteen characters were used, ten binary and five multistate (see character descriptions below). All species of *P.* (*Xerophasma*) were coded,

with *Perdita (Perdita) lateralis* Timberlake used as the outgroup. In the only phylogenetic analysis of *Perdita*, Danforth (1996) found a combined *Perdita (Perdita) ventralis* group + *P. (Alloperdita)* as the sister group to *P. (Xerophasma)*. *Perdita (P.) lateralis* is a common and typical member of the *ventralis* group. An input matrix was constructed using WinClada (BETA) version 0.9.99m10.1 (Nixon 2000). All characters were treated as unweighted and non-additive. Parsimony analysis was performed using NONA version 2.0 using Ratchet (Island Hopper), fast optimization and default parameters (Goloboff 1997).

Character descriptions.

1. Ocellar size

- 0, normal, width of median ocellus 1/9 interocular distance at level of median ocellus
- 1, slightly enlarged, width of median ocellus 1/5 interocular distance at level of median ocellus (Fig. 1)
- 2, moderately enlarged, width of median ocellus 1/4 interocular distance at level of median ocellus (Fig. 2)
- 3, greatly enlarged, width of median ocellus 1/3 interocular distance at level of median ocellus (Fig. 4)

2. Marginal cell length on wing margin

- 0, less than or equal to 1.5 apical width
- 1, twice apical width

3. Number of submarginal cells

- 0, two (intercalary cell absent)
- 1, three (intercalary cell present)

4. Female mandible

- 0, with preapical tooth (Fig. 1)
- 1, simple, without preapical tooth (Fig. 2)

5. Female face

- 0, with dark marks (Fig. 1)
- 1, without dark marks (Fig. 2)

6. Female frontal line

- 0, strongly raised
- 1, weakly raised

7. Female facial fovea

- 0, with dense velvety hair
- 1, with moderate amount of velvety hair
- 2, without hair

8. Female vertex length posterior to lateral ocellus

- 0, greater than ocellar diameter
- 1, slightly less or equal to ocellar diameter
- 2, one-fourth of ocellar diameter

9. Female mesoscutum

- 0, entirely dark
- 1, light in part
- 2, entirely light

10. Female mesepisternum with ventral hair

- 0, long, hooked, erect
- 1, short, simple, obliquely directed

11. Female pygidial plate apically

- 0, narrowly to broadly rounded
- 1, truncate
- 2, acutely angled

12. Male supraclypeal area

- 0, planar, without erect hair tuft
- 1, with low tubercle and erect tuft of hair

13. Male S8 apical margin
 - 0, bluntly angled (Fig. 17)
 - 1, emarginate (Fig. 16)
 - 2, broadly rounded (Fig. 18)
14. Male gonostylus in lateral view
 - 0, broad, tapering toward apex (Fig. 11)
 - 1, slender, parallel sided (Fig. 12)
15. Male gonostylus apically
 - 0, straight (Fig. 11)
 - 1, bent (Fig. 12)

Results

Subgenus *Xerophasma*

Perdita (*Xerophasma*) Cockerell

Xerophasma Cockerell 1923: 1. Type species: *Xerophasma bequaerti* Cockerell 1923.

Diagnosis. *Xerophasma* can be distinguished from all other subgenera of *Perdita* by the enlarged ocelli (each about 1/5 to 1/3 width of interocular distance at level of median ocellus) and from all except some members of the subgenus *Alloperdita* Viereck, (restricted to the eastern United States) by the small triangular, petiolate submarginal cell intercalated between the two submarginal cells normal for *Perdita*. This third submarginal cell is likely a derived character not homologous to the second submarginal cell found in many Andrenidae (Michener 2007). It is unclear whether it is a synapomorphy for the two subgenera (Danforth 1996, Michener 2007). In *Xerophasma*, the body color is largely pale caramel-colored, with extensive dark markings on the head and mesosoma in some species, and all species have some degree of light to dark brown tergal banding.

Description. *Female.* Length: 6.5–11.5 mm; forewing length: 4.5–8.3 mm. Body off-white to caramel-colored except dark brown pygidial plate and tergal bands and sometimes on face and mesosoma. Pubescence white, fine, mostly short and inconspicuous except long on gena, legs, mesepisternum. Sculpture finely reticulate, shallow on anterior third of mesoscutum. Head slightly wider than long, no wider than mesosoma. Mandible slender, tapering to acute apex (except with subapical tooth in *P. celadona*), base pale caramel-colored, apex brown. Inner eye orbits parallel to slightly convergent below. Antenna long, slender, with length of flagellomeres equal to or greater than their width. Facial fovea shallowly impressed, dull, linear or elliptical, darker than rest of face. Ocelli enlarged, median ocellar diameter 1/5 to 1/3 width of interocular distance at level of median ocellus. Gena in lateral view about 1/2 as wide as eye (except as wide in *P. rhondae*), widest above middle of eye. Tibial spurs long, straight, slender, tarsal claws with medial tooth. Scopal hairs of hindtibia long, straight, rather sparse, hair on outer side of hindbasitarsus shorter but otherwise similar. Forewing extending to or beyond apex of metasoma. Stigma large, width equal to or slightly broader than first submarginal cell. Marginal cell as long as stigma but not quite reaching halfway to apex of wing. Small triangular, petiolate intercalary submarginal cell almost always present between the normal first and second. Wings hyaline, veins and stigma light brown, except subcostal vein dark brown. Branched hairs surrounding pygidial plate, long hairs on gena and mesepisternum. Pygidial plate acutely angled.

Male. Length: 5.5–10.5 mm. Forewing length: 4.0–7.1 mm. Similar to female except body sometimes darker colored, gena slightly wider in lateral view; tarsal claws bifid, pygidial plate absent.

Variation. Occasional specimens of *P. vespertina* and *P. celadona* are missing the petiolate intercalated submarginal cell on one or both wings. Such specimens of *P. vespertina* from Riverside, Nevada, May 1983 are as follows: 3 females and 1 male missing on left wing only, 1 female incomplete on right wing only, 2 females with incomplete right and missing left, 1 female incomplete left, 4 males missing cell on both wings. One *P. vespertina* male from Mesquite, Nevada 1998 is missing the third submarginal cell on both wings.

Distribution. Previously known only from the Sonoran and Chihuahuan Deserts (Timberlake, 1953, 1954, 1958), *Xerophasma* is now known to occur in the Colorado Plateau and the Mojave Desert and on the western margin of the Great Plains (Figs. 26–28). All *Xerophasma* are crepuscular visitors to Onagraceae of the genera *Camissonia* and *Oenothera* in desert and semi-desert regions of southwestern North America. They are frequently found associated with sand dunes and vegetated sands.

TABLE 1. Character matrix for *Perdita* (*Xerophasma*).

Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>P. lateralis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. celadona</i>	1	0	1	0	0	0	0	1	0	0	2	0	1	0	0
<i>P. rhondae</i>	1	0	1	1	0	1	0	0	1	0	1	1	1	0	0
<i>P. vespertina</i>	2	1	1	1	0	0	1	1	1	1	0	0	2	0	0
<i>P. pallida</i>	2	1	1	1	1	0	1	1	2	1	0	0	0	1	1
<i>P. bequaertiana</i>	3	1	1	1	1	0	2	2	2	1	0	0	2	1	1

Key to species of *Perdita* (*Xerophasma*)

- 1 Female..... 2
- Male 6
- 2 Entirely pallid, cream to tan on head and mesosoma 3
- Dark brown above antennal sockets, dark brown markings on mesoscutum, propodeum..... 4
- 3 Ocelli greatly enlarged, ocellar diameter nearly 1/3 width of interocular distance at level of median ocellus (Fig. 4); large (forewing length > 7 mm) *bequaertiana* Cockerell
- Ocelli moderately enlarged, ocellar diameter approximately 1/5 width of interocular distance at level of median ocellus (Fig. 2); small (forewing length < 7mm) *pallida* Timberlake
- 4 Frons dark throughout (Fig. 1, 3); gena narrower than eye in lateral view; mesoscutum either dull or densely punctate 5
- Frons with small dark mark above each antennal socket (Fig. 5); gena broader than eye in lateral view; mesoscutum polished and sparsely punctate *rhondae* Griswold
- 5 Mandible without preapical tooth (Fig. 3); clypeus entirely cream-colored; mesoscutum golden brown or dark with 'U' shaped yellow marking, surface shiny, rather densely punctate..... *vespertina* Griswold & Miller
- Mandible with preapical tooth (Fig. 1); clypeus with medial dark band; mesoscutum entirely dark, surface dull, very sparsely punctate..... *celadona* Griswold & Miller
- 6 Supraclypeal area with conical protuberance and dense tuft of erect, apically bent hair; clypeus densely punctate..... *rhondae* Griswold
- Supraclypeal area flat, without tuft of hair; clypeus very impunctate medially 7
- 7 Face cream or golden brown above antennal sockets, with little contrast to clypeus and paraocular area; facial fovea distinct, tear-drop shaped, or ellipsoid 8
- Face dark brown or black above antennal sockets, in distinct contrast to yellow clypeus and paraocular area; facial fovea indistinct, slightly oval *celadona* Griswold & Miller
- 8 Ocelli not greatly enlarged, 1/5 width of interocular distance at level of median ocellus; frons cream to pale yellow above antennal sockets 9
- Ocelli large, 1/3 width of interocular distance at level of median ocellus; frons golden brown above antennal sockets *bequaertiana* Cockerell
- 9 Ocelli not bordered by dark lines except sometimes a single fine line medially between two lateral ocelli; prestigma pale in contrast to dark vein R; stigma without dark posterior margin; facial fovea tear-drop shaped *pallida* Timberlake
- Dark markings present at least anterior to lateral ocelli, often more extensive in ocellar region; prestigma dark, similar to vein R; stigma with dark posterior margin; facial fovea elongate ellipsoid *vespertina* Griswold & Miller

Species accounts

Perdita (Xerophasma) celadona Griswold & Miller, new species

(Figs. 1, 6, 11, 16, 21)

Female. Length: 6.5–8.0 mm. Forewing length: 4.5–5.0 mm. Head, mesosoma dark brown except: cream-colored on mandible basally, lateral margin of clypeus, paraocular area below level of antennal socket, flagellum ventrally, pronotum dorsally, pronotal lobe, tegula, sometimes scutellum; dark reddish brown on labrum, mandible apically; greenish metallic reflections on dark areas of head and mesosoma except barely visible on mesoscutum medially; scutellum sometimes caramel-colored. Legs cream-colored except: light brown on coxae, fore and midfemora basoventrally, midtibia dorsally, mid tarsi except midbasitarsus ventrally, hindtibia; dark brown on hind tarsi. Costal vein, prestigma dark. Stigma with brown margins, center clear. Brown apical bands on T2–T4 or T5. Frons reticulate but shiny. Mesoscutum, scutellum dull, very sparsely, indistinctly punctate. Hair on mesoscutum sparse, except for dense, short hair anterior to scuto-scutellar suture.

Mandible with preapical tooth. Labrum with apical margin scarcely convex. Clypeal width dorsally 1.5–2X as wide as subantennal area. Frontal line slightly raised halfway to median ocellus then slightly depressed to median ocellus. Facial fovea dull, linear, densely pubescent, extending from middle of antennal socket 2/3 or more of distance to median ocellus. Ocellar area not inflated. Median ocellar diameter equal to 1/5 width of frons. Length of vertex behind lateral ocellus less than ocellar diameter. Forecoxa, mesepisternum ventrally with long, simple, erect, apically bent hair. Length of marginal cell on wing margin less than or equal to 1.5 apical width. Pygidial plate acutely angled.

Male. Length: 5.5 mm. Forewing length: 4 mm. Head, mesosoma black except: cream-colored on clypeus, paraocular area below level of fovea, spot medially on supraclypeal area, subantennal area, flagellum dorsally and basally, sometimes along dorsal margin of eye, pronotum except dark spot anterior to pronotal lobe, mesepisternum ventrally near forecoxal cavity. Slight metallic green reflections on dark integument of head, almost no metallic reflection on mesoscutum or mesepisternum. Foreleg, midleg entirely caramel colored except tibiae with brown posterior longitudinal stripe, faint on foreleg. Hindleg caramel-colored except hindfemur dark distally and dorsally, hindtibia, hindbasitarsus and hindtarsi brown dorsally. Brown bands apically on otherwise cream colored terga. T2 lateral fovea forming fine dark line. Sculpture, punctuation, pubescence as in female except mesoscutum, scutellum polished.

Clypeal width dorsally greater than width of subantennal area. Supraclypeal area not protuberant, without tuft of hair. Facial fovea appearing glabrous, indistinct, barely visible as small, slight oval indentation where light and dark markings meet. Frontal line, ocellar diameter, forewing as in female. T7 with pygidial plate ill-defined, without apical tuft of hair protruding from beneath apical margin. S8 as in Fig. 16. Genitalia as in Figs. 6, 11.

Type material. Holotype female: USA NEVADA, Clark County, St. Thomas Gap, 36°24.35' N 114°5.62' W, 8 Jun 1998, *Camissonia*, T. Griswold. Paratypes: NEVADA, Clark County: 1 male, 6 females, same label data as holotype; 1 female, Grand Gulch Road, 22 air mi S Mesquite, 11–21 May 1983, F. D. & J. H. Parker; 4 females, Mesquite, 25 May 1973, *Oenothera*, G. Bohart; 3 females, same except 8 May 1994, *Oenothera*, P. Torchio, D. Veirs; 4 females, Toquap Wash, W Mesquite, 36°46'34"N 114°11'10"W, 24 May 2003, *Camissonia*, D. Yanega; 3 females, Toquap Wash, 1 mi N Hwy I-15, 485 m, N36°46'39" W114°11'10", 25 May 2003, *Camissonia*, D. Yanega. Holotype deposited in the U.S. National Pollinating Insects Collection, Logan, Utah; paratypes in Logan and Riverside.

Diagnosis. *Perdita celadona* differs from other *Xerophasma* by the darker body and truncate rather than rounded or angled apical margin of the labrum. The female pygidial plate is pointed, rather than rounded or truncate as in other *Xerophasma*, and the mandible has a preapical tooth whereas other species lack a preapical tooth.

Range. Apparently endemic to the eastern Mojave Desert in Clark County, Nevada (Fig. 26) where it was active at dusk. Known only from the Virgin River drainage ranging from Mesquite south to St. Thomas Gap.

Specimens labeled as collected on *Oenothera* are actually on plants now assigned to *Camissonia* (F. D. Parker, personal communication).

Variation. A single female from Mesquite has the dark clypeus interrupted by a pale longitudinal line. The size of the intercalated second submarginal cell varies among individuals. In three (14%) of the females it is missing on one wing. The female from Grand Gulch Road and all the females from St. Thomas Gap have the scutellum dark, while those from Mesquite have the scutellum pale in contrast to the dark metanotum. T5 may be all brown except for two oval light spots.

Etymology. From the French “celadon” meaning a sea green color, in reference to the metallic green reflections on most areas of dark integument.

***Perdita (Xerophasma) vespertina* Griswold & Miller, new species**

(Figs. 3, 8, 13, 18, 22)

Female. Length: 7.0–8.5 mm. Forewing length: 6.2–7 mm. Head, mesosoma dark brown to nearly black except: cream-colored labrum, clypeus, paraocular area below level of fovea, spot on vertex between and slightly dorsal to lateral ocelli (sometimes reduced to point), postgenal area along margin of eye, pronotum except spot laterally, 'U'-shaped markings on mesoscutum with base of 'U' at scuto-scutellar margin, arms of 'U' running longitudinally between parapsidal and admedial lines, scutellum, metanotum, tegula, propodeum laterally, legs. Costal vein, prestigma dark. Stigma slightly darkened, ventral margin distinctly darkened. T1-5 with subapical brown bands on otherwise caramel-colored terga. Frons finely reticulate. Mesoscutum, scutellum shiny, mesoscutum anteriorly and laterally slightly reticulate. Mesoscutum moderately densely, distinctly punctate, evenly covered with sparse long pale hair. Propodeal triangle somewhat shiny, finely reticulate.

Mandible simple, without preapical tooth. Labrum with apical margin obtusely angulate. Clypeal width dorsally slightly greater than width of each subantennal area. Frontal line strongly raised halfway to median ocellus then strongly depressed to median ocellus. Facial fovea dull, linear, densely pubescent, extending from middle of antennal socket nearly to level of median ocellus. Ocellar area slightly inflated. Median ocellar diameter 1/4 width of interocular distance at level of median ocellus. Length of vertex behind lateral ocellus less than ocellar diameter. Forecoxa with long, erect, slightly plumose, straight hair; mesepisternum ventrally with short, obliquely directed, straight hair. Length of marginal cell on wing margin twice apical width. Pygidial plate narrowly rounded.

Male. Length: 7.5–9.0 mm. Forewing length: 5.3–5.9 mm. Head, mesosoma, legs cream colored except: entire head slightly yellowed; dark brown on facial fovea, markings anterior to each of lateral ocelli, medially between lateral ocelli, line extending dorsally from median ocellus, marks sometimes forming “V” between hindocelli on vertex, occasionally as rings around ocelli, sometimes along dorsal margin of eye orbit; brown subapical band on T1 and sometimes T2–4. T2 lateral fovea forming fine, sometimes dark, line. Sculpture, punctuation, pubescence as in female.

Clypeus dorsally about 1.5X width of subantennal area. Supraclypeal area not protuberant, without tuft of hair. Facial fovea pubescent, elliptical, minutely depressed, sometimes slightly tear-shaped with narrow end ventral, extending from level of ventral margin of median ocellus to slightly more than halfway to dorsal margin of antennal socket. Frontal line, ocellar diameter, forewing as in female. T7 with pygidial plate ill-defined, with apical tuft of hair protruding from beneath apical margin. S8 as in Fig. 18. Genitalia as in Figs. 8, 13.

Type material. Holotype female: USA NEVADA, Clark County, Mesquite, 36°48.98' N 114°04.22' W, 26 May 1998, *Camissonia*, T. Griswold, BBSL289459. Paratypes: NEVADA, Clark County: 2 females, 7 males, same data as holotype; 1 female, St. Thomas Gap, 36°24.35' N 114°5.62' W, 8 Jun 1998, *Camissonia*, T. Griswold; 2 females, 2 males, St. Thomas Gap, 36°24.45' N 114°05.58' W, 7 Jun 1998, pantrap, F. D. Parker; 2 females, Las Vegas Dunes Rec. Lds., 36°17.27' N 114°58.00' W, 22 May 1998, light blue pantrap, M. Andres, K. Receveur, K. Keen, C. Shultz; 1 female, 1 male, same except white pantrap; 1 male, same except

dark blue pantrap; 1 female, SE of Overton, 36°31.32' N 114°26' W, 21 May 1998, yellow pantrap, C. Shultz, K. Receveur, K. Keen, M. Andres; 1 female, same except white pantrap; 2 females, same except light blue pantrap; 1 female, same except dark blue pantrap; 21 females, 13 males, Riverside, 11–21 May 1983, F. D. & J. H. Parker; 21 females, 55 males, Mesquite, 25 May 1973, at dusk, *Oenothera*, G. Bohart; 6 females, 12 males, Glendale, 2 Jun 1973, P. F. Torchio; 12 females, 6 males, Toquap Wash, W Mesquite, 36°46'34"N 114°11'10"W, 24 May 2003, 19:30 h., *Camissonia*, D. Yanega; 2 males, Toquap Wash, 1 mi N Hwy I-15, 485 m, N36°46'39" W114°11'10", 25 May 2003, *Camissonia*, D. Yanega; 1 female, 3 males, Kaolin Wash, S Overton, 36°30'42"N 114°26'39"W, 25 May 2003, D. Yanega; 1 female, 2.16 mi SW Wechech Basin, 11S E755235 N4038290, 13 May 2005, fluorescent yellow pantrap, R. Andrus, S. Higbee; 1 female, 0.4 mi E St. Thomas Gap, 11S E760620 N4032979, 12 May 2005, white pantrap, D. Allen, E. Ahlstrom, R. Andrus, S. Higbee; 2 males, 3.9 mi SSW Whitney Pocket, 11S E755045 N4039308, 26 May 2005, white pantrap, R. Andrus, S. Higbee; 1 male, same except fluorescent yellow pantrap; 1 male, same except fluorescent blue pantrap. Holotype deposited in the U.S. National Pollinating Insects Collection, Logan, Utah; paratypes in Logan and Riverside.

Diagnosis. Timberlake recognized this as a new species and gave it a manuscript name that remained unpublished at his death. *Perdita vespertina* differs from all other *Xerophasma* except *P. celadona* in the largely dark mesoscutum. The ocelli of *P. vespertina* are larger than in *P. celadona*. Females differ from *P. celadona* in the simple mandible, pale clypeus, and rounded rather than acute pygidial plate. Males differ in the absence of dark marks above the antennal sockets and the rounded rather than emarginate apex of S8. The scopa on the hindtibia is denser than in other *Xerophasma*.

Range. Apparently endemic to Clark County, Nevada in the eastern Mojave Desert (Fig. 27) where it was active at dusk. Known only from scattered low elevation, sandy localities from Las Vegas Dunes to Mesquite and St. Thomas Gap. Some specimens were labeled as collected on *Oenothera* but these were from plants now assigned to *Camissonia* (Parker, personal communication).

Variation. Some individuals lack the intercalated second submarginal cell on one or both wings. The incidence varies among populations. In the Riverside population (n = 36) 22% have intercalated submarginal cell absent or incomplete on one wing; 11% missing on both wings. The cell was absent in only one specimen (1 %) of the Mesquite sample (n = 82) and none of the Glendale sample (n = 17). Two females from Glendale, Nevada 1973 had the mesoscutum light, with the mesepisternum light dorsally but brown ventrally.

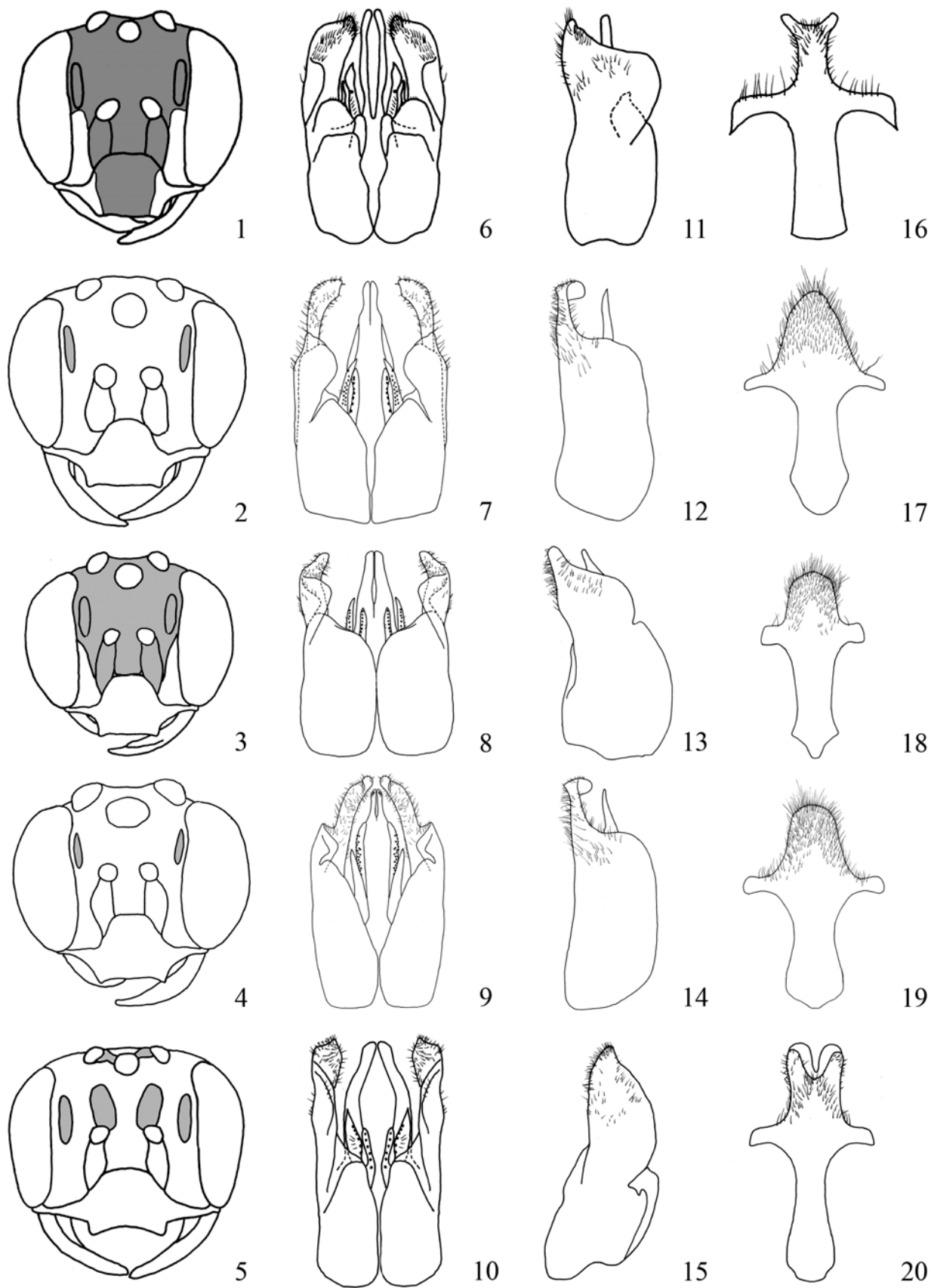
Etymology. From the Latin, “vesper”, meaning evening and west, in reference to the evening flight period and southwestern origin of the bee.

***Perdita (Xerophasma) rhondae* Griswold, new species**

(Figs. 5, 10, 15, 20, 23)

Female. Length: 7.0–7.5 mm. Forewing length: 5–5.5 mm. Head, mesosoma pale caramel-colored except: most of face cream-colored; dark-brown longitudinal mark above antennal socket, interocellar area, ventral area of mesepisternum; brown lateral longitudinal mark on mesoscutum, U-shaped mark on propodeum. Costal vein, prestigma dark. Stigma slightly stained, ventral margin distinctly darkened. T1–3 with subapical brown bands widened laterally on otherwise caramel-colored terga, on T4 reduced to lateral spot. Frons shiny. Mesoscutum impunctate, with sparse long pale hair present only anteriorly and laterally. Mesoscutum, scutellum shiny. Propodeal triangle somewhat shiny, finely reticulate.

Mandible simple, without preapical tooth. Labrum with apical margin slightly convex. Clypeal width dorsally slightly greater than width of each subantennal area. Frontal line scarcely raised, grooved. Facial fovea dull, linear, densely pubescent, extending from middle of antennal socket two-thirds distance to median ocellus. Ocellar area not inflated. Median ocellar diameter 1/6 width of interocular distance at level of median ocellus. Length of vertex behind lateral ocellus greater than ocellar diameter. Forecoxa, mesepisternum ventrally with long, simple, erect, apically bent hair. Length of marginal cell on wing margin less than or equal to 1.5 apical width. Pygidial plate broadly truncate.



FIGURES 1–20. Female heads (1–5), dorsal (6–10) and lateral (11–15) views of male genitalia, and male sternum 8 (16–20) of *Perdita* (*Xerophasma*). *Perdita celadona* (1, 6, 11, 16), *P. pallida* (2, 7, 12, 17), *P. vespertina* (3, 8, 13, 18), *P. bequaertiana* (4, 9, 14, 19), *P. rhondae* (5, 10, 15, 20). Shaded areas indicate dark markings on female heads.



FIGURES 21–23. Habitus of female *Perdita* (*Xerophasma*). *Perdita celadona* (21), *P. vespertina* (22), *P. rhondae* (23).

Male. Length: 5.5 mm. Forewing length: 4 mm. Head, mesosoma, legs pale caramel-colored except: entire face yellow; dark brown between ocelli, posterior to eye, longitudinal line laterally on mesoscutum, propodeum dorsally and posteriorly; brown subapical band on T1, less distinct bands on T2–4 broadened into spots laterally. T2 lateral fovea sometimes forming fine dark line. Sculpture, punctation, pubescence as in female except clypeus densely punctate.

Clypeal width dorsally approximately two times greater than width of each subantennal area. Supraclypeal area conically protuberant, with tuft of erect, apically bent hair. Facial fovea pubescent, elliptical, minutely depressed, equidistant from level of ventral margin of median ocellus and dorsal margin of antennal socket.

Frontal line, ocellar diameter, forewing as in female. T7 with pygidial plate well defined, with apical tuft of hair protruding from beneath apical margin. S8 as in Fig. 20. Genitalia as in Figs. 10, 15.

Type material. Holotype female: **USA** California, Inyo Co., Stovepipe Wells, 1.76 mi ENE; Stovepipe Main Dunes, near S margin, 11S E489743 N4051323, 26 Apr 2003, *Camissonia*, T. & R. Griswold. Paratypes: 6 males, 2 females, same data as holotype. Holotype is the property of the National Park Service and is indefinitely deposited in the U.S. National Pollinating Insects Collection, Logan, Utah; paratypes in Logan and the Death Valley National Park collection.

Diagnosis. Females with head more robust than in other *Xerophasma*, with the vertex longer. The conical protuberance and tuft of hair on the supraclypeal area in the male is not found in other *Xerophasma* or elsewhere in the genus.

Range. Apparently endemic to Death Valley (Fig. 23). Known only from dunes near Stovepipe Wells where it was active at dusk.

Variation. The size of the dark markings varies slightly in both sexes.

Etymology. This species was discovered after we thought we had completed this manuscript. It is a great pleasure to name this bee after my wife Rhonda, who has been my companion on many an entomological quest, and who discovered these bees on *Camissonia* as we were leaving the dunes near Stovepipe Wells at dusk.

***Perdita* (*Xerophasma*) *pallida* Timberlake**
(Figs. 2, 7, 12, 17, 24)

Perdita pallida Timberlake 1954:349. Holotype female, Hopkins Well, Riverside Co., California. (San Francisco) (examined).

Female. Length: 7.5–9.5 mm. Forewing length: 5.4–6.7 mm. Head, mesosoma, legs entirely pale caramel-colored, except: face cream-colored; facial fovea dark golden brown; fine dark line sometimes present on vertex medially between lateral ocelli. Costal vein dark, prestigma light, stigma evenly stained, without dark margins. Terga pale caramel-colored except light brown subapical bands on T1–4. Frons, mesoscutum, scutellum shiny; propodeal triangle dull with finely carinulate triangular area basally. Mesoscutum

moderately densely punctate, covered with moderately dense hair. Forecoxa, mesepisternum with long apically straight hair, sparse on forecoxa, dense on mesepisternum.

Mandible simple, without preapical tooth. Labrum with apical margin obtusely angled. Clypeal width dorsally equal to or slightly greater than width of each subantennal area. Frontal line strongly raised halfway to median ocellus then strongly depressed to median ocellus. Facial fovea sparsely pubescent, linear, shiny to dull, extending from ventral margin of median ocellus to middle of antennal socket. Ocellar area inflated. Median ocellar diameter 1/4 interocular distance at level of median ocellus. Length of vertex behind lateral ocellus less than ocellar diameter. Forecoxa with long, erect, slightly plumose, straight hair; mesepisternum ventrally with short, obliquely directed, straight hair. Length of marginal cell on wing margin twice apical width. Pygidial plate narrowly to broadly rounded.



FIGURES 24, 25. Habitus of female *Perdita* (*Xerophasma*). *Perdita pallida* (24), and *P. bequaertiana* (25).

Male. Length: 8.0–8.5 mm. Forewing length: 5.2–5.7 mm. Head, mesosoma, legs pale caramel-colored except: entire head slightly yellow; golden antenna; light brown integumental line on vertex medially between lateral ocelli; dark brown facial fovea, terga without preapical bands except sometimes quadrate brown mark on T1. T2 lateral fovea forming fine undarkened line. Sculpture, punctation, pubescence as in female.

Clypeus dorsally as wide as subantennal area. Supraclypeal area not protuberant, without tuft of hair. Facial fovea tear-shaped, extending half distance from ventral margin of median ocellus to dorsal margin of antennal socket, indistinct ridge defining fovea. Frontal line, ocellar diameter, forewing as in female. T7 with pygidial plate ill-defined, without apical tuft of hair protruding from beneath apical margin. S8 as in Fig. 17. Genitalia as in Figs. 7, 12.

Diagnosis. *Perdita pallida* can be distinguished from all other *P.* (*Xerophasma*) except *P. bequaertiana* by the entirely pale integument. It differs from *P. bequaertiana* by the smaller ocelli. Females further differ in the presence of very short hair on the facial fovea and the greater postocellar distance on the vertex; males in the cream to pale yellow frons and the shape of S8.

New material. MEXICO SONORA: El Golfo, 6 mi N, 10 Apr 1975, M. Wasbauer. USA NEVADA Clark County: 2 females, 2 males, 0.4 mi E St. Thomas Gap, 11S E760620 N4032979, 12 May 2005, fluorescent blue pantrap, D. Allen, E. Ahlstrom, R. Andrus, S. Higbee; 2 males, 1 female, same except fluorescent yellow pantrap; 2 males, same except white pantrap; 4 males, 3 females, same except 25 May 2005, fluorescent yellow pantrap, E. Ahlstrom, S. Higbee; 1 male, 1 female, same except 25 May 2005, white pantrap, E. Ahlstrom, S. Higbee; 1 female, same except 20 May 2004, fluorescent blue pantrap, S. Higbee, E. Ahlstrom, D. Skandilis, L. Saul; 1 male, same except fluorescent yellow pantrap; 1 male, white pantrap; CALIFORNIA Imperial County: 1 male, 23 females, Algodones Dunes, 3.5 mi SE Glamis, 28 Apr 1978, at light, A. Hardy, F. Andrews; 1 female, Algodones Dunes, 9.5 mi NW Glamis, Site 37, 32°4'27"N 115°12'45"W, 19 Apr 1979; 1 female, Algodones Dunes, S Ruthven, 32°55'30"N 114°59'34"W, 6 Apr 2000, at light, D. Yanega; Riverside County: 1 female, Blythe, 22 May 1969, at light, J. Johnson, R. Gill; San Bernardino County: 2 males, 1 female, Kelso Dunes, Mojave National Park, 770m, 34°35'20"N 115°43'02"W,

19 May 2001, *Oenothera*, D. Yanega; 1 male, 1 female, Palen Dunes, 27 Apr 1978, at light, F. G. Andrews, A. R. Hardy; 2 males, Parker Dam, dunes SW, 150m, 34° 155'N 114°08'W, 8 Apr 2005, L. Packer. New records are from the following institutions: Riverside, Sacramento, Davis, and Toronto.

Range. Northwestern Sonoran Desert and eastern Mojave Desert in California and adjacent Nevada (Fig. 28).

Variation. Two females in poor condition from north of the known range of *P. pallida* (California, San Bernardino Co., near Saratoga Springs; Davis collection) may represent this species. They differ by the presence of dark markings on the head. These include a stripe above the antennal socket connected with markings in the interocellar region, and markings on the vertex behind the eye.

Perdita (Xerophasma) bequaertiana Cockerell

(Figs. 4, 9, 14, 19, 25)

Xerophasma bequaerti Cockerell 1923:2. Preoccupied. Holotype female, Fabens, El Paso County, Texas. (New York).

Perdita bequaertiana Cockerell 1951 (*In*: Michener 1951:1089). N. Name.

Female. Length: 9.5–11.5 mm. Forewing length: 7.0–8.3 mm. Head, mesosoma, legs pale caramel colored except frons, facial fovea, vertex reddish brown; scutellum slightly paler than surrounding areas. Costal vein dark. Prestigma light. Stigma evenly stained, without dark margins. Preapical dark bands on otherwise caramel-colored terga. Frons, mesoscutum, scutellum, propodeal triangle dull, reticulate except shiny centrally on mesoscutum, scutellum. Basal area of propodeal triangle with carinulate triangular area.

Mandible simple, without preapical tooth. Labrum with apical margin obtusely angulate. Clypeal width dorsally slightly to 1½ times greater than width of each subantennal area. Frontal line strongly raised halfway to median ocellus, then strongly depressed to median ocellus. Facial fovea rather shiny to dull, appearing glabrous, linear, sometimes narrowed dorsally with slight bend toward eye, extending from dorsal 1/3 of antennal socket to level of ventral margin of median ocellus. Ocellar area strongly inflated. Ocelli greatly enlarged, the trio taking up nearly entire width of interocular distance at level of median ocellus, median ocellus 1/3 interocular distance at level of median ocellus. Length of vertex behind lateral ocellus equal to one-fourth of ocellar diameter. Forecoxa with long, erect, slightly plumose, straight hair; mesepisternum ventrally with short, obliquely directed, straight hair. Length of marginal cell on wing margin twice apical width. Pygidial plate narrowly rounded.

Male. Length: 9.5–11.0 mm. Forewing length: 6.1–7.1 mm. Head, mesosoma, legs pale caramel colored except: paraocular area sometimes pale; facial fovea dark brown; scutellum pale. Indistinct, light brown preapical band on T1, sometimes with lateral spots on T2–4. T2 lateral fovea sometimes forming fine undarkened line. Sculpture, punctation, pubescence as in female.

Clypeal width dorsally greater than width of each subantennal area. Supraclypeal area not protuberant, without tuft of hair. Facial fovea appearing glabrous, elliptical, depressed, narrower and shorter than in female, extending half distance from dorsal margin of antennal socket almost to ventral ocellar margin. Frontal line, ocellar diameter, forewing as in female. T7 with pygidial plate ill-defined, without apical tuft of hair protruding from beneath apical margin. S8 as in Fig. 19. Genitalia as in Figs. 9, 14.

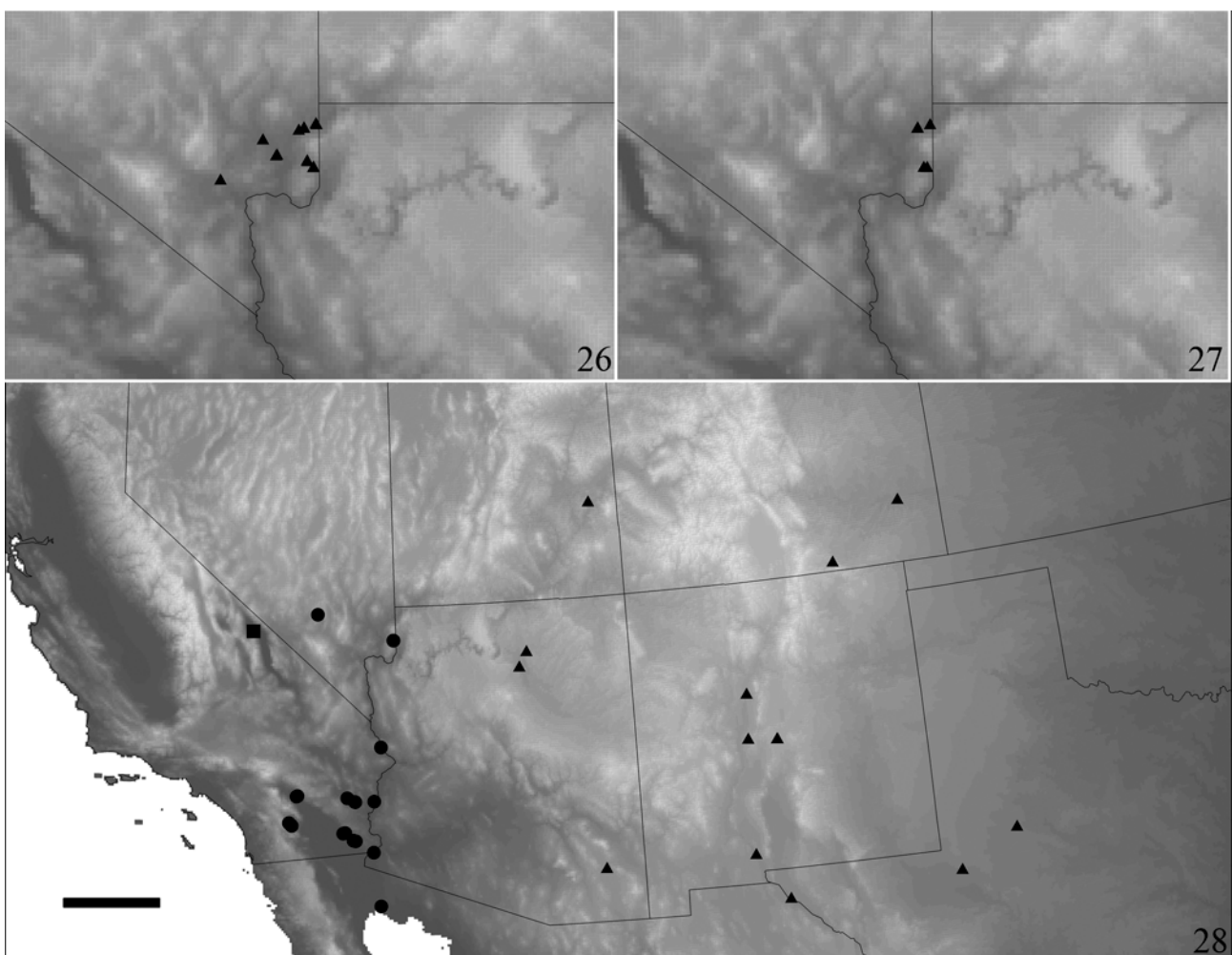
Diagnosis. The greatly enlarged ocelli are unique among *Perdita*. *Perdita bequaertiana* is larger than other *P. (Xerophasma)*.

New material. USA ARIZONA, Coconino County: 7 females, Moenkopi, 16 Jul 1994, L. G. Bezark, D. E. Russell; 1 male, Cameron, 1 Aug 1978, R. C. Miller; 1 male, same except 4 July 1977; 1 female, same except 5 Aug 1978; 1 female, same except 15 Aug 1977; Cochise County: 4 females, Willcox, Browntaren 90-33, black light, 18 Aug 1990, J. Schmidt; COLORADO, Bent County: John Martin Reservoir, sand dunes near dam, H. E. Evans, B. Kondratieff, D. & M. Leatherman, M. Weissman, H. Kneuttel; Las Animas County: 1 male, 22 Jul 1963, R. Allen; NEW MEXICO, Bernalillo County: 1 male, 2 females, Albuquerque, 16 Aug 1962, at light, G. E. Bohart, D. C. Heninger; 1 female, same except, 4 Aug 1962, D. C. Heninger; Dona Ana County: 1 female, Las Cruces, 5 Jul 1961, D. C. Heninger; Roosevelt County: 2 males, 2 females, Oasis State

Park, 4.0 mi N Portales, 4200 ft, 29 Jul 1975, to light among *Oenothera pallid runcinata*, 2045-2100 MST, T. J. Zavortink; Socorro County: 11 males, 3 females, La Joya Wildlife Preserve, 1 Jul 1976, W. Rubink; 1 male, 1 female, same except 1–14 July 1976, malaise trap; 2 females, same except 10 Jun 1977; 1 female, same except 13 Jul 1976; 1 female, same except 25 Jul 1976; 1 female, same except 1 Jul 1976, W. Rubink, H. Evans; 1 female, same except 25 Jun 1977, W. Rubink, H. Evans, D. Gwynne; 1 female, same except 17 Aug 1977, W. Rubink, J. Buchholz; Torrence County: Gran Quivira, 1 female, 8 Aug 1965, H. B. Leech; 1 female, same except 6500 ft., 19 Aug 1967; 1 male, 4 females, same except 20 Aug 1967, UV light; 1 male, 3 females, same except 18 Aug 1967; TEXAS Ward County: 1 male, 1 female, Monahans Dunes, 12 Jun 1976, H. Evans, W. Rubink, D. Gwynne; UTAH, Grand County: 2 females, 2 males, 9 mi NW Moab, 14 Jul 1994, L. G. Bezark, D. E. Russell. New records are from the following institutions: Davis, Ft. Collins, and Logan.

Range. Southern Great Plains, northern Chihuahuan Desert, and Colorado Plateau (Fig. 28). Known from El Paso and Howard Counties, Texas to Coconino County, Arizona, and Grand County, Utah.

Variation. One specimen from Albuquerque, New Mexico is darker than the rest, with the trochanter and femur of forelegs darkened rather than golden brown.



FIGURES 26–28. Distributions of *Perdita* (*Xerophasma*) in the southwestern United States and adjacent Mexico. *Perdita celadona* (26), *P. vespertina* (27), *P. rhondae* (■), *P. pallida* (●), and *P. bequaertiana* (▲) (28). Bar equals 100 km.

Discussion

In the phylogenetic analysis a heuristic search found one most parsimonious tree ($L = 24$, $Ci = 91$, $Ri = 86$; Fig. 29). Results show good support for a monophyletic *Xerophasma*. Synapomorphies include the triangular

second submarginal cell (character 3) and enlarged ocelli (character 1, states 2–4). The phylogeny suggests evolution toward crepuscular, and perhaps nocturnal, habits in *Perdita* (*Xerophasma*) from the typical diurnal behavior found in all other *Perdita*. This is reflected in increasingly pale integument (Fig. 29, characters 5, 9) and incremental enlargement of the ocelli (Fig. 29, character 1). Increase in ocellar size in bees is correlated with decreasing light during flight activity (Kerfoot 1967). Enlarged ocelli are rare among bees but do occur sporadically. Moderate enlargement of the ocelli occurs in other *Oenothera/Camissonia* oligoleges such as *Andrena* (*Onagandrena*) (LaBerge & Thorp 2005), *Svastra* (*Anthedonia*), and *Lasioglossum* (*Sphecodogastra*) (McGinley 2003), but only in some *L.* (*Sphecodogastra*) are they as greatly enlarged. Other matinal or vespertine bees of the southwestern deserts (*Colletes stephensi* Timberlake, *Ancylandrena koebelei* Timberlake, *Simanthesdon*, *Martinapis*) and the tropical *Megalopta*, *Megaloptidia*, *Caupolicana* (Kerfoot 1967), *Ptiloglossa* and its cleptoparasite *Odyneropsis* (Rozen 1984), and some *Xylocopa* (Kerfoot 1967) have moderately enlarged ocelli. None of these has evolved a pale integument, though a reddish metasoma occurs in *Megalopta* and some *Lasioglossum* (*Sphecodogastra*).

The Mojave Desert appears to be the origin of *Perdita* (*Xerophasma*). Not only is it the center of diversity with four of the five species present, but the basal members of the clade are restricted to this region. The expansion of the subgenus into the typically hotter Sonoran and Chihuahuan Deserts is accompanied by increasingly large ocelli and possibly nocturnal behavior (Kerfoot 1967). Many *P. pallida* and *P. bequaertiana* have been collected at black lights.

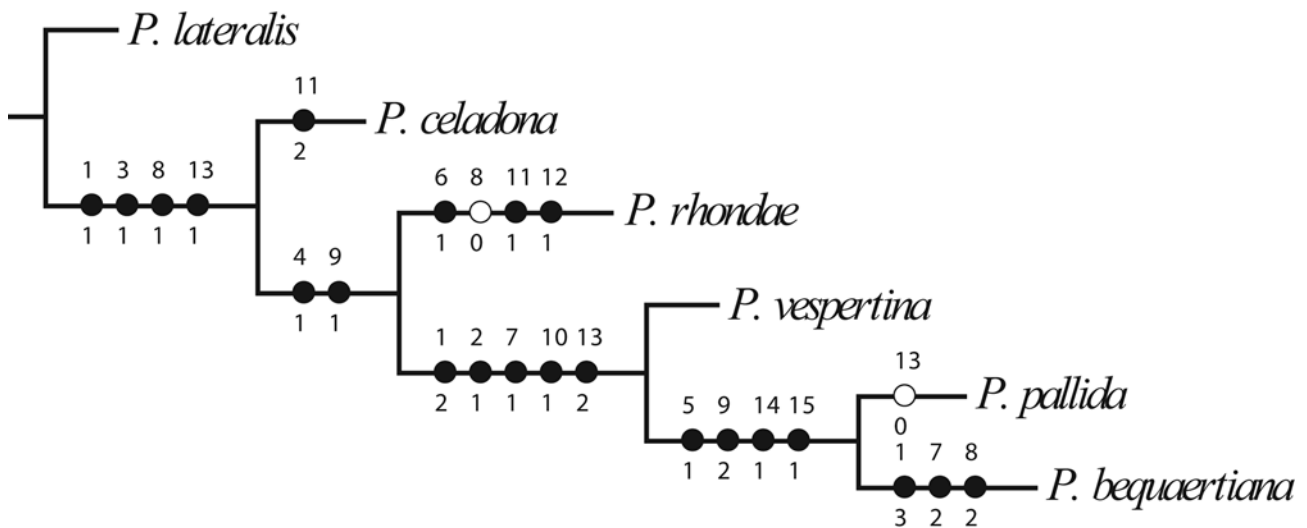


FIGURE 29. Cladogram of *Perdita* (*Xerophasma*). Characters are shown above circles, character states below. L=24; Ci=91; Ri=86.

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