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Natural history, ecology, and conservation of the genus *Polyphylla* Harris, 1841. 1. New species from the southwestern United States and Baja California, Mexico, with notes on distribution and synonymy (Coleoptera: Scarabaeidae: Melolonthinae)

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Natural history, ecology, and conservation of the genus *Polyphylla* Harris, 1841. 1. New species from the southwestern United States and Baja California, Mexico, with notes on distribution and synonymy (Coleoptera: Scarabaeidae: Melolonthinae)

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Abstract. Four **new species** of the genus *Polyphylla* Harris (Coleoptera: Scarabaeidae: Melolonthinae) from the southwestern United States and Baja California, Mexico, are described and illustrated: *Polyphylla anivallis*, *P. koso*, *P. morroensis*, and *P. socorrana*. Two nomenclatural changes are proposed: *Polyphylla ratcliffi* Young is placed into synonymy with *P. avittata* Hardy and Andrews, **new synonymy**; *P. uteana* Tanner is removed from synonymy and reinstated as a valid species, **reinstated status**. The females of *P. monahansensis* Hardy and Andrews and *P. stellata* Young are described and illustrated. New distributional records and ecological associations are amended for *P. avittata* Hardy and Andrews, *P. cavifrons* LeConte, *P. concurrens* Casey, *P. crinita* LeConte, *P. diffracta* Casey, *P. mescalerensis* Young, *P. petittii* (Guérin-Méneville), and *P. rugosipennis* Casey. A checklist of the “Western Clade” species of *Polyphylla*, north of Mexico, is included.

Key words. Relict species, sand dunes, microrefugia, “sky island” ecosystems, endemism, June beetles

Resumen. Cuatro **especies nuevas** del género *Polyphylla* Harris (Coleoptera: Scarabaeidae: Melolonthinae) del suroeste de los Estados Unidos y Baja California, México, se describen e ilustran: *Polyphylla anivallis*, *P. koso*, *P. morroensis*, y *P. socorrana*. Se proponen dos cambios de nomenclatura: *Polyphylla ratcliffi* Young se coloca en sinonimia con *P. avittata* Hardy y Andrews, **nueva sinonimia**; *P. uteana* Tanner es removido de la sinonimia y reinstalado como una especie válida, **estado reinstalado**. Las hembras de *P. monahansensis* Hardy y Andrews y *P. stellata* Young se describen e ilustran. Nuevos registros de distribución y asociaciones ecológicas se complementan para *P. avittata* Hardy y Andrews, *P. cavifrons* LeConte, *P. concurrens* Casey, *P. crinita* LeConte, *P. diffracta* Casey, *P. mescalerensis* Young, *P. petittii* (Guérin-Méneville), y *P. rugosipennis* Casey. Se incluye una lista de las especies del “Clado Occidental” de *Polyphylla*, al norte de México.

Palabras clave. Especies relictas, dunas de arena, microrefugia, ecosistemas “insulares del cielo”, endemismo, escarabajos de Junio

Introduction

The profound effect of Pleistocene glaciation upon the distributions of indigenous biota in western North America has far reaching implications for understanding adaptive and evolutionary responses to climate shifts. Paleoecologic data inferred from palynological analyses, oxygen isotope ratios in marine and ice core samples, lacustrine sedimentary sequences, and packrat (*Neotoma* Say and Ord: Cricetidae) paleomidden plant assemblages indicate that dramatic climate changes during the Pleistocene produced an array of distinct biogeographic patterns (Spaulding and Graumlich 1986; Betancourt et al. 1990; Van Devender 1990a, 1990b; Elias and Van Devender 1992; MacKay and Elias 1992; Riddle et al. 2000; Thompson and Anderson 2000; Harrison et al. 2003; Holmgren et al. 2003; Smith and Farrell 2005). While new climatic regimes became established, glacial-interglacial oscillations of the continental ice sheets formed isolated regions of ameliorated habitats in which populations of species survived outside of their main distribution. As a result, many organisms that were once contiguously distributed experienced extreme range reduction, becoming progressively restricted to unique microrefugia creating disjunct relict populations (Milstead 1960; Johnson 1977; Péwé 1983; Mayr and O’Hara 1986; Rull 2009; Dobrowski 2010; Loera et al. 2012). The isolation of these populations to a deglaciated environment would prohibit their dispersal under regionally changing climates and allow a progressive loss of genetic diversity and thus speciation as they adapted to previously inhospitable terrain (Hewitt 1996; Hewitt and Nichols 2005; Loehle 2007; Loera et al. 2012).

Herein, four new species of the melolonthine genus *Polyphylla* Harris, 1841, are described and hypothesized to be precinctive to Pleistocene refugia representing allopatric peripheral isolates of more widespread and divergent proto-taxa: *Polyphylla anivallis* from Animas Valley Sand Dunes, Hidalgo County, New Mexico; *P. koso* from the Coso Mountain Range, Mojave Desert, Inyo County, California; *P. morroensis* from Baywood Fine Sands, Morro Bay, San Luis Obispo County, California, and *P. socorriana* from El Socorro Sand Dunes, Baja California, Mexico.

Young (1967, 1988) separated the species of *Polyphylla* north of Mexico, into four complexes based primarily upon similarities of the male genitalic morphology supplemented with various secondary characters and geographic distribution. To some extent, this methodology had previously been used by Horn (1881), Casey (1914), and Fall (1928). However, those and other authors remarked upon the intra- and interspecific inconsistencies of those criteria (e.g. Mutchler 1919; Cazier 1938; Hardy 1974, 1981; Hardy and Andrews 1978; La Rue 1998; Russell 2000; Skelley 2003). Although recent molecular phylogenetic data and mitochondrial lineages of Nearctic *Polyphylla* (Russell 2000) revealed unsuspected relational complexities within the genus, they refute the putative species complexes and morphological relationships proposed by Young (1967, 1988). Despite these significant research efforts, the Nearctic taxa are still plagued with numerous taxonomic difficulties. While some species are easily recognized by their unique set of morphological characters and familiarity (e.g. *P. decemlineata* (Say), the most common and frequently collected western species), few can be identified authoritatively and must be evaluated from a series of individuals and populations to assess intraspecific variation.

The present descriptive study follows the evolutionary framework based on mitochondrial DNA (mtDNA) sequence data of Russell (2000) indicating an inclusive, monophyletic New World *Polyphylla* assemblage with the Nearctic taxa comprised of five species clades:

- (I.) the *P. occidentalis* (Linnaeus)/*P. variolosa* (Hentz) clade;
- (II.) a combination of the *P. decemlineata* (Say) and *P. diffracta* Casey species complexes of Young (1988);
- (III.) the *P. hammondi* LeConte clade;
- (IV.) the *P. cavifrons* LeConte/*P. anteronivea* Hardy and Andrews clade; and
- (V.) the *P. gracilis* Horn clade.

The integration of the *P. decemlineata* and *P. diffracta* complexes of Young (1967, 1988) resolves the prior taxonomic incongruity of taxa that share morphological characteristics of both species groups. For example, *P. aeolus* La Rue and *P. monahansensis* Hardy and Andrews, provisionally associated with the decemlineata species complex, exhibit pronotal setae, a morphological characteristic of the diffracta species group. Despite extreme morphological divergence, many of the former diffracta complex species appear more closely related molecularly to their regional *P. decemlineata* demes than to other *P. diffracta*-related species (Russell 2000).

Members of species clade II, with which the four new species are associated, share a guild of characters and hypothesized synapomorphies presumably derived from a common proto-*P. decemlineata* genotype that distinguish it as one of the most morphologically distinctive and speciose groups in the genus. All species exhibit pronotal discal setae (except *P. decemlineata* and *P. arguta* Casey); presence or absence of elytral setae, excluding suture; elytra avittate, strongly vittate or vittae composed of non-linear squamal groupings; typically white or ochraceous setal and/or squamal vestiture; light testaceous to deep rufotestaceous or black dorsal integument; unidentate to tridentate protibia; diminutive to large species (15–35 mm); and restricted distribution in western North America (the “western clade”, Russell 2000).

Materials and Methods

Initial taxonomic assessment of the new species described herein required perusal of prior literature (Casey 1891, 1895, 1914; Fall 1908, 1928; Tanner 1928; Cazier 1939; von Bloeker 1939; Van Dyke 1947; Young 1966, 1967, 1986, 1988; Hardy and Andrews 1978; Hardy 1981) and evaluation of diagnostic characters based on type specimens and other material of, or selected taxa synonymized under, *P. crinita* LeConte, *P. decemlineata*, and *P. diffracta* to which the new species appear most similar. In addition, forms synonymized under *P. nigra* Casey, reinstated to species status by Young (1988),

which formerly applied to *P. crinita*, were also reviewed. Consequently, salient diagnostic characters of the new taxa were considered sufficiently distinctive to warrant species recognition as well as being consistent with Russell's molecular data (2000) indicating that several cryptic species exist within the current taxonomic definitions of both *P. decemlineata* and *P. diffracta*.

For purposes of this paper, the phylogenetic species concept of Wheeler and Platnick (2000) is applied. The Nearctic region is defined as America, north of Mexico.

Measurements were taken in a straight line, except curvilinear measurements of the male lamellate antennomeres (distance from basal constriction to apex in dorsal aspect) using an ocular micrometer or digital calipers and rounded to the nearest 0.5 mm. Length was measured at the greatest longitudinal distance from anterior clypeal margin to elytral apices. Width was measured at the greatest transverse distance across both elytra supplemented with humeral measurement. Color was determined under white fiber optic illumination and magnification (10–15×).

Quantitative aspects of integumental vestiture (setae, squamae, and punctation) are expressed as form, density, and length as viewed under magnification (10–20×). The appearance of vestiture is defined as either setae (simple, circular in cross section, trichoid), squamae (opaque, acuminate, rarely lanceolate) or spiculae (small, thickened, pointed, generally translucent). Due to inherent fossorial behavior, the vestiture is subject to abrasion sometimes removing or modifying these character states.

Setal density is defined as solitary (single, sparsely distributed), scattered (randomly distributed), dense (nearly obscuring integument), or devoid of setae. Squamal density is defined as solitary (single, separated), contiguous (clustered, adjoined at margins), or imbricate (overlapping as in roof shingles). Puncture density is defined as coarse (separated by less than 1–2 puncture diameters), moderate (separated by 3–4 puncture diameters), sparse (separated by more than 4 puncture diameters), or impunctate.

Male *Polyphylla* have uniformly well sclerotized phallobases and parameres with a simple endophallus which is considered the primitive genitalic state in Scarabaeoidea (d'Hotman and Scholtz 1990). Interspecific similarities combined with intraspecific variation in Nearctic *Polyphylla* demonstrate that these characters provide negligible diagnostic support for species determination or secondary groupings. Consequently, no taxonomic emphasis is given to the male genitalic morphology.

In recent decades the American Southwest and adjacent northwestern Mexico have become an important study area for biology, ecology, and conservation management (Bainbridge and Virginia 1990, and references therein). Because many species of *Polyphylla* are stenotopic (ecologically specialized) they may be highly suitable as indicators of environmental change and as umbrella species in conservation efforts. *Polyphylla barbata* Cazier, endemic to the Zayante Sandhills, Santa Cruz County, California, has been federally listed as endangered because more than 60% of the ecoregion has been lost to human exploitation. Three additional species, *P. anteronivea* Hardy and Andrews, *P. erratica* Hardy and Andrews, and *P. nubila* Van Dyke, are listed as "critically imperiled" by the California Department of Fish and Game. For purposes of disseminating conservation information, common names for each new species are proposed to facilitate inclusion in concurrent habitat conservation plans, environmental assessment and impact statements, inventories and monitoring of species of special concern, and consideration as candidate species under the Endangered Species Program by the United States Fish and Wildlife Service or the Official Mexican Norm for environmental protection (NOM-059).

Conservation status of the species described herein are defined as "special concern," a species which is not presently threatened or endangered but warrants careful monitoring of its status in the event of future stochastic or anthropogenic disturbance, or "critically imperiled," a species at risk of becoming endangered or extinct if immediate measures are not taken to protect it and the habitat where it occurs.

The country, state, department, or county representing new distribution records are indicated in **bold**. Multiple specimen labels are separated by a double slash ("*//*"); brackets ("*[]*") include explanatory information. The following codens denote depositories for specimens examined herein:

BYUC	Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT, USA.
CASC	California Academy of Sciences, San Francisco, CA, USA.
DALC	Delbert A. La Rue, Entomology Research Museum, University of California, Riverside, CA, USA.
EAPZ	Escuela Agrícola Panamericana, El Zamorano, Francisco Morazán, Honduras.
FSCA	Florida State Collection of Arthropods, Gainesville, FL, USA.

JMMC	Jean-Michel Maes, Museo Entomológico de León, León, Nicaragua.
JWSC	James W. Saulnier, Indio, CA, USA.
MXAL	Miguel A. Morón, Xalapa, Veracruz, Mexico.
PESC	Paul E. Skelley, Florida State Collection of Arthropods, Gainesville, FL, USA.
PKLC	Paul K. Lago, University of Mississippi, University, MS, USA.
POKC	Paul O. Kaufman, Morristown, AZ, USA.
RACC	Richard A. Cunningham, Chino, CA, USA.
RHMC	Ronald H. McPeak, Vancouver, WA, USA.
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, CA, USA.
UCRC	Entomology Research Museum, University of California, Riverside, CA, USA.
UNAM	Universidad Nacional Autónoma de México, Mexico City, Distrito Federal, Mexico.

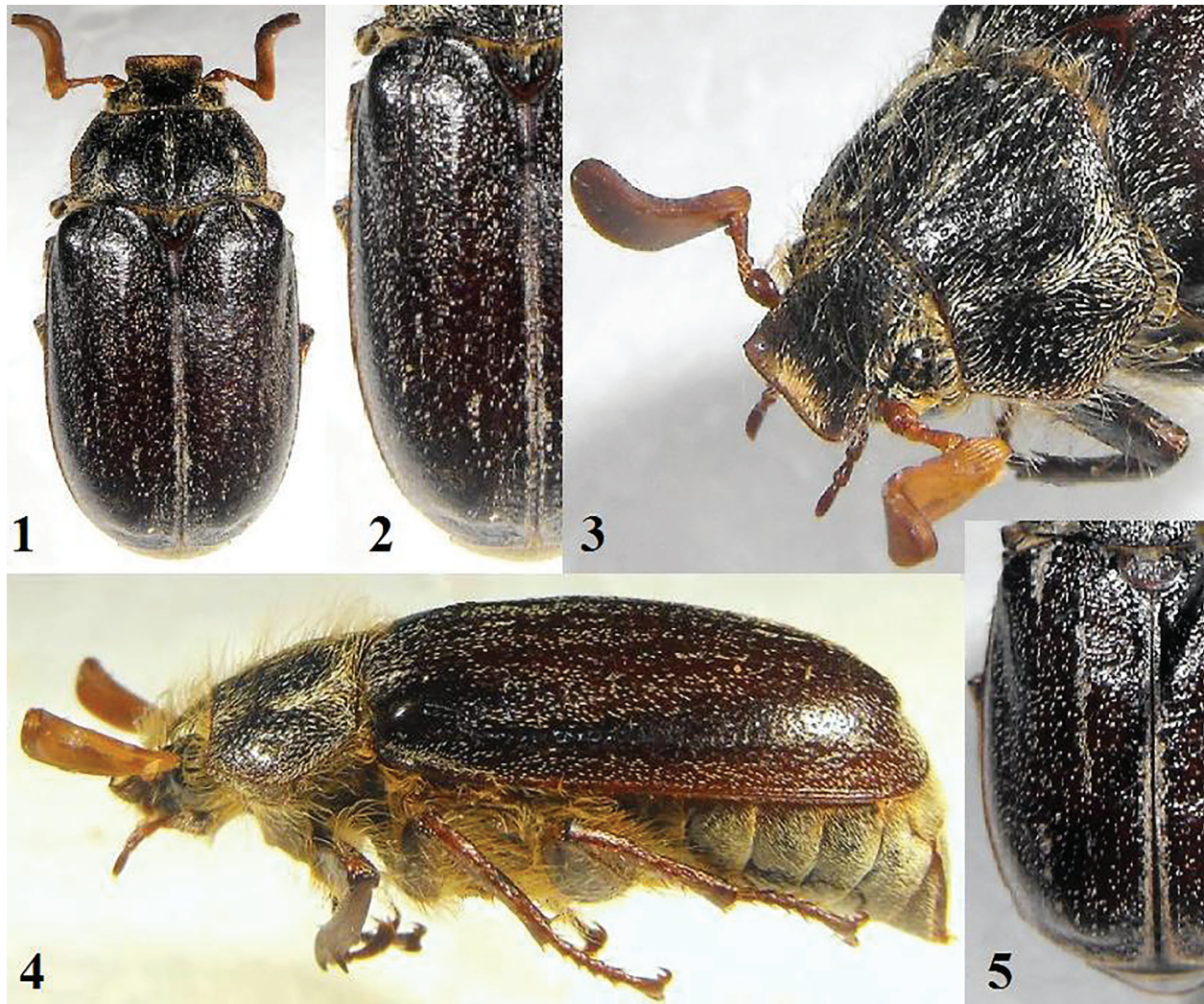
Species descriptions

Polyphylla anivallis La Rue, new species

(Fig. 1–5, 50–51)

Type material. Holotype. Male (CASC #18361). Labeled “USA, NEW MEXICO: Hidalgo County, 3 mi E. Jct. St. Hwys. 338 & 79, Diamond-A-Ranch - Juniper Trap, sand dunes, 25-26.VII.2005 // 1584m elev., Oak-Juniper-Mesquite, D.A. La Rue collector, 175w HgVL.” **Paratypes.** (32). Labeled as holotype (31 males); “USA, NEW MEXICO: Hidalgo County, 3 mi ENE Fitzpatrick’s, 5-6.VIII.2002, 1585m, K.H. Osborne collector, MV” (1 male). BYUC, CASC, JWSC, MXAL, PESC, PHLC, POKC, RACC, RHMC, SBMNH, UCRC.

Description. Holotype. Male (Fig. 1–4). Length 19.5 mm. Greatest width 9.0 mm. Humeral width 8.0 mm. **Form.** Elongate, parallel-sided, diminutive. **Color.** Head, eyes, pronotum, protibial dentition black; antennomeres, other appendages of head, scutellum, and legs rufotestaceous; elytral integument black, deep rufotestaceous to rufopiceous under magnification (10.5×); pygidium, pterothoracic integument, exposed abdominal sternites rufopiceous; except where noted, setal and squamal vestiture pale yellow. **Head.** Subconvex; clypeus transverse with strongly reflexed, bisinuate anterior margin; anterior angles obtuse, lateral margins convergent basally; disc deeply concave, coarsely punctate, with long, suberect setae and acuminate scales. Frontoclypeal suture sinuate, obscured medially by coarse punctation. Frons and vertex shallowly punctate, provided with long, erect, setae. Maxillary palpomere-4 cylindrical, anteriorly depressed, finely rugose with translucent, golden yellow setae; subequal in length to three basal palpomeres combined. Mentum subquadrate, anteriorly emarginate, angles broadly rounded. **Antennae.** Scape elongate, distally bulbous, convergent basally, provided with a dense scopula of long setae; lamellate antennomeres 4–10 distally curved obtusely outward, provided with randomly distributed translucent, golden yellow setae. Antennal club 2.7× (linear measurement) or 4× (curvilinear measurement) longer than basal antennomeres combined. **Pronotum.** Strongly convex, transverse, 2.5× wider than length at midline, widest at posterior 1/2; anterior angles obtuse, basal angles broadly arcuate and explanate; marginal bead lacking anteriorly, feebly reflexed and coarsely serrate posterolaterally, evanescent posteriorly. Disc coarsely to moderately punctate; punctures provided with either a single, recumbent, acuminate scale or long seta; medially sulcate dividing a transverse tumidity; appearing trivittate, medial vitta longitudinally complete, lateral vittae eroded at apical 1/2, basally formed as two distinct patches of imbricate, white scales. **Scutellum.** Oblong, broadly rounded; margins glabrous, disc medially provided with solitary to imbricate, acuminate white scales. **Elytra.** 3.2× greater in length than width; humeral angles obtusely rounded, posterolateral angles broadly arcuate and feebly explanate. Marginal bead evanescent posterolaterally, sutural bead posteriorly cristate with apices acuminately produced. Disc moderately to coarsely punctate; calli gibbous, impunctate; vestiture composed of acuminate scales and widely scattered, suberect setae; appearing nearly avittate, an indication of vittae composed of widely separated glomerate patches of contiguous to imbricate, acuminate, white scales and suberect setae. Metathoracic wings functional. **Pygidium.** Subtriangular, convex, length subequal to width; distal apex broadly rounded; disc coarsely punctate, vestiture composed of acuminate scales



Figures 1–5. *Polyphylla anivallis*. 1–4) Holotype male. 5) Left elytron of paratype male.

and suberect setae. **Venter.** Densely pubescent obscuring pterothorax; exposed abdominal sternites convex, penultimate and ultimate sternites with a basal glabrous band; vestiture composed of solitary to imbricate acuminate, white scales and scattered, suberect setae throughout. **Legs.** Protibia strongly bidentate, basal third tooth feebly indicated as an angular projection; dentition widely separated, projecting obliquely forward from longitudinal tibial axis; inner margin with a coarse, serrated ridge; outer margin with a longitudinal carina; surfaces coarsely to finely punctate, variably covered with solitary to contiguous acuminate scales and scattered setae. Meso- and metatibia with an incomplete transverse carina; dorsally coarsely to finely punctate, margins diverging toward apex at distal 1/3, provided with a fringe of thick spiculae. All femora flattened, margins parallel, surface vestiture as in protibiae. Apices of tarsomeres coronate with a fringe of short, translucent spiculae; tarsomere-5 elongate, subequal in length to four basal tarsomeres combined, ventral surface bearing a sharp carina extending 1/2 length of tarsomere; tarsal claws with basal proximal tooth. **Phallobase and parameres.** Number examined (3). In dorsal aspect, symmetrical with two simple parameres narrowing distally, apices convergent; median notch sharply rounded, separated approximately 1/2 length of parameres; lateral aspect, apical 1/3 cristate; apices smoothly rounded ventrally; caudal aspect, subconvex, obliquely depressed; distal tips nearly adjoined anterodorsally.

Female. Unknown.

Variation. Males (32). Length 17.0–20.5 mm. Greatest width 8.0–10.5 mm. As holotype except: **Color.** Scutellum, antennal scape and protibial surface black. **Head.** Clypeus feebly emarginate anteriorly, angles rounded. **Pronotum.** Lateral marginal bead feebly serrate, angulate medially; setal vestiture densely distributed. **Scutellum.** Setal and squamal vestiture reduced. **Elytra.** Vittae represented as a linear pattern of solitary to contiguous scales or with short vittal fragments; setal vestiture reduced (abrasion?). **Pygidium.** Setal vestiture reduced. **Venter.** Squamal vestiture of exposed abdominal sternites obscuring surface. **Legs.** Distal tips of protibial dentition worn.

Diagnosis. The avittate elytral vestiture and black to deep brown dorsal integument of *P. anivallis* are similar to *P. stellata* Young (Fig. 45). Some specimens of *P. anivallis* have discontinuous elytral vittal fragments with edges coarsely eroded (Fig. 5), whereas, males of *P. stellata* have at most small, irregular-shaped spots of contiguous to imbricate squamae in normally vittate areas. In addition, protibial dentition in male *P. stellata* varies from bidentate to tridentate (bidentate in *P. anivallis*); and lacks the cristate elytral sutural apices of *P. anivallis*. The presence or absence (presumably abraded) of elytral discal setae is variable in *P. stellata* (present in *P. anivallis*). Both species share a mixture of white and pale yellowish-brown elytral squamae; presence of pronotal and pygidial setae; and similar ecological requisites: *P. stellata* is associated with sandy alluvial substrates of the American, Sacramento, and San Joaquin River Deltas, Contra Costa to Sacramento Counties, California (La Rue 1998) while *P. anivallis* is restricted to a geographically isolated sand dune complex in the Chihuahuan Desert of southwestern New Mexico. These morphological similarities may be the result of identical adaptive solutions to similar environmental pressures prevalent in psammophilous ecosystems.

In dorsal habitus and distribution, *P. anivallis* may be confused with avittate concolorous *P. diffracta* (*s.l.*). However, that species is devoid of elytral setae; has light yellowish brown to dark brown (rarely olivaceous) integumental color; white (rarely yellow) squamae; and absence of acuminately produced elytral sutural apices. Ecologically, *P. diffracta* (*s.l.*) is a highly facultative species.

Natural history. *Polyphylla anivallis* is ecologically associated with relictual pinyon-juniper-oak woodland refugia growing in deep semi-stabilized, low relief sand dunes (Lanner and Van Devender 1981; Thompson and Anderson 2000; Smith and Farrell 2005).

Adult emergence of *P. anivallis* is apparently prompted by the onset of the summer monsoon that typically begins during July, indicative of “phenotypic plasticity” (*i.e.* any change in an organism’s characteristics in response to an environmental signal, Schlichting and Smith 2002). Earlier collection attempts during the drier months of May and June were unsuccessful. At the time the type series was collected, during late July, there were standing pools and puddles of monsoonal rain throughout the area and the sand was damp to a depth of 2 to 7 cm. Just prior to dusk, in faint diffused light, males were observed flying rapidly in open areas between dune vegetation approximately one meter above the sand surface. Most males were attracted to a 175 watt mercury vapor light station while other males were encountered crawling on the sand surface after twilight. Females are unknown and presumed flightless.

Ecology. Animas Valley Sand Dunes (Fig. 50–51) are located in the Chihuahuan Desert of southwestern New Mexico, 1580 m elevation. The northwest-southeast oriented basin where they occur is bordered on the west by the Peloncillo Mountains and the Animas, Pyramid and San Luis Mountains to the southeast. Due to internal drainage, most of Animas Valley contains fine textured Pleistocene alluvial deposits (Kottlowski 1965). Sediments and alluvia, including those from two ephemeral playas, remnants of Pleistocene Lakes Animas and Cloverdale, are subject to saltation by southerly prevailing winds and subsequent downwind accretion at the southeast margin of the valley. These accumulations form diminutive rounded lunette dunes in an elongated arcuate-shaped mass which essentially follow the basal contours of the southern Animas Mountains. The pale ecru sand color is a result of this amalgam of aggregates.

A complex of transitional floristic elements representing Chihuahuan desert scrub, oak savanna, oak woodland, and pinyon-juniper woodland occur near or within the dunes. Dominant vegetation in the immediate habitat includes *Quercus* sp. (oak: Fagaceae), *Pinus engelmannii* Carrière (apache pine: Pinaceae), *P. leiophylla* var. *chihuahuana* Englemann (chihuahuan pine: Pinaceae), *Juniperus deppeana*

von Steudel (alligator juniper: Cupressaceae), *Arctostaphylos* sp. (manzanita: Ericaceae), scattered *Yucca* sp. (Asparagaceae), with an understory of numerous forbs and grasses depending on precipitation levels.

Climate is characterized by high amounts of solar radiation, wide diurnal ranges in ambient temperature, low relative humidity, and highly variable precipitation with subsequent elevated rates of evaporation. The dry early summer months of May and June are typically the hottest part of the year with average temperatures of 16° to 32° C. Winters are generally cool with average daytime temperatures between 4° and 14° C., and occasional snow at higher elevations. Average annual precipitation of 24 to 38 cm primarily occurs during July through September as brief localized convective thunderstorms. As much as 90% of annual rainfall occurs during this period (Holmgren et al. 2003).

Conservation. Because of varied topography, unique floral diversity, and geographic isolation of Animas Valley, the ecoregion is recognized as a refugium for many threatened and endangered indigenous species (Dinerstein et al. 2000). The area comprising the type locality is under the jurisdiction of the Diamond-A-Ranch (formerly the Gray Ranch) which is administered by the Animas Foundation, a private conservation agency dedicated to protecting the abundance of biological diversity and natural and historical values of the area. As a result, public access to the area is carefully regulated which affords *P. anivallis* some protection. However, because of its apparent endemism, *P. anivallis* should be considered a species of “special concern.”

Etymology. From a combination of the prefix of “Animas” and the Latin *vallis*, “valley.”

Common name. The Animas Valley polyphyllan scarab beetle.

Polyphylla koso La Rue, new species

(Fig. 6–10, 52–53)

Type material. Holotype. Male (CASC #18339). Labeled “USA, CALIFORNIA, Inyo County, China Lake NAWS [Naval Air Weapons Station], Coso Mountains, Coso Bridge, 25.VII.1998, G. Pratt, C. Pierce, MV light” [phallobase and parameres mounted on card]. **Paratypes.** (8). Same data as holotype except 18.VII.1998, G. Pratt, M. van Tilborg (6 males); 19.VII.1999 (1 male); Mill Spring, 07.VI.2003, G. Pratt, C. Pierce, MV light (1 male). CASC, UCRC.

Description. Holotype. Male (Fig. 6–9). Length 28.0 mm. Greatest width 12.0 mm. Humeral width 11.5 mm. **Form.** Elongate, robust, parallel-sided. **Color.** Head, eyes, pronotum, elytral calli, pygidium, and abdominal sternites black; elytra, scutellum, anterior clypeal margin deep rufotestaceous; basal antennomeres, other appendages of head, and legs rufotestaceous; lamellate antennomeres light testaceous; except where noted, setal and squamal vestiture white. **Head.** Subconvex; clypeus transverse with highly reflexed, feebly emarginate anterior margin; anterior angles obtuse; lateral margins basally reflexed and sinuate; disc deeply concave, coarsely punctate, with acuminate scales and recumbent setae. Frontoclypeal suture obscured medially by rugose punctation and contiguous acuminate scales and suberect setae. Frons depressed on either side of a longitudinal tumidity, surface moderately to coarsely punctate, provided with solitary to contiguous, acuminate scales and scattered setae. Vertex coarsely punctate, with similar vestiture as frons. Maxillary palpomere-4 elongate, cylindrical, anteriorly depressed, densely setose with minute, golden spiculae; 1/2 length of three basal palpomeres combined. Mentum subquadrate, anteriorly deeply emarginate, angles broadly rounded, disc posterolaterally with long setae. **Antennae.** Scape subtriangular, constricted basally, apex bulbous, provided with a dense scopula of long setae; lamellate antennomeres 4–10 distally recurved outward attaining a right-angle, provided with translucent, golden setae. Antennal club 2.5× (linear measurement) or 3.3× (curvilinear measurement) longer than basal antennomeres combined. **Pronotum.** Broadly convex, transverse, 2× wider than length at midline, widest at posterior 1/2; anterior angles sharply rounded, basal angles broadly obtuse and explanate; marginal bead absent anteriorly, serrate and explanate laterally, evanescent posteriorly. Disc moderately to coarsely punctate, punctures provided with an acuminate scale



Figures 6–10. *Polyphylla koso*. 6–9) Holotype male. 10) Left elytron of paratype male.

or suberect seta; medially sulcate, dividing a transverse tumidity at posterior 1/2; trivittate; vittae longitudinally complete, edges eroded, composed of contiguous to imbricate, acuminate scales. **Scutellum.** Oblong, broadly rounded; margins glabrous, disc obscured by imbricate scales; devoid of setae. **Elytra.** 2.2× greater in length than width; humeral angles obtusely rounded, posterolateral angles broadly arcuate. Marginal bead explanate and reflexed posterolaterally, evanescent posteriorly, sutural bead obscured by dense acuminate scales. Disc rugosely punctate; calli tumose, glabrous, moderately punctate; vestiture composed of solitary to imbricate, acuminate scales; devoid of setae; distinctly vittate; vittal edges coarsely eroded, composed of contiguous to imbricate, acuminate scales; sutural and subsutural vittae discontinuous; submarginal vittae complete; subhumeral vittae absent; interstitial area between discal and submarginal vittae with a series of disconnected, glomerate patches of squamae. Metathoracic wings functional. **Pygidium.** Subtriangular, convex; length subequal to width; angles obtusely rounded; disc moderately punctate, depressed behind reflexed margins; vestiture composed of contiguous, acuminate scales; devoid of setae. **Venter.** Densely pubescent obscuring pterothorax; exposed abdominal sternites subconvex with a basal glabrous band, vestiture composed of solitary to imbricate scales and solitary setae. **Legs.** Protibia bidentate, lacking any indication of a basal third tooth; dentition moderately separated, projecting obliquely forward from longitudinal tibial axis; inner margin rounded, outer margin with a sharp longitudinal carina; surfaces moderately to coarsely punctate with solitary, acuminate scales and setae. Meso- and metatibia lacking any indication of a transverse carina, dorsally coarsely to finely punctate, margins diverging toward apex at distal 1/3, provided with a fringe of thick spiculae. All femora flattened, margins converging toward apex, sur-

face vestiture as protibiae. Apices of tarsomeres coronate with a fringe of short, translucent spiculae; tarsomere-5 elongate, subequal in length to four basal tarsomeres combined, ventral surface bearing a fine carina extending length of tarsomere; tarsal claws with basal proximal tooth. **Phallobase and parameres.** Number examined (3). In dorsal aspect, symmetrical with two simple parameres narrowing distally, apices diverging outward; median notch sharply rounded, separated less than 1/2 length of parameres; lateral aspect, apical 1/4 cristate with apices smoothly rounded ventrally; caudal aspect, obliquely depressed; distal tips separated, gradually diverging outward at apex.

Female. Unknown.

Variation. Males (8). Length 26.0–28.0 mm. Greatest width 11.5–12.5 mm. As holotype except: **Color.** Pronotal discal surface rufotestaceous; tarsal claws and protibial dentition black; femora deep rufotestaceous. **Head.** Setal and squamal vestiture pale yellow, variably reduced or obscuring disc; antennal lamellae broadly obtuse. **Pronotum.** Squamal vestiture pale yellow; setal vestiture reduced; posterolateral bead coarsely serrate. **Elytra.** Discal vittae incomplete, coarsely eroded, reduced to clumps of imbricate squamae (Fig. 10); subhumeral vittae present. **Pygidium.** Surface obscured by dense, squamal vestiture. **Legs.** Apices of protibial dentition worn; setal and squamal vestiture reduced (abrasion?).

Diagnosis. The coarsely eroded elytral vittae, deep rufotestaceous integument, and eastern California distribution of *P. koso* are similar to its adelphotaxon, *P. aeolus*. However, males of *P. aeolus* have pale yellow setae; a combination of pale yellow or white squamae (setal and squamal vestiture white in *P. koso*); interstitial squamae contiguous with elytral vittae (intermittent in *P. koso*); elytral sutural vittae continuous and complete (fragmented and eroded in *P. koso*); elytral discal setae (absent in *P. koso*); and distinctly larger antennal structure than in *P. koso*. Ecologically, *P. aeolus* is a psammophilous obligate endemic to the Kelso Sand Dunes, San Bernardino County, California, whereas, *P. koso* is a montane isolate associated with relictual pinyon-juniper woodlands.

In some respects, *P. koso* is similar in appearance to some phenotypes of *P. arguta* which lacks pronotal setae; has a light testaceous to black elytral integument; and is primarily restricted to the Great Basin in Nevada and Utah.

Natural history. Males of *P. koso* were collected at mercury vapor lights in pinyon-juniper woodlands between 2100–2300 m during July with one record during early June. Other specimens have been collected during early August (Ballmer 2003). *Polyphylla koso* is sympatric with the southwestern montane form of *P. decemlineata*.

An unidentified species of *Pyrgota* Wiedemann (Diptera: Pyrgotidae), a dipteran genus of endoparasitoids of Melolonthinae, has been observed to parasitize *P. koso* while avoiding the more abundant *P. decemlineata* (G.F. Pratt, *in litt.*). Typically, the female pyrgotid oviposits on the exposed abdomen of the beetle while in flight possibly utilizing one or a combination of olfactional mechanisms, microhabitat association, or synchrony with the host life cycle to localize and distinguish its preferred host. Pratt (1943), Young (1967, 1988), Salehi (1984), and Skelley (2009) described similar dipteran parasitism on other *Polyphylla* species.

Ecology. The Coso Mountain Range is located in the Mojave Desert in east central California with elevations from 610 to 2490 m at Coso Peak. These remote mountains are part of the Great Basin “sky island archipelago,” a complex of high desert ranges that were geographically and ecologically isolated during the Pleistocene (Heald 1951; Smith and Street-Perrot 1983; Warshall 1995; Baldwin and Martens 2002). Because of an array of soils, microclimates, and topographic complexities, these isolated mountain ranges provide habitats for many rare and endemic species and are among the most biodiverse ecosystems in North America. Consequently, their associated faunas are highly divergent from other closely related taxa (Marshall 1957; MacArthur and Wilson 1963, 1967; Warshall 1995; Coblentz 2005).

At the type locality, Coso Bridge (Fig. 52), southwest of Coso Peak at approximately 2286 m elevation, *Pinus monophylla* Torrey and Frémont (single-leaf pinyon: Pinaceae) is predominant with a mixed understory of *Artemisia tridentata* ssp. Nuttall (big sagebrush: Compositae), *Eriogonum nudum* Benth (naked buckwheat: Polygonaceae), *E. umbellatum* Torrey (sulphur-flower buckwheat: Polygonaceae), *E.*

wrightii Torrey ex Benth (wright's buckwheat: Polygonaceae), *Purshia glandulosa* Curran (desert bitterbrush: Rosaceae), and *Ribes velutinum* E. Greene (desert gooseberry: Grossulariaceae) (G.F. Pratt, *in litt.*).

At Mill Springs (Fig. 53), approximately 2130 m elevation where a single specimen was collected in early June, vegetation is primarily *Juniperus occidentalis* Hooker (western juniper: Cupressaceae) (G.F. Pratt, *in litt.*).

Because the mountains lie within the rain shadow of the Sierra Nevada Range, annual precipitation averages between 12.5 and 30.5 cm. Much of this occurs as snow at higher elevations which is often present until late spring. Average annual temperatures range from 4.0° to 19° C., with 125 to 250 frost-free days. Soils are well drained with rapid surface runoff from alluvial fans that lead to either the adjacent Owens or Panamint Valleys.

Despite the generally dry conditions, the areas surrounding Coso and Mill Springs support areas of unique flora including species that exemplify vastly disjunct distributional ranges (G.F. Pratt, *in litt.*). In arid regions where moisture availability constrains species distributions, a locally damp site will act as an ecological refugium.

The Coso pinyon-juniper woodland represents a relictual population of a more widespread coniferous forest that dominated much of southwestern North America during the Pleistocene. *Polyphylla koso* may have been more widely distributed at that time when this region of eastern California was a broad savanna dominated by shallow pluvial lakes with scattered woodlands occurring at all elevations (Axelrod and Ting 1960; Woodcock 1986; Mensing 2001). As climate transitioned to interstadial conditions between 14,000 and 10,000 years ago, large contiguous areas of cooler temperate habitats were fragmented into mountain-top refugia and replaced at lower elevations by a cactus-legume-dominated desert scrub (Wells and Woodcock 1985; Thompson et al. 1993; Thompson and Anderson 2000).

Conservation. The distribution of *P. koso* lies within the boundaries and jurisdiction of the China Lake Naval Air Weapons Station. As a result, public access to the area is extremely limited which affords it some protection. However, because it occupies a very limited geographic range, *P. koso* should be considered a species of “special concern.”

Remarks. *Polyphylla koso* is the second species of Nearctic *Polyphylla* restricted to a small area of an isolated mountain complex. The other species is *P. hirsuta* Van Dyke (1933) of the Patagonia Mountains, Santa Cruz County, Arizona.

Although the type locality of *P. barbata* is “Mt. Hermon, Santa Cruz County, California” (Cazier 1938), the name “Mount Hermon” was chosen for a Christian retreat site for its biblical significance rather than montane characteristics (elevation 178 m).

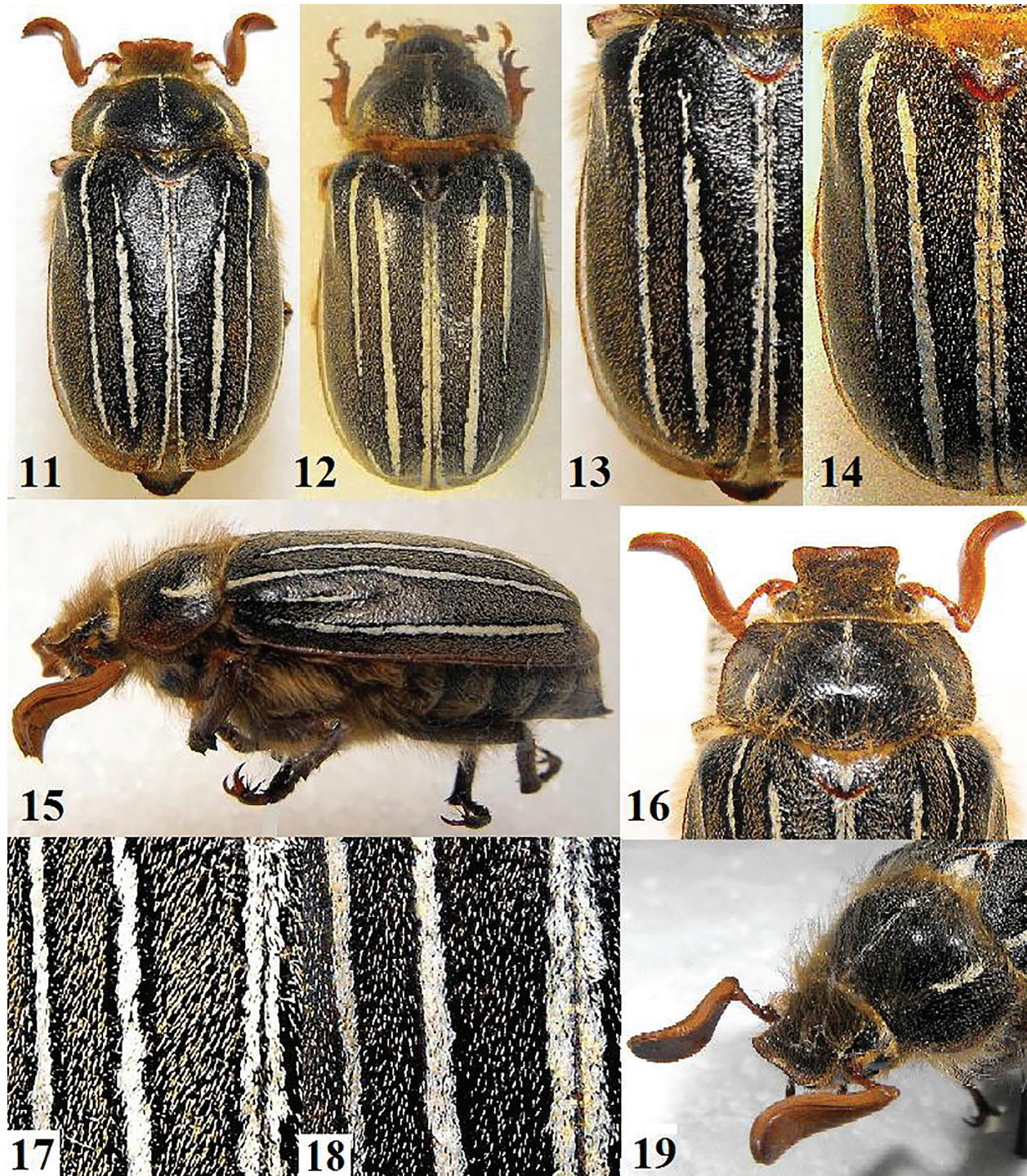
Etymology. From the Tümpisa Shoshone language, *kosoowah* meaning “to be steamy,” referring to the numerous hot springs throughout the area and its indigenous paleo-inhabitants, the Koso. The name is applied as a noun in apposition.

Common name. The Koso Mountains polyphyllan scarab beetle.

***Polyphylla morroensis* La Rue, new species**

(Fig. 11–19, 54–55)

Type material. Holotype. Male (CASC #18340). Labeled “USA, CALIFORNIA, San Luis Obispo County, Los Osos, private residence, 20.VIII.2007, Baywood Fine Sands, Elev. 133', M. Walgren” [phallobase and parameres mounted on card]. **Allotype.** Female. (CASC). Labeled “USA, CALIFORNIA, San Luis Obispo County, Baywood Park, VII.1968, J.D. Pinto.” **Paratypes.** (11). Labeled as holotype (1 male); as allotype (2 males); Los Osos, 05.VI.1979, C. Meichart (1 male); 07.VII.1980, D. Overman (1 male); 01.IX.1984, J. Wagner (1 male); 22.VII.1986, E.M. Saylor (1 male); private residence, various dates between 30.VII.-08.VIII.2008, M. Walgren, L. Andreano (2 males, 1 female); 11.VIII.2008, M. Walgren, L. Andreano, shopping center lights (1 male). CASC, RHMC, SBMNH, UCRC.



Figures 11–19. *Polyphylla morroensis*. 11, 13, 15–16, 19) Holotype male. 12, 14) Allotype female. 17–18) Section of male left elytron, dorsal aspect, illustrating distribution of interstitial squamae (150 \times). 17) *Polyphylla crinita*, dense. 18) *Polyphylla morroensis*, sparse.

Four additional male specimens excluded from the type series because of excessive damage labeled as holotype (3); USA, CALIFORNIA, San Luis Obispo County, Los Osos, vacant lot, 10.VIII.2008, M. Walgren, L. Andreano (1).

Description. Holotype. Male (Fig. 11, 13, 15–16, 19). Length 28.0 mm. Greatest width 12.0 mm. Humeral width 11.5 mm. **Form.** Elongate, robust, parallel-sided. **Color.** Head, eyes, and exposed abdominal sternites black; pronotum, scutellum, and elytra deep olive green, rufopiceous to black under magnification (10.5×); pygidium deep rufotestaceous; basal antennomeres, other appendages of head, pterothoracic integument, and legs rufotestaceous; lamellate antennomeres light testaceous; except where noted, setal vestiture pale rubiginous brown to yellowish-brown; squamal vestiture white; interstitial squamae pale yellowish-brown. **Head.** Subconvex; clypeus transverse with highly reflexed bisinuate anterior margin; anterior angles obtuse, lateral margins reflexed and convergent basally; disc deeply concave, coarsely punctate, densely setose with long pale setae and imbricate, acuminate scales. Frontoclypeal suture rugosely punctate, obscured medially by dense setal vestiture. Frons depressed on either side of a longitudinal tumidity, surface moderately to coarsely punctate, densely setose with solitary acuminate scales. Vertex glabrous and shining. Maxillary palpomere-4 cylindrical, anteriorly depressed, apex truncate, finely punctate and densely setose with minute, golden spiculae, 1/3 length of three basal palpomeres combined. Mentum subquadrate, anteriorly deeply emarginate, angles broadly rounded, disc posterolaterally with long setae. **Antennae.** Scape subtriangular, constricted basally, apex bulbous, provided with a dense scopula of long setae; lamellate antennomeres 4–10 distally recurved outward attaining a right-angle, provided with translucent, golden setae. Antennal club 2.5× (linear measurement) or 3.3× (curvilinear measurement) longer than basal antennomeres combined. **Pronotum.** Broadly convex, transverse, 2× wider than length at midline, widest at posterior 1/2; anterior angles obtuse, basal angles broadly obtuse and explanate; marginal bead absent anteriorly, serrate and explanate laterally, evanescent posteriorly. Disc moderately to coarsely punctate, punctures provided with an acuminate, recumbent scale or suberect setae, medially sulcate, dividing a transverse tumidity at posterior 1/2; trivittate; vittae longitudinally complete, edges eroded, composed of contiguous to imbricate, acuminate scales. **Scutellum.** Oblong, broadly rounded, margins glabrous, disc obscured by imbricate scales; devoid of setae. **Elytra.** 2.2× greater in length than width; humeral angles obtusely rounded, posterolateral angles broadly arcuate. Marginal bead explanate and reflexed posterolaterally, evanescent posteriorly, sutural bead obscured by dense acuminate scales. Disc rugosely punctate; calli tumose, glabrous, moderately punctate; vestiture composed of solitary to imbricate, acuminate scales; devoid of setae; distinctly vittate; vittae narrow, edges coarsely eroded, composed of contiguous to imbricate, acuminate scales; sutural vittae incomplete; subsutural vittae fragmented and discontinuous; submarginal vittae complete; subhumeral vittae evanescent. Interstitial squamae evenly, sparsely distributed (Fig. 18), intermittently contiguous with vittae. Metathoracic wings functional. **Pygidium.** Subtriangular, convex, length subequal to width; angles obtusely rounded; disc moderately punctate, depressed behind reflexed margins; vestiture composed of contiguous, acuminate scales; devoid of setae. **Venter.** Densely pubescent obscuring pterothorax; exposed abdominal sternites subconvex with a basal glabrous band, vestiture composed of solitary to imbricate scales and solitary setae. **Legs.** Protibia bidentate, lacking any indication of a basal third tooth; dentition moderately separated, projecting obliquely forward from longitudinal tibial axis; inner margin rounded, outer margin with a sharp longitudinal carina, surfaces moderately to coarsely punctate with evenly distributed acuminate scales and long setae. All femora flattened, margins converging toward apex, surface vestiture as protibiae. Apices of tarsomeres coronate with a fringe of short, translucent spiculae; tarsomere-5 elongate, subequal in length to four basal tarsomeres combined, ventral surface bearing a short, fine carina basally; tarsal claws with basal proximal tooth. **Phallobase and parameres.** Number examined (3). In dorsal aspect, symmetrical with two simple parameres narrowing distally, apices convergent, median notch sharply rounded, separated less than 1/2 length of parameres; lateral aspect, parameres cristate length of median notch, apices smoothly rounded ventrally; caudal aspect, obliquely rounded; distal tips separated, acutely angled, diverging outward at apex.

Allotype. Female (Fig. 12, 14). Length 24.5 mm. Greatest width 12.5 mm. Humeral width 12.0 mm. Excluding sexual dimorphic variation as holotype except: **Form.** Robust, ovate, widest at posterior 1/3. **Head.** Anterior clypeal margin deeply bisinuate, lateral angles sharp; basal antennomeres approximately 2.5× longer than lamellate club. **Pronotum.** Sharply convex; disc densely covered with long yellow setae; feebly trivittate; lateral vittae agglomerate, composed of contiguous to imbricate acuminate scales. **Scutellum.** Bearing a dense scopula of pale setae. **Elytra.** Subdiscal vittae interrupted at

posterior 1/3; interstitial squamae lanceolate in form. **Pygidium.** Setae present at posteriorly margin. **Legs.** Protibia strongly tridentate, projecting perpendicular to longitudinal tibial axis; right protarsomeres-4 and 5, left and right metatarsomeres missing; metatibial dorsal surface with two prominent dentiform projections.

Variation. Males (12). Length 22.0–27.5 mm. Greatest width 11.5–13.0 mm. As holotype except: **Color.** Elytra rufo-olivaceous. **Pronotum.** Medial vittae eroded. **Scutellum.** Squamal vestiture reduced or confined medially. **Elytra.** A shallow parascutellar sulcus present in some specimens. **Pygidium.** Long setae present.

Female (1). Length 23.0 mm. Greatest width 12.5 mm. Remarkably similar to allotype except: **Color.** Legs testaceous, protibial dentition black. **Pronotum.** Vittae more pronounced. **Pygidium.** Devoid of setae.

Diagnosis. The combination of deep olive green dorsal coloration; sparsely distributed yellowish-brown elytral interstitial squamae (Fig. 18); reddish-brown to deep yellowish-brown setae; narrow elytral vittae with coarse edges; evanescent submarginal vittae; and long, densely distributed pronotal setae (Fig. 15–16, 19) are sufficient to distinguish *P. morroensis* from all other species of *Polyphylla*.

Polyphylla morroensis may possibly be confused with *P. crinita* or its adelphotaxon, *P. nigra*, that are similar in general appearance. Males of those species have a black, reddish-black, or brown (sometimes olivaceous yellowish-brown in *P. crinita*) dorsal integument; pale yellow to yellowish-brown setae; densely distributed elytral interstitial squamae (Fig. 17); elytral vittae with sharply defined (*P. nigra*) or uneven (*P. crinita*) edges; submarginal vittae longitudinally complete; and sparsely distributed pronotal discal setae. The presence (LeConte 1856; Horn 1881; Casey 1914; Fall 1928, Hardy 1981) or absence (Young 1988) of pronotal discal setae in male *P. crinita* is apparently subjective and open to interpretation as is the presence of elytral discal setae (present in syn. *P. ruficollis perversa* Casey 1914).

Both *P. crinita* and *P. nigra* are distributed from the Pacific northwest to Baja California, Mexico, and are associated with a variety of habitats including mixed conifer forest, mixed riparian woodland, ancient volcanic soils, and urban environs indicating diverse facultative ecologies.

Due to its littoral proximity, the dark olive green coloration; reduced, sparsely distributed interstitial vestiture; and narrow, eroded vittae of *P. morroensis* may be a selective response to the cooler, moist, coastal environment.

Natural history. Males of *P. morroensis* were collected at lights of private dwellings and a shopping center complex immediately adjacent to areas of open Baywood Fine Sands habitat. Females are presumed flightless as none were encountered at lights but were found within their burrows 5 to 7.5 cm below the soil surface by observing male flight behavior. *Polyphylla decemlineata* was encountered in the coastal-dune scrub floral community south of the Baywood Fine Sands ecosystem but was not sympatric in the known distribution of *P. morroensis* (M. Walgren, *in litt.*).

Ecology. Baywood Fine Sands (Fig. 54–55) are located on the southeast shore of Morro Bay, San Luis Obispo County, on the central California coast. The sand dunes were deposited during the Pleistocene when eustatic sea levels were approximately 10 to 170 meters lower than at present exposing continental shelf sands to eolian accretion further inland (Cooper 1967; Orme 1990; Knott and Eley 2006).

The sand appears dark grayish brown to dark brown with fine particle size corresponding to high organic content. These deep, well drained soils provide the foundation for an endemic coastal ecosystem that supports remnants of maritime chaparral and coastal-dune scrub floral communities including several federal- and state-listed endangered or threatened species.

Areas of maritime chaparral are dominated by a dense canopy of *Arctostaphylos morroensis* Wislender and Schreiber (morro manzanita: Ericaceae), a federally endangered species. Understory vegetation is minimal as the environment under this chaparral complex is one of negligible solar penetration and deep leaf litter. In some areas *Ceanothus cuneatus* (Hook) Nuttall (buckbrush: Rhamnaceae), *Eriophyllum confertiflorum* de Candolle A. Gray (golden yarrow: Compositae), *Mimulus aurantiacus* Curtis (monkey flower: Phrymaceae), *Prunus fasciculata* var. *punctata* Jepson (desert almond: Rosaceae),

Quercus agrifolia Nee (coast live oak: Fagaceae), and *Salvia mellifera* Greene (black sage: Lamiaceae) are present (M. Walgren, *in litt.*).

Coastal-dune scrub is the most imperiled habitat because of its location on relatively flat terraces adjacent to the Pacific Ocean where development is prevalent. During different seasons, *Abronia umbellata* Lamark (pink sand verbena: Nyctaginaceae), *Amsinkia spectabilis* Fischer and Meyer (seaside fiddleneck: Boraginaceae), *Corethrogyne filaginifolia* (Hooker and Arnott) Nuttall (california aster: Asteraceae), *Ericameria ericoides* (Lessing) Jepson (goldenbush: Asteraceae), *Eriogonum parvifolium* Smith (coast buckwheat: Polygonaceae), *Eriophyllum staechadifolium* la Gasca (yellow yarrow: Asteraceae), and numerous other ephemeral annual species predominate. The floral community is threatened by the invasive exotic, *Ehrharta calycina* Smith (veldt grass: Poaceae), which supplants native species and can cover the dunes in dense expanses (M. Walgren, *in litt.*).

Ambient climate is characterized as subhumid mesothermal with cool, foggy summers and cool, moist winters. The climate provides frequent periods of fog drip that is a critical factor in limiting the distribution of endemic species of the ecosystem. Mean annual precipitation is approximately 37 cm at the coast to nearly 90 cm further inland. Average annual temperature is 5.5° to 26° C., with an average of 250 to 350 frost-free days. Elevation ranges from mean sea level in areas adjacent to Morro Bay, at the northwest margin of the dunes, to approximately 250 m in the southern dune area.

Conservation. The major threat to *P. morroensis* is urban development. Much of the area with moderate topographic gradients supporting Baywood Fine Sands has been subject to unprecedented urban expansion. In addition to direct removal and modification of the habitat, development has had detrimental effects on the quality of remaining habitat including fragmentation, deterioration due to increased recreational activity, and the introduction of invasive non-native vegetation (M. Walgren, *in litt.*).

Remnants of the dunes support several federal- and state-listed endangered or threatened species including *Helminthoglypta walkeriana* (Hemphill) (morro shoulderband snail: Helminthoglyptidae), *Anniella pulchra* Gray (silvery legless lizard: Anniellidae), *Dipodomys heermanni morroensis* (Merriam) (morro bay kangaroo rat: Heteromyida), *Eriodictyon altissimum* P.V. Wells (indian knob mountainbalm: Hydrophyllaceae), and *A. morroensis*, clearly emphasizing the unique composition of the ecosystem.

Because of limited geographic range and imminent threat of extirpation from habitat modification, *P. morroensis* should be considered a “critically imperiled” species.

Etymology. From a combination of “Morro” and the Latin adjectival suffix *-ensis*, “originating in or from.”

Common name. The Morro Bay polyphyllan scarab beetle.

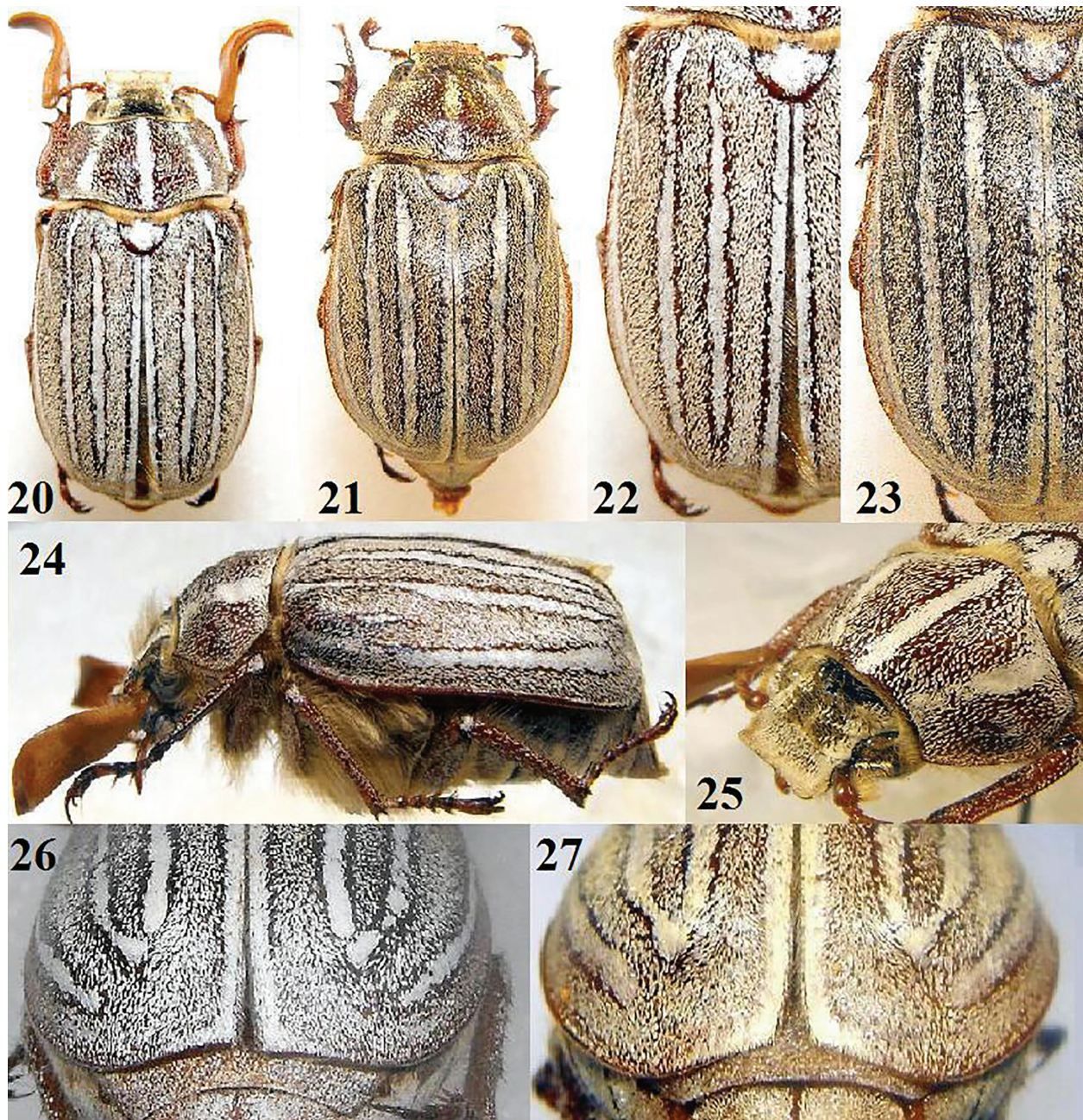
***Polyphylla socorriana* La Rue, new species**

(Fig. 20–27, 56–57)

Type material. Holotype. Male (UNAM). Labeled “MEXICO, Baja California, Highway 1, south of San Quintín, Socorro Sand Dunes, 10 m, 3.VII.1998, at blacklight, J.D. Beierl collector.” **Allotype.** Female (UNAM). Labeled “MEXICO, Baja California, Socorro Sand Dunes, north of San Quintín at 1 mi. W. Hwy. 1, 30' el., 26.VIII.2002, R.A. Cunningham, G. Nogueira.” **Paratypes.** (14). Labeled as holotype (4 males); as allotype except “MV” (5 males); “MEXICO, Baja California, 1 mile N. El Socorro, 10 m, El Socorro Dunes, 2.VII.1996, R.A. Cunningham” (1 male); “MEXICO, Baja California, San Ramon, 4 mi W of Colonia Guerrero, 3.VII.1969, L.F. La Pré, UV light” (4 males). CASC, MXAL, RACC, RHMC, UCRC.

One additional male specimen excluded from the type series because of considerable dorsal abrasion and disparate locality: “MEXICO, Baja California, 2.7 mi E. EJ [Ejido] Bonfil, Rio San Rafael, 27.VI.1986, Faulkner, Bloomfield”.

Description. Holotype. Male (Fig. 20, 22, 24–26). Length 26.5 mm. Greatest width 12.5 mm. Humeral width 11.0 mm. **Form.** Elongate, robust, slightly ovate at basal 1/3. **Color.** Head, eyes, elytral humeri, protibial dentition black; pronotum, scutellum, pygidium, legs, abdominal sternites, pterothoracic integument, basal antennomeres, and other appendages of head rufotestaceous; elytra deep rufotestaceous;



Figures 20–27. *Polyphylla socorriana*. 20, 22, 24–26) Holotype male. 21, 23, 27) Allotype female.

lamellate antennomeres light testaceous; except where noted, setal and squamal vestiture white. **Head.** Convex; clypeus transverse with reflexed bisinuate anterior margin; anterior angles obtuse, lateral margins sinuate, converging basally; disc depressed, coarsely punctate, densely setose with long pale setae and contiguous to imbricate acuminate scales. Frontoclypeal suture arcuate, variably obscured by coarse punctation. Frons feebly depressed medially, coarsely punctate with long, recumbent setae, and solitary, acuminate scales. Vertex medially tumid and glabrous. Maxillary palpomere-4 cylindrical, anteriorly depressed, distally truncate; finely punctate and variably setose; $2/3$ length of three basal palpomeres combined. Mentum transverse, anteriorly emarginate, angles rounded, disc slightly concave, with scattered setae and solitary scales. **Antennae.** Scape bulbous, constricted basally, provided with a dense, scopula of long setae; lamellate antennomeres 4–10 distally recurved obtusely outward, provided with randomly distributed setae. Antennal club $2.2\times$ (linear measurement) or $3.2\times$ (curvilinear

measurement) longer than basal antennomeres combined. **Pronotum.** Broadly convex, transverse, 2× wider than length at midline, widest at posterior 1/2; anterior angles obtuse, basal angles broadly arcuate and explanate; marginal bead absent anteriorly, coarsely serrate laterally, feebly indicated to evanescent posteriorly. Disc moderately to coarsely punctate, an acuminate scale arising from each puncture, medially with long, suberect to recumbent setae; medially sulcate, dividing a transverse tumidity at posterior 1/2; trivittate; medial vitta longitudinally complete, submarginal vittae eroded at apical 1/3, basally with two distinct glomerate patches of dense, imbricate, acuminate scales and solitary setae. **Scutellum.** Oblong, broadly rounded, margins glabrous, disc coarsely punctate, provided with contiguous to imbricate scales and suberect setae. **Elytra.** 2.5× greater in length than width; humeral and posterolateral angles broadly arcuate. Marginal bead reflexed, explanate anteriorly, evanescent posterolaterally, sutural bead obscured by dense acuminate scales. Disc shallowly punctate; calli tumose, glabrous, sparsely punctate; vestiture composed of contiguous acuminate scales and solitary, suberect setae; distinctly vittate; vittae longitudinally continuous with edges eroded, composed of dense imbricate, acuminate scales obscuring integument; each with a parallel, glabrous band on either side; discal and subsutural vittae adjoined basally (Fig. 26). Metathoracic wings functional. **Pygidium.** Subtriangular, convex, length subequal to width, angles obtusely rounded; disc finely punctate, depressed behind greatly reflexed margins; vestiture composed of contiguous to imbricate, acuminate scales and short, recumbent setae. **Venter.** Densely pubescent obscuring pterothorax; exposed abdominal sternites convex, with a basal glabrous band, depressed medially; vestiture composed of solitary, acuminate scales basally and solitary, pale yellow setae. **Legs.** Protibia strongly bidentate, basal third tooth feebly indicated as an obtuse angular projection; dentition widely separated, projecting perpendicular to longitudinal tibial axis; inner margin rounded, outer margin with a sharp, longitudinal carina; surfaces finely to coarsely punctate with solitary to contiguous, acuminate scales and scattered, pale yellow setae; meso-, metatibia with a dentiform projection and acuminate spines. All femora flattened, margins parallel, surface vestiture as protibiae. Apices of tarsomeres coronate with a fringe of translucent spiculae; tarsomere-5 elongate, less than length of basal tarsomeres combined, ventral surface bearing a fine carina extending length of tarsomere; tarsal claws with basal proximal tooth. **Phallobase and parameres.** Number examined (3). In dorsal aspect, symmetrical with two simple parameres narrowing distally, apices convergent; median notch sharply rounded, separated approximately 1/3 length of parameres; lateral aspect, apical 1/4 cristate with apices smoothly rounded ventrally; caudal aspect, subconvex, obliquely depressed; distal tips of parameres adjoined anterodorsally.

Allotype. Female (Fig. 21, 23, 27). Length 23.0 mm. Greatest width 12.0 mm. Humeral width 10.0 mm. Excluding sexual dimorphic variation as holotype except: **Form.** Robust, subovate, widest at posterior 1/2. **Head.** Subconvex; clypeal disc shallow, devoid of setae; setal vestiture of lamellate antennomeres translucent golden yellow. **Pronotum.** Sharply convex; lateral marginal bead coarsely, deeply serrate; squamal vestiture pale yellow. **Scutellum.** Squamation evenly distributed. **Pygidium.** Triangular. **Legs.** Protibia strongly tridentate; dentition projecting obliquely forward from longitudinal tibial axis; tarsal claws with proximal tooth centrally positioned.

Variation. Males. (14). Length 22.0–27.0 mm. Greatest width 10.0–13.0 mm. As holotype except: **Head.** Clypeal squamae obscuring disc. **Pronotum.** Setal vestiture limited to discal margins (abrasion). **Scutellum.** With solitary pale setae. **Legs.** Protibial basal tooth variably developed.

Diagnosis. The prominent white dorsal vestiture and dense continuous elytral vittae of *P. socorriana* are similar to some disjunct psammophilous populations of *P. decemlineata* with heavy white dorsal squamation (= syn. *P. comstockiana* von Bloeker 1939). However, *P. decemlineata* lacks pronotal and elytral discal setae (present in *P. socorriana*); has sharply defined, smooth-edged elytral vittae (uneven to eroded in *P. socorriana*); yellowish-brown to black integument (deep rufotestaceous in *P. socorriana*); and is a larger, robust species (length usually greater than 30 mm; type specimens of *P. socorriana* are between 22–27 mm).

Specimens of *P. socorriana* exhibiting an abraded dorsal vestiture may be confused with *P. crinita* which shares a proximal but allopatric distributional range (Hardy 1981). That species has an olivaceous yellowish-brown to black integument (deep rufotestaceous in *P. socorriana*); yellowish-brown interstitial

squamae (white in *P. socorriana*); and lacks the basally adjoined discal and subsutural elytral vittae. The presence or absence of pronotal discal setae is apparently variable in male *P. crinita* (present in *P. socorriana*).

Although infrequent in some western clade species, the basally adjoined discal and subsutural elytral vittae of *P. socorriana* (Fig. 26–27) is statistically stable and diagnostic. In addition to the types, twelve of fourteen paratypes (85%) exhibit this character.

The dorsal coloration of *P. socorriana* is presumably a selective response to the distinctive white sand color of the El Socorro Sand Dunes ecosystem and contiguous sand areas suggesting an adaptation toward parasemantic crypsis.

Natural history. Based on field observations and specimen data, *P. socorriana* is a psammophilous obligate ecologically associated with coastal sand dunes. Males were attracted to black, ultraviolet, and mercury vapor light stations placed adjacent to, or a slight distance away from, the leeward side of the dunes shortly after twilight. The allotype female was encountered crawling on the sand surface at dusk (R.A. Cunningham, personal communication).

Locality data of the specimen excluded from the type series, “2.7 mi E. Ejido Bonfil, Rio San Rafael,” is slightly inland and ecologically dissimilar to that of the type series. This would suggest the possibility that *P. socorriana* may not be entirely restricted to a coastal ecosystem. However, the arenaceous substrates of Rio San Rafael, an ephemeral desert riparian wash that drains to the Pacific Ocean, are consistent with the psammophilous requisites of *P. socorriana* and may provide an ecologically suitable corridor for the species to disperse, albeit, marginally inland.

Ecology. El Socorro Sand Dunes (Fig. 56–57) are located on the Pacific coast of the state of Baja California, Mexico, at an elevation of 10 to 45 m. Their pronounced white coloration is directly related to high carbonate content (aragonite and calcite) from skeletal marine invertebrates. High carbonate sand dunes are rare in North America occurring only along the Yucatan Peninsula, the Channel Islands of California, and Baja California (Muhs et al. 2009).

The coastal strip from 32° to 29.5° north latitude, encompassing the type locality, has been documented to be an area of high floristic diversity with a conservation status of endemic (25%), sensitive (40%), or rare (35%) species (Johnson 1977; Riemann and Ezcurra 2005, 2007; Vanderplank 2010).

Adolphia californica S. Watson (california prickbush: Rhamnaceae), *Funastrum arenarium* (Decaisne ex Benth) Liede (talayote: Apocynaceae), *Heteromeles arbutifolia* (Lindley) M. Roem (davis gold toyon: Rosaceae), *Rhamnus crocea insula* (Kellogg) (buckthorn: Rhamnaceae), and *Yucca schidigera* Roez ex Ortega (splinter yucca: Agavaceae) are found only on the El Socorro Dunes.

Abronia maritima Nuttall ex. S. Watson (red sand verbena: Nyctaginaceae) is predominant on active dunes with *A. umbellata* Lamark (pink sand verbena: Nyctaginaceae), *Atriplex julacea* S. Watson (saltbush: Amaranthaceae), *Eulobus californicus* Torrey and A. Gray (california primrose: Onagraceae), *Funastrum arenarium* Decaisne ex Benth (climbing milkweed: Apocynaceae), *Helianthus niveus* (showy sunflower: Compositae), and *Heteromeles arbutifolia* (Lindley) M. Roem (toyon: Rosaceae) in stabilized dune areas (Vanderplank 2010).

Ambient climate is classified as mediterranean (cool moist winters, hot dry summers) with average annual precipitation of approximately 13.5 cm and mean temperature of 17.5° C. The area experiences frequent moisture laden fog providing additional water resources and associated humidity which is critical in supporting the endemic species of the ecosystem (Markham 1972; Delgadillo 1998).

Conservation. The unique high carbonate content, unusual floristic composition, high species diversity, and percentage of endemic taxa clearly indicate the El Socorro Sand Dunes a priority for conservation. The imminent threat to *P. socorriana* is habitat degradation. The entire dune system has been proposed for development to allow egress from Mexico Peninsular Highway 1. Other impending threats include trash dumping, recreational off-road vehicle use, invasive floristic species, and vegetation clearing (Vanderplank 2010).

To underscore the negative impact of cumulative human encroachment and habitat modification of the region, the endemic tule shrew (*Sorex ornatus juncensis* Nelson and Goldman: Soricida) is now extinct and the San Quintín kangaroo rat (*Dipodomys gravipes* Huey: Heteromyidae) is presumed ex-

tirpated as no individuals have been found since the 1980s (Best and Lackey 1985; Álvarez-Castañeda and Patton 1999).

Because of limited geographic range and imminent threat of extirpation from habitat modification, *P. socorriana* should be considered a “critically imperiled” species.

Remarks. *Polyphylla socorriana* is the second species of *Polyphylla* described from a coastal sand dune complex of the Baja California Peninsula. The other species is *P. multimaculata* Hardy (1981) from Dunas de Soledad, north of Guerrero Negro.

The *Polyphylla* fauna of the Baja California Peninsula now consists of seven species. Of these, five also occur in the southwestern United States (*P. cavifrons*, *P. crinita*, *P. decemlineata*, *P. nigra*, *P. rugosipennis* Casey), and two are endemic (*P. multimaculata*, *P. socorriana*).

Etymology. From a combination of “Socorro” and the Latin adjectival suffix, *-iana*, “belonging or related to.”

Common name. The El Socorro Sand Dunes polyphyllan scarab beetle.

Taxonomic proposals

Polyphylla avittata Hardy and Andrews

(Fig. 28–32)

Polyphylla avittata Hardy and Andrews 1978:1

Type locality. “Utah, Washington Co., 6 mi. S of Hurricane, Hurricane Dunes.”

Type repository. Holotype. Male. CASC #13098 [examined].

Polyphylla ratcliffei Young 1986:49 **NEW SYNONYMY**

Type locality. “Utah, Grand Co., 9 mi. NW of Moab.”

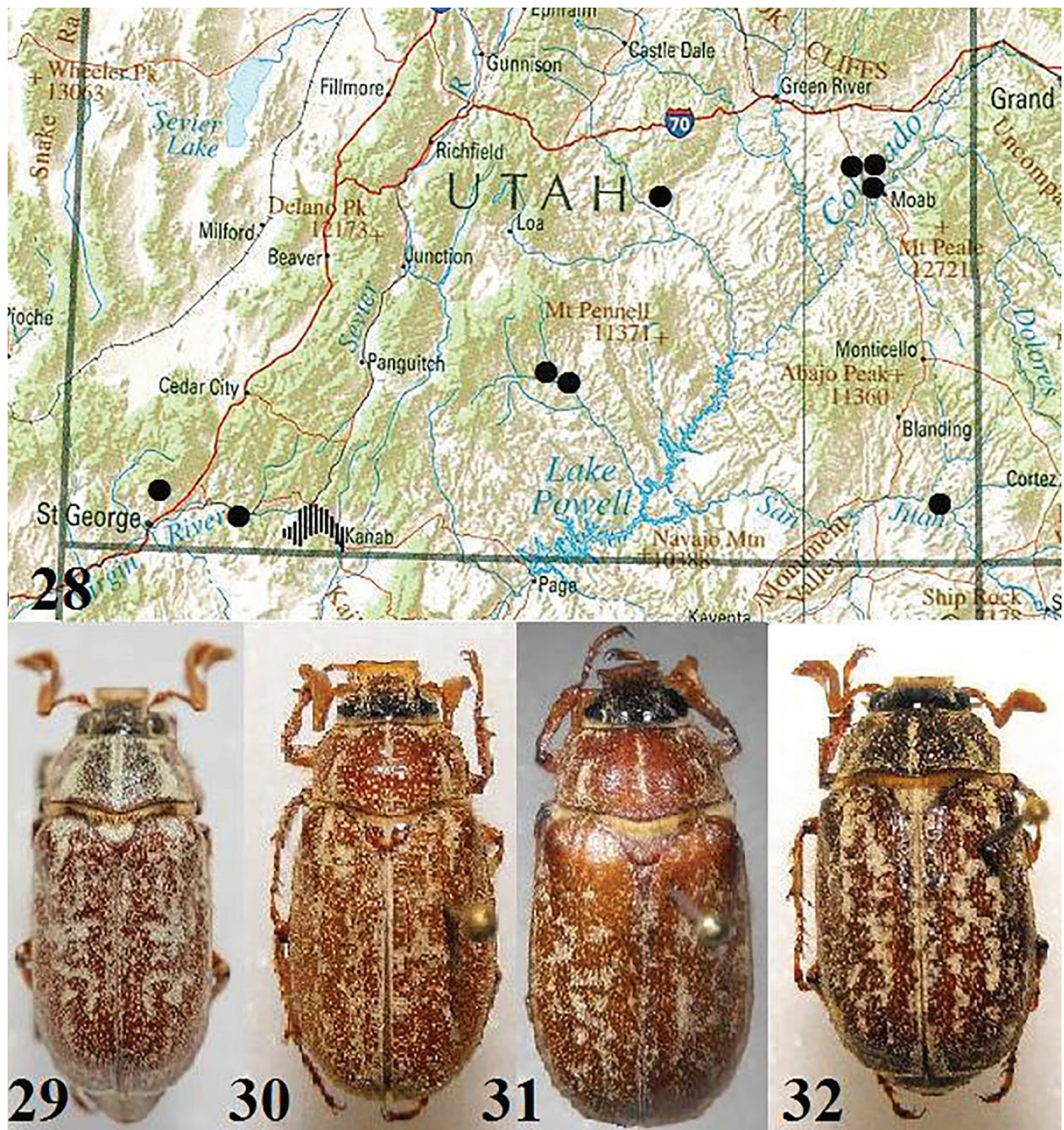
Type repository. Holotype. Male. CASC #15999 (not University of Idaho, Young 1986:49) [examined].

Notes on synonymy. The basis for this synonymy is that the putatively diagnostic characters of *P. ratcliffei* (differences of parameres, protibial dentition, and geographic distribution) are within the range of morphological variation of *P. avittata*, as determined by comparison of the types and other material examined from several institutional and private collections.

In the original description, Young (1986) stated that *P. ratcliffei* could not be distinguished from *P. avittata* solely upon external morphological characters. However, he separated the two species based on “unique” male parameres, differences in protibial dentition, and disjunct distribution: southwestern Utah (*P. avittata*) and east central Utah (*P. ratcliffei*). All three criteria are not diagnostic and vary intraspecifically as follows:

Parameres. Young (1986, 1988) considered the parameres in *P. avittata* asymmetrical (“unequal” Young 1986). In caudal aspect, he regarded the tips as dorsally cristate (*i.e.* bearing a raised carina, what Young referred to as a “dorsal flange”) with apices adjoined distally, whereas, in *P. ratcliffei*, he considered the parameres symmetrical (“equal” Young 1986) lacking any raised carina with the apices clearly separated.

Examination of geographically intermediate samples from Emery and Garfield Counties, Utah (21 males), 16 displayed some indication of cristate parameres. In all samples, the parameres were symmetrical with the dorsal surface obliquely depressed outward, in contrast to those illustrated by Young (1986:49 Fig. 7). Consequently, the genitalic differences between these two species are regarded as intraspecific variation and unreliable to validate species recognition on this character.



Figures 28–32. *Polyphylla avittata* 28) Distribution of *P. avittata* Hardy and Andrews (solid circles) and *P. uteana* Tanner (black vertical lines). 29–32) Variation of male. 29) Hurricane Sand Dunes, Washington Co., UT (topotype). 30) Goblin Valley State Park, Emory Co., UT. 31) Grand Staircase-Escalante National Monument, Garfield Co., UT. 32) 3 miles N of Moab, Grand Co., UT.

Protibial dentition. Cazier (1938) and Young (1988) indicated that protibial dentition was rarely applicable in distinguishing species and rejected the character as diagnostic because of intraspecific and geographic variation.

Hardy and Andrews (1978) stated that nine of twelve male paratypes of *P. avittata* exhibit an indication of a third protibial tooth, the other three apparently bidentate as in the holotype. Young (1986) remarked that protibial dentition of the holotype and four paratypes of *P. ratcliffei* varied from weakly

(i.e. bidentate with some indication of a third protibial tooth) to strongly tridentate. Assessment of available samples clearly demonstrates that protibial dentition within these two species is entirely variable and without any geographic correlation. Eleven of 25 *P. avittata* examined showed a slight indication of a third basal tooth. The remaining 14 were bidentate as the holotype. Only one of four *P. ratcliffei* was distinctly tridentate with the remaining three samples bidentate. The third basal tooth indicated as a slight lateral flange. Geographically intermediate samples from Emery and Garfield Counties (19 males) were all bidentate.

Distribution. The amended distribution (Fig. 28) establishes that both putative taxa are more widely distributed than previously recognized. As a result, distribution is irrelevant in separating these species as used by Young (1986, 1988). In effect, Young's comparative material upon which *P. ratcliffei* was established actually represented geographical extremes of a single taxon, *P. avittata*. Accordingly, it is expected that with continued field efforts in intervening sandy environments, the distribution between both type localities will prove to be one relatively continuous track.

In view of the continuity of variation among available samples, the amended geographical range, and the absence of other morphological characters to distinguish the two taxa, there are insufficient criteria to warrant their separation into distinct species. On the basis of the above analyses, *P. ratcliffei* is reduced to synonymy with *P. avittata*.

Materials examined. In addition to the holotypes, 37 males labeled USA, Utah: **Emery County**, S. Temple Wash, Goblin Valley State Park, 8.VII.1995, Holmes and Liu (1 male); **Garfield County**, Calf Creek Campground, 7 miles S. of Boulder, Grand Staircase-Escalante National Monument, 10.VI.1978 (4 males), 4.VIII.1983 (1 male), 19.VI.1986 (5 males), R.W. Baumann; 3.VI.2001, D.J. Cavan (2 males); 19.VI.2002, S.M. Clark, R.W. Baumann (8 males); Grand County, Arches National Park, 3.VII.1964, EDW [collector initials?] (1 male); 3 miles N of Moab, 5.VI.1993, Liu and Kremer (1 male); (all BYUC); **San Juan County**, Montezuma Creek Trading Post, no date or collector (2 males, BYUC); Washington County, Snow Canyon State Park, 14-15.VII.1978 (2 males), 30.VI.1986 (2 males), G.H. Nelson, at blacklight (FSCA); Hurricane Dunes, 6 mi. SW Hurricane, Flora Tec Rd., 28.VI.1986, 15w BL, R.A. Cunningham, D.A. La Rue (4 males, RACC); 26.VI.1993, R.A. Cunningham, J.D. Beierl (2 males, RACC); 12.VII.1993, no collector (2 males, BYUC).

Conservation. The type locality of *P. avittata*, Hurricane Dunes, Washington Co., Utah (Hardy and Andrews 1978) has recently been modified to create Sand Hollow State Park, which includes a 1,322 acre reservoir. Although remnants of the former dune field remain, there have been no provisions to constrain off-road-vehicle use to specific designated areas. It is probable that this population of *P. avittata* has already experienced irreparable habitat degradation and is likely in imminent peril of extirpation.

***Polyphylla uteana* Tanner, REINSTATED STATUS**

(Fig. 28, 33-41)

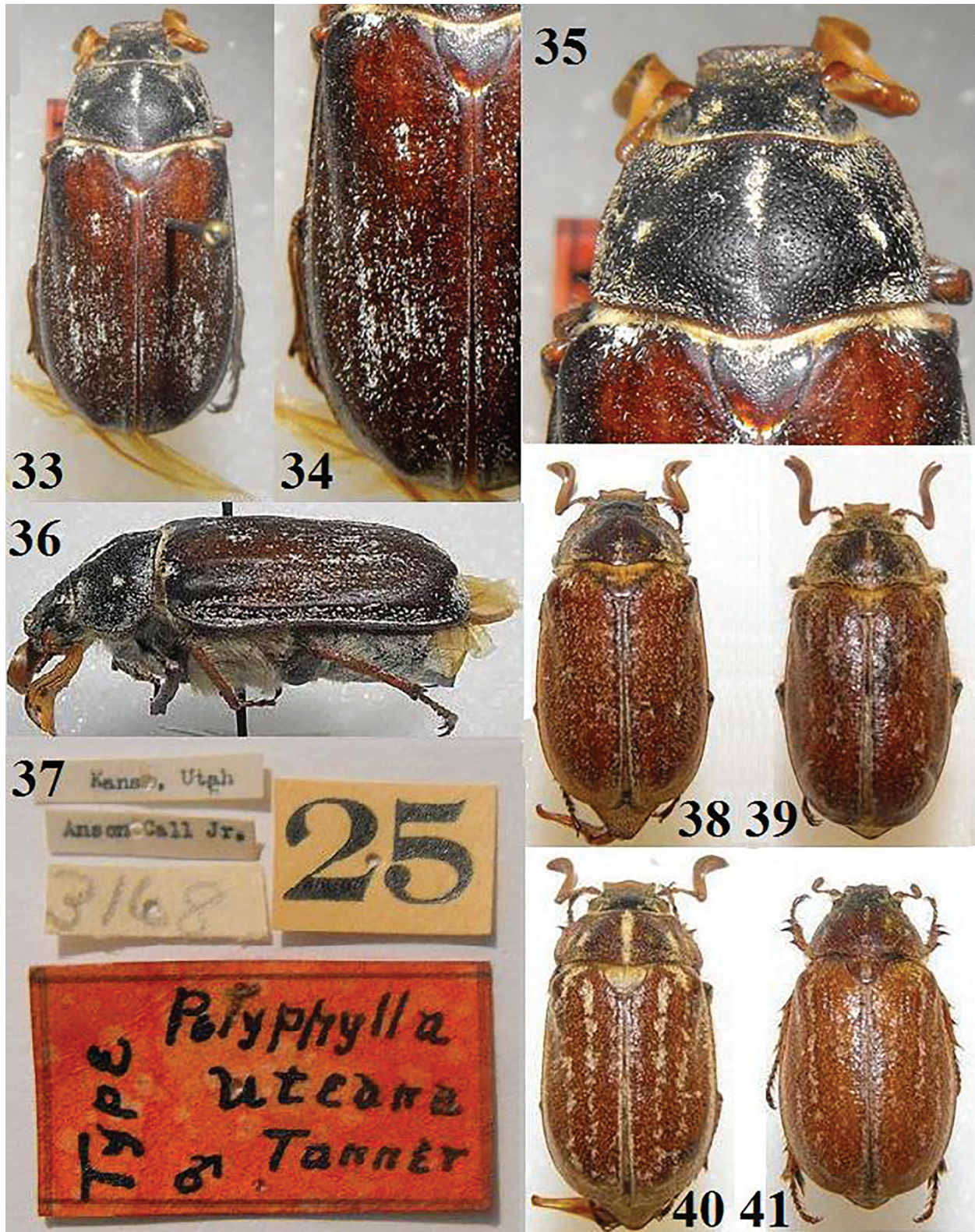
Polyphylla uteana Tanner 1928:276.

Type locality. "Kanab, Utah, about thirty miles southeast of Zion Park" [Kane County].

Type repository. V. M. Tanner Collection, BYUC #25. Holotype. Male. [examined].

Comments on the holotype. Male. Labeled (Fig. 37) [in descending order] (1) "Kanab, Utah" rectangular, white, black type-set; (2) "Anson Call Jr." rectangular, white, black type-set; (3) "3168" rectangular, white, hand-printed in pencil; (4) "25" square, white, black type-set; (5) "Type" hand-printed perpendicular at left margin, "*Polyphylla uteana* Tanner" with male gender symbol at lower left corner, rectangular, red with black border, hand-printed in black ink.

No label reference to a collection date is present, however, Tanner (1928) stated "July 13, 1927" as well as an additional collector: "D. Irvin Rasmussen."



Figures 33–41. *Polyphylla uteana* Tanner. 33–36) Holotype male. 37) Holotype labels. 38–40) Male variation. 41) Female.

The holotype is an aged specimen, abraded anterodorsally, with heavily worn protibial dentition, and the left apical fourth and fifth metatarsomeres missing.

It is briefly characterized as follows: Length 25.0 mm. Greatest width 14.5 mm. Head and pronotum piceous; elytra deep rufotestaceous, grading to rufopiceous at humeri; pygidium, exposed abdominal sternites, and legs rufotestaceous; antennae and other appendages of head light testaceous; squamal and setal vestiture pale white; head and pronotum moderately to deeply punctate; clypeal disc shallow, anterior margin slightly emarginate and weakly reflexed, lateral margins parallel; maxillary palpomere-4 3/4 length of three basal palpomeres combined; head, pronotal, elytral, and pygidial discs bearing setae; elytral sutural apices feebly acuminose; disc nearly avittate, vittae heavily eroded; protibia bidentate, dentition widely separated, significantly worn (age and abrasion), indicated by short protuberances; tarsal claws with basal proximal tooth.

Tanner (1928) stated “pronotum without erect hairs,” presumably referring to the central pronotal disc that is heavily abraded (Fig. 35). However, under magnification (10.5×), there are thin, recumbent, pale setae randomly distributed on the pronotal disc. Also, he regarded the protibial dentition as unidentate. Although heavily worn, there are two distinct remnants of dentition on each protibia.

Taxonomy. According to the original description (Tanner 1928), *P. uteana* was based on a single male specimen labeled “Kanab, Utah.” Young (1967, 1988) synonymized *P. uteana* with *P. diffracta* based on the purported similarity of the “relative size of the antennal club, lack of elytral hairs, closely punctate pronotal disc, and a ‘unicolorous black’ (Young 1967) or ‘unicolorous brown’ (Young 1988) elytral coloration.” In comparing it to *P. hirsuta*, Young (1967) stated that *P. uteana* was “totally without vittae.”

Contrary to Young’s observations, however, upon closer scrutiny and magnification (20×), there are, in fact, short, suberect, randomly distributed, pale setae present on the elytral surface of the holotype. In addition, the specimen is distinctly bicolored displaying a deep rufopiceous head and pronotum, and deep rufotestaceous elytra with vestiges of former vittae (Fig. 33–36), clearly in contrast to Young’s evaluation.

The holotype of *P. uteana* is conspecific with, and well within the morphological range of variation of, specimens from the Coral Pink Sand Dunes, Kane County, Utah, approximately 12 km (7.5 air miles) west of Kanab, the type locality. In addition, molecular sequence data of mitochondrial 16S, COI, and COII cytochrome oxidase genes of this deme (Russell 2000) conclusively establishes the distinctness of this species and strongly supports reinstatement to species status.

Remarks. The known range of *P. uteana* appears to represent a southwest to northeast morphological cline which also corresponds to the dune slip-face orientation and eolian migration alignment.

Males from the southwest lower dune field (~1600 m elevation) (Fig. 40) display lighter integumental coloration (light testaceous to rufotestaceous); coarsely eroded, fragmented elytral vittae; lamellate antennomeres strongly recurved, nearly attaining a right-angle; and shorter overall body length (< 22.0 mm). Ecologically, this area is a mixed Mountain-Brush plant community primarily within semi-stabilized barchanoid dune hummocks.

Males from the northeast upper dune field (~1900 m elevation) (Fig. 3–39) tend to be darker in coloration (deep rufotestaceous); consistently avittate; lamellate antennomeres feebly recurved; and greater in body length (> 22.0 mm). Collection localities from this area are in pinyon/juniper uplands in stabilized or active parabolic and transverse dune types.

The coloration of *P. uteana* closely resembles the distinctive sand color particularly during crepuscular hours, at low solar angle, when adults are most active suggesting predator evasion adaptations through parasemantic crypsis or spectral properties in flight. For desert arthropods, crepuscular activity may be an effective way of avoiding thermal stress and/or predation while still utilizing available light.

Based on morphological similarities, Tanner’s holotype was most likely collected somewhere in the northeast upper dune field within the Sand Hills region where large areas of arenaceous substrates are common. The specific locality of “Kanab, Utah” may have been used simply because it was the closest point of reference since very few roads, towns or other geographic points were established in this area of south-central Utah during the early part of the twentieth century. This was common practice as early collectors and authors were less precise about specimen labeling methodologies as compared

to modern standards. Usually, a nearby town, prominent landmark or geographic form were used as demonstrated by Tanner's reference (1928), "about thirty miles southeast of Zion Park."

Materials examined. In addition to the holotype, 85 males and 2 females variously labeled "USA, Utah: Kane County, Coral Pink Sand Dunes" with dates and additional data as follows: 14.VII.1991, G.R. Ballmer (4 males, UCRC); Ponderosa Grove Campground, 8.VII.1992, R.W. Baumann (18 males, BYUC), L.J. Liu (5 males, BYUC), J.T. Zenger (12 males, BYUC); 2.5 rd. mi. NE Jct. Hancock Rd. and Coral Pink Sand Dunes Rd., County Road 43, 25.VI.1993, R.A. Cunningham, J.D. Beierl (10 males, 1 female, RACC); 10.VII.2005, 1827m elev., N37°02'33" W112°43'32", D.A. La Rue, 175w HgVL (36 males, 1 female "dune hummocks at dusk", DALC).

Redescription. Males (Fig. 38–40). Length 18.0–24.5 mm. Greatest width 10.0–15.5 mm. Humeral width 9.0–11.5 mm. **Form.** Elongate, robust, subparallel-sided. **Color.** Head, eyes black; pronotum deep rufopiceous to rufotestaceous; pygidium, tibiae, tarsomeres, exposed abdominal sternites and appendages of head rufotestaceous; scutellum and elytra deep rufotestaceous to light testaceous; pterothoracic integument and antennae light testaceous; except where noted, setal vestiture pale yellow, squamal vestiture white. **Head.** Convex; clypeus transverse with reflexed bisinuate anterior margin; anterior angles obtuse, lateral margins parallel to subconvergent basally; disc depressed, coarsely punctate, densely setose with dense setae and imbricate, acuminate scales. Frontoclypeal suture obscured by rugose punctuation, suberect setae and contiguous, acuminate scales. Frons evenly convex, surface coarsely, punctate; provided with contiguous to imbricate, acuminate scales and long, suberect setae. Vertex glabrous and shining. Maxillary palpomere-4 elongate, cylindrical, anteriorly depressed, apex truncate, densely setose with minute, golden yellow spiculae, 2/3 to subequal in length to three basal palpomeres combined. Mentum subquadrate, anteriorly emarginate, angles broadly rounded, disc deeply depressed, rugosely punctate, posterolaterally with long setae and acuminate squamae. **Antennae.** Scape short, constricted basally, apex bulbous, provided with a dense scopula of long, golden yellow setae; lamellate antennomeres 4–10 distally recurved obtusely outward, provided with scattered setae. Antennal club 2.2× (linear measurement) or 2.5× (curvilinear measurement) longer than basal antennomeres combined. **Pronotum.** Broadly convex, transverse, 2× wider than length at midline, widest at posterior 1/2; anterior angles obtuse, basal angles broadly arcuate and explanate; marginal bead absent anteriorly, heavily serrate posterolaterally, evanescent posteriorly. Disc coarsely to moderately punctate, an acuminate scale or long setae arising from each puncture; medially sulcate, dividing a transverse tumidity at posterior 1/2; trivittate; medial vitta longitudinally complete or coarsely eroded, when present, composed of contiguous to imbricate, acuminate scales; submarginal vittae eroded at apical 1/2, formed as two distinct glomerate patches of dense, imbricate, acuminate scales. **Scutellum.** Oblong, broadly rounded, margins glabrous, disc obscured by imbricate scales and long, suberect setae. **Elytra.** 2.4× greater in length than width; humeral angles obtusely rounded, posterolateral angles broadly arcuate. Marginal bead explanate and reflexed anterolaterally, evanescent posteriorly, sutural bead obscured by dense acuminate scales and suberect setae. Disc shallowly, rugosely punctate; calli tumose, coarsely punctate; vestiture composed of solitary to imbricate acuminate scales and long, recumbent to erect setae; avittate or with faint longitudinal squamal lines to the unaided eye, fragmented microscopically (10×). Metathoracic wings functional. **Pygidium.** Subtriangular, convex, length subequal to width, angles obtusely to acutely rounded; disc finely punctate, depressed behind reflexed margins; vestiture composed of contiguous, acuminate, scales and recumbent setae. **Venter.** Densely pubescent obscuring pterothorax; exposed abdominal sternites convex, depressed medially; with a basal glabrous band, vestiture composed of solitary to imbricate scales and scattered setae. **Legs.** Protibia bidentate, basal third tooth indicated as a slight angular projection; dentition widely separated, projecting obliquely forward from longitudinal tibial axis; inner margin rounded; outer margin with a raised, longitudinal dentiform carina; surfaces finely punctate with solitary, acuminate scales and scattered setae. All femora flattened, margins parallel, rounded anteriorly, surface vestiture as protibiae. Apices of tarsomeres coronate with a fringe of golden translucent spiculae, solitary setae, and acuminate scales; tarsomere-5 elongate, arcuate, ventral surface bearing a fine carina extending 1/2 length of tarsomere; tarsal claws with basal proximal tooth. **Phallobase and parameres.** Number examined (3). In dorsal aspect, symmetrical with two simple parameres narrowing distally, convergent at apical 1/3, apices

diverging outward, median notch sharply rounded, subequal to 1/2 length of parameres; lateral aspect, apical 1/4 cristate, tapering to a faint carina length of median notch, apices smoothly rounded ventrally; caudal aspect, obliquely depressed outward; distal tips adjoined anterodorsally, acutely angled at apex.

Females (Fig. 41). Length 19.5–22.0 mm. Greatest width 10.5–11.0 mm. Humeral width 8.5–9.5 mm. Excluding sexual dimorphic variation as male except: **Form.** Robust, ovate, widest at posterior 1/3. **Color.** Pronotum black to rufotestaceous; elytra, exposed abdominal sternites, pygidium, and tarsomeres brown to testaceous; legs rufotestaceous. **Head.** Clypeus broadly rounded, anterior margin arcuate; frontoclypeal suture absent; squamal vestiture sparse; lamellate antennomeres straight. **Pronotum.** Sharply convex; faintly trivittate; vittae fragmented, setal and squamal vestiture reduced. **Scutellum.** Medially with contiguous, acuminate scales and setae. **Elytra.** Vittae fragmented, forming indistinct lines; subhumeral vittae faintly indicated. **Pygidium.** Setal and squamal vestiture reduced exposing discal integument. **Legs.** Protibia strongly tridentate; dentition sharply acute, projecting obliquely forward from longitudinal tibial axis; mesotibial margin distally bearing two short projections.

Natural history. Males were first observed flying at or just before twilight and continued late into the evening except on one occasion ceasing abruptly at 23:15 hrs. PST when no additional males were seen at light stations nor encountered upon the sand surface. Similar to the behavior reported for *P. aeolus* (La Rue 1998) and *P. arguta* (Young 1988). Although flight activity of *P. uteana* had ceased, males of *P. arguta* and *P. decemlineata* continued to be attracted to light stations for several hours.

Approximately 20 minutes prior to dusk, preceding male flight, female *P. uteana* were found crawling or stationary on the sand surface with antennae extended and lamellae in a splayed position. Despite attempts to induce flight by releasing them just above the sand surface, females would not fly suggesting they are flightless as in other *Polyphylla* species restricted to cryptic ecosystems (La Rue 1998; Russell 2000; Skelley 2009). No adult feeding activity was observed and no specimen was encountered on vegetation. Adult longevity is presumably based upon metabolic reserves accrued during larval development. As in other psammophilous *Polyphylla*, adults of *P. uteana* undoubtedly spend diurnal hours at varied depths within the microenvironment of damp sand (La Rue 1998).

Ecology. The Kanab and Coral Pink Sand Dunes are part of a larger sand dune regime located in the Colorado Plateau region of south-central Utah. The dunes are connected by sheet sand deposits to the Sand Hills region that extend northeast between Kanab Creek and the Sevier fault. Smaller sand accumulations have developed on the lee sides of numerous ridges, escarpments, and cliffs throughout the area. Estimates place the sand origin to the Pleistocene (Gregory 1950) or possibly during the middle Holocene (Shafer 1989). The salmon-colored sand is derived from a mixture of red and white Navajo Sandstone grains.

The vegetation at Coral Pink Sand Dunes is largely transitional with elements of cool desert shrub, pinyon-juniper, mountain brush, and ponderosa pine floral communities (Welsh et al. 1993). Predominant species include *Artemisia tridentata* ssp. Nuttall (big sagebrush: Compositae), *Juniperus osteosperma*, and widely distributed *Pinus edulis*. A varied understory of extensive *Calamovilfa gigantea* (Nuttall) Scribner and Merrill (giant sand reed: Gramineae), *Ericameria nauseosus* (Pallas) (rabbitbrush: Asteraceae), *Sophora stenophylla* A. Gray (fringeleaf necklacepod: Leguminosae), and *Wyethia scabra* Hooker (rough mulesears: Compositae), with many annual species present at various times of the year depending on precipitation levels.

Climate is characterized as a cold desert (cold winters and hot, dry summers). Mean annual precipitation, which fluctuates greatly from year to year, averages 34.5 cm with occasional snowfall. In late summer, brief monsoonal cloudbursts are common. Ambient temperatures range from 7° to 32° C. In recent decades there has been increased available moisture but precipitation has become exceedingly variable (Welsh et al. 1993).

Conservation. The major threat to *P. uteana* is habitat destruction from off-road vehicle activity which has greatly increased in recent decades. The use of three- and four-wheel off-road vehicles on the more vegetated dune areas adversely modifies and destroys critical habitat. Irreparable destabilization of vegetated dunes accelerates sand movement to a point that exceeds the tolerance of dune-adapted plants

on which larvae of *P. uteana* are dependent. Surveys of other sand dune ecosystems in the Great Basin have established that *P. uteana* is endemic to a small region of contiguous sand dune areas in south-central Utah. This would indicate that it is highly vulnerable to extinction from continued anthropogenic disturbance and should be considered a “critically imperiled” species.

Common name. The Coral Pink Sand Dunes polyphyllan scarab beetle.

Female descriptions

Except for a few common, widely distributed species, females are poorly represented for the majority of Nearctic *Polyphylla* and those of species restricted to isolated cryptic ecosystems are rarely encountered. Most are exemplified by a single specimen or remain unknown. Consequently, the paucity of comparative females has precluded quantitative morphological assessment and taxonomic consideration.

Nearctic females exhibit an accentuated sexual dimorphism characterized by a heavy, robust, ovate form; large, convex abdominal sternites with strongly arcuate sutures; reduced antennal structure with five-segmented, ovate, straight or feebly divergent lamellate antennomeres; reduced number and distribution of antennal sensory receptors (sensilla); shortened apical maxillary palpomeres; pronotum sharply convex, often bearing a pronounced setigerous and/or squamal vestiture (excluding the pubescens species group, Skelley 2003, 2009); clypeus shallow, transverse to subquadrate with variably reflexed margins; short, robust protibia with corresponding dentition, typically tridentate with proximal tooth prominent; meso-, and metatibia distally divergent with greater number of apical spines; meso-, and metatibial spurs spatulate; enlarged metafemora; and shortened tarsomeres. Several of these latter characters are presumably adaptations associated with inherent fossorial behavior.

The reproductive system of female *Polyphylla* is of the “tubular type” consisting primarily of a genital chamber, accessory glands, oviduct, median oviduct, bursa copulatrix, spermatheca, and spermathecal gland (Dupuis 2005). Four simplified sclerotized genital plates, two superior and two inferior, with several sensory setae and membranous folds are everted during copular intromission with the male parameres remaining external and only the aedeagus penetrating between the female genital sclerites, as observed in other closely related genera of Nearctic Melolonthini (e.g. *Phyllophaga* Harris, Polihronakis 2006; *Dinacoma* Casey, in preparation). The apical sensory setae of the female genital plates and apices of the male parameres are presumed to interact during male “internal courtship” (Eberhard 1992; Zunino 1987). The manner in which a female determines a potential mate and complexities of pheromonal recognition and discrimination are unknown.

Female *Polyphylla* restricted to cryptic ecosystems have greatly histolysed wing musculature and reduced wing venation explicative of flightlessness. For flight capability, insects require flight muscles that comprise at least 12–20% of their total mass (Roff 1990; Marden 2000). However, flight muscles are metabolically exigent to produce and maintain and their development seriously constrains certain aspects of adult function, most particularly, female fecundity (Marden 2000). As a result, loss of flight may be favored among females because it permits greater allocation of energy and protein toward ova development and provision, while flight is retained in males because it increases the probability of mate location. In addition, flightless females reach sexual maturity more rapidly and attain higher fecundity (Marden 2000). Consequently, flightless *Polyphylla* females have adapted a semelparous life history strategy presumably as a result of limited energy expended toward reproduction.

Polyphylla monahansensis Hardy and Andrews

(Fig. 42–44)

Female description. Based on one specimen labeled “USA, Texas: Andrews Co., dunes, 1.3 miles E. Jct. Texas 115 and Farm Road 181, 24.VII.1996, C.S. Wolfe, D.G. Marqua” (DALC).

Length 20.5 mm. Greatest width 10.5 mm. Humeral width 9.0 mm. Excluding sexual dimorphic variation as male except: **Form.** Robust, slightly ovate, widest at posterior 1/2. **Color.** Clypeus deep rufotestaceous; pygidial disc rufopiceous; venter and exposed abdominal sternites pale testaceous. **Head.**

Anterior clypeal margin medially tumescent; frontoclypeal sutural margins coarsely eroded. **Pronotum.** Lateral margins and bead more acutely angled and explanate. **Scutellum.** Slightly narrower basally. **Elytra.** Squamal vestiture more evenly distributed; vittae more uniform, edges not as coarse as in male, sutural vittae absent anteriorly; subsutural and discal vittae adjoined basally. **Venter.** Squamal and setal vestiture reduced. **Legs.** Protibia strongly tridentate; dentition widely separated, distal tooth strongly recurved.

Remarks. The distribution of this species was previously amended (La Rue 1998).

The female was encountered crawling on the sand surface at dusk in an area of semi-stabilized parabolic and barchan dunes with scattered *Calamovilfa gigantea* and *Quercus harvardii* Rydberg (sand shinnery oak: Fagaceae) (C.S. Wolfe, personal communication). This locality is associated with the Monahans and Andrews dune fields, in Andrews, Ward, and Winkler Counties, west Texas, and are part of the Southern High Plains dune system (Machenberg 1984; Muhs and Holliday 2001).

Polyphylla stellata Young

(Fig. 45–47)

Female description. Based on two specimens labeled “USA, California: Contra Costa Co., East Antioch, 14.V.1994, S.E. Haskins” same data except 10.VI.1994 (DALC).

Length 21.0–24.5 mm. Greatest width 10.5–12.0 mm. Humeral width 9.5–10.0 mm. Excluding sexual dimorphic variation as male except: **Form.** Robust, slightly ovate, widest at posterior 1/2. **Color.** Head and pronotum rufotestaceous; elytra appearing black to piceous, rufotestaceous to deep rufotestaceous under magnification (10.5×); venter and exposed abdominal sternites pale testaceous to rufotestaceous. **Head.** Anterior clypeal margin feebly to strongly bisinuate; lateral clypeal margins subparallel. **Pronotum.** Pale setae uniformly distributed over entire disc; lateral marginal bead crenulate. **Elytra.** Vittate, vittae fragmented, sublinear, composed of fragmented patches of small, white squamae; short, recumbent pale setae randomly scattered over disc or confined to elytral declivities. **Pygidium.** Pale setae uniformly distributed over disc. **Venter.** Squamal and setal vestiture reduced. **Legs.** Protibia strongly tridentate, dentition widely separated; pale straw-colored setae uniformly distributed over anterior surface, or nearly glabrous; distal tooth strongly recurved; anterior mesotibial surface with coarse dentiform projections.

Remarks. The distribution and ecological associations of this species were previously amended (La Rue 1998).

The females were encountered within or partially emerged from their burrows in hard-packed clay soil while observing male flight behavior at dusk. Males were attracted to a blacklight placed in an area of sandy alluvial soil (S.E. Haskins, personal communication).

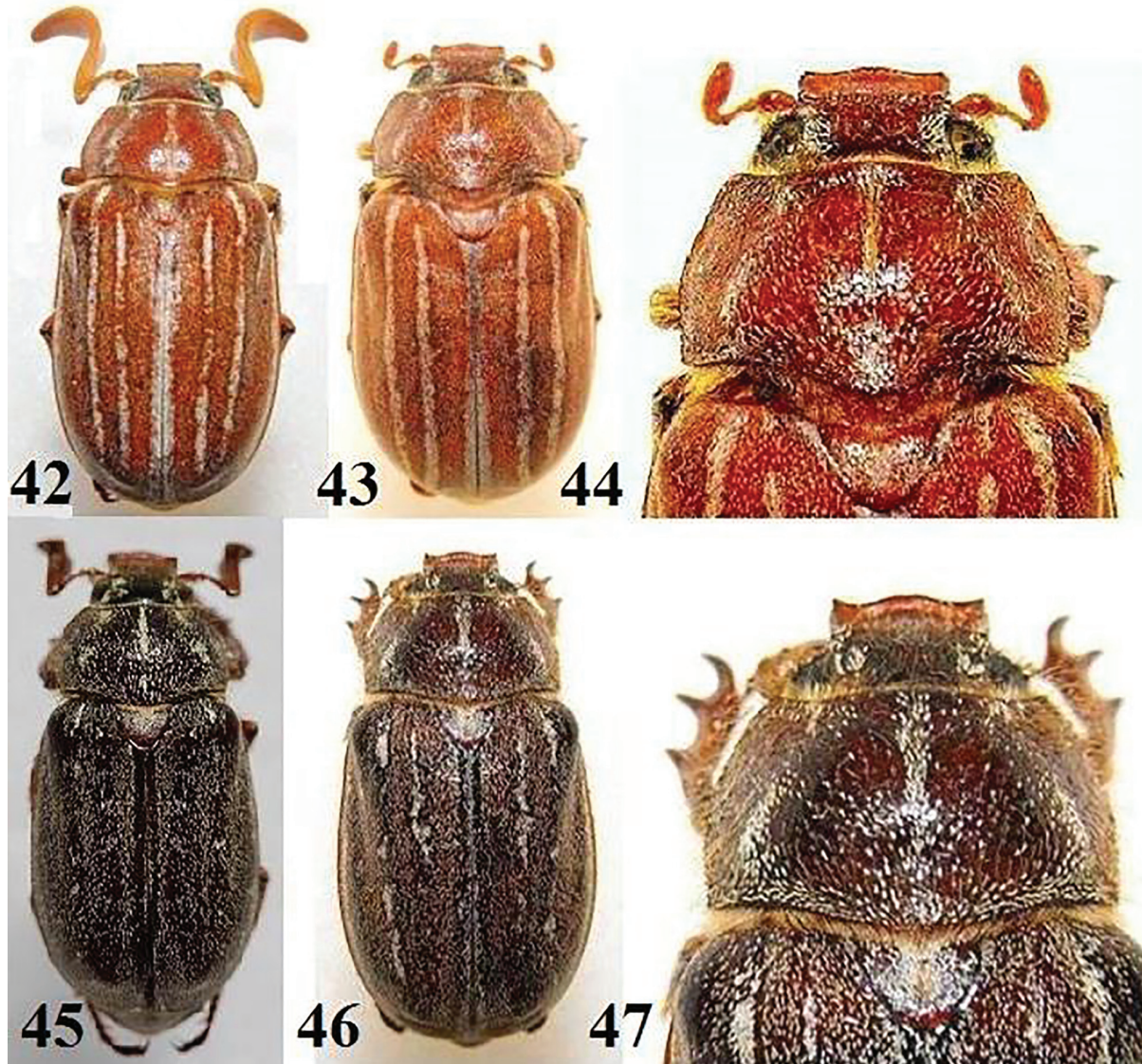
Remnants of the Antioch Sand Dunes continue to support what remains of an oak-willow woodland canopy with a ground cover of scattered forbs and grasses. Ecologically, these habitat parameters correspond to extant populations of *P. stellata* in Sacramento County, CA (La Rue 1998).

Distribution and ecological amendments

Polyphylla cavifrons LeConte

Materials examined. USA, Nevada: Clark County, Warm Springs, 19.VII.1990, R.W. Baumann (1 male, BYUC); Overton, 19.VII.1997, L.A. Hedquist (1 male, BYUC); Moapa Valley, Muddy Springs, 18.VIII.1997, Baumann and Huilett, lights (2 males, BYUC); Muddy River, 6.VIII.2000, Winkler and Waite (1 male, DALC).

Remarks. This distinctive species is ecologically associated with desert riparian or similar habitats including isolated desert springs, agricultural and urban canals, and irrigation channels (La Rue 1998).



Figures 42–47. Described females and comparative male. *Polyphylla monahansensis* Hardy and Andrews. 42) Male. 43–44) Female. *Polyphylla stellata* Young. 45) Male. 46–47) Female.

Young (1988) cited a single record of this species from Nevada: “Mesquite, Clark County,” which is adjacent to the Virgin River.

***Polyphylla concurrens* Casey**

Materials examined. GUATEMALA, El Quiché: Chichicastenango, central market, 10.X.1998, H. E. Mayne (1 male, DALC).

Remarks. This species was originally described from Honduras (Casey 1889, 1914). Morón (2010, 2015 *in litt.*) records it from the states of Chiapas, Morelos, Oaxaca, Puebla, and Vera Cruz, Mexico. Accounting for phenotypic variation and sexual dimorphism (the holotype is a female, #35640, United States National Museum), the specimen cited above agrees in all essential morphological respects to Casey (1889, 1914) and Morón (2010, 2015 *in litt.*).

Polyphylla crinita LeConte

Materials examined. CANADA, British Columbia: Terrace, 28.VIII.2002, S. Schulte (1 male, DALC).

Remarks. Terrace is located within the Coast Mountains in an area of extensive coastal-interior rainforests.

Young (1988) indicated the northernmost record of the genus in the New World was a specimen of *P. crinita* from Quesnel, British Columbia, south of 53° north latitude. The Terrace record extends the known distribution of the genus and species nearly 700 km northwest to west central British Columbia at approximately 54°30'40" north latitude.

Polyphylla diffracta Casey

Materials examined. MEXICO, Chihuahua: 86 km NE Nácori Chico (Sonora), Rancho Arroyo El Cocono, 1660m, 7.VIII.1982, S. McCleve, G.E., K.E. Ball [12 males, not examined, depository unknown].

USA, Colorado: **Bent County**, 3.5 mi S of Caddoa, 3.VII.1990, B. Kondratieff, M. Kippenhan, H.E. Evans (1 male, DALC).

Remarks. The Mexico locality was previously reported by Young (1988) as from the state of Sonora. Revised locality data cited by McCleve and Kohlmann (2005) indicate this locality is actually within the southwestern border of the state of Chihuahua.

This species was not listed from Colorado by Young (1967, 1988). Krell (2010) cites "Mesa County, Colorado." Records of its occurrence in California (Young 1967, 1988; Evans 1992) certainly represent misidentified or mislabeled specimens. For example, examination of a male specimen in the SBMNH determined as this species and labeled "Calif: San Bernardino Co., San Bernardino NF, nr. Deer Crk. 34.1741-116.9844, July 2, 2005, specimen #CBP0031851, M. Caterino collector" shows that, in fact, it represents *P. crinita* with fragmented elytral vittae (see comments regarding this character under *P. rugosipennis* below).

Polyphylla mescalerensis Young

(Fig. 48–49)

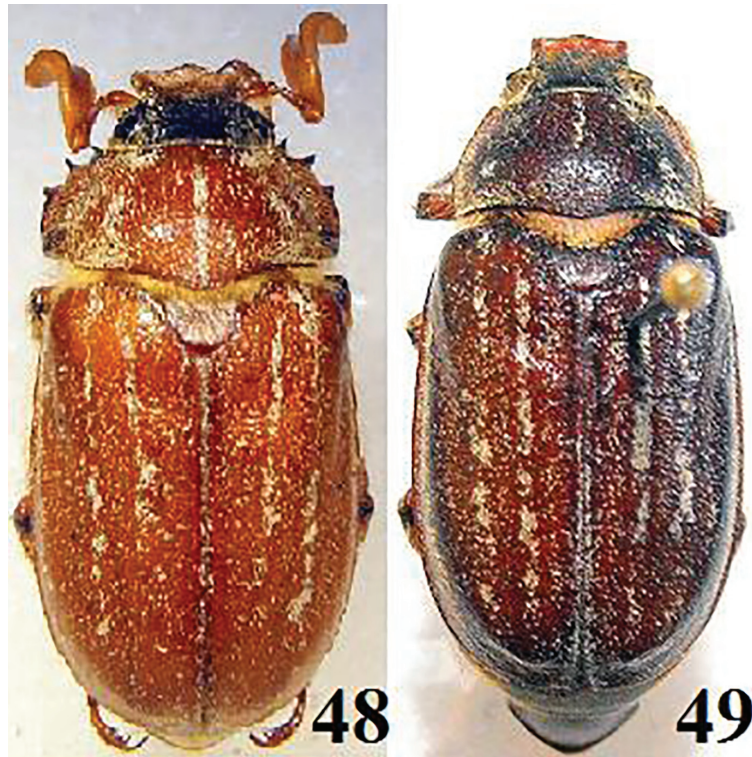
Remarks. Based on a series of 19 males, Young (1988) described *P. mescalerensis* from the Mescalero Sand Dunes, Chaves County, New Mexico. The female was subsequently described by La Rue (1998).

In Young's key to the North American species of *Polyphylla* (1988), the concluding couplet for *P. mescalerensis* (#18, p.24) includes the distributional note, "Chihuahua, Mexico." Inexplicably, no further reference to the Chihuahuan record appears anywhere in the publication nor, in the intervening years since Young's publication, have any supporting references documenting its occurrence there been reported (Morón 1997, 2010, 2015 *in litt.*).

A purported male specimen of *P. mescalerensis* examined is labeled "MEX: Chihuahua, Cerro San Luis, VIII-13-1981, 1767m at light, S. McCleve // *P. mescalerensis* Young, det. R. M. Young 1988" (DALC). The coincidental year of Young's determination suggests the possibility that this was a specimen on which he validated the Chihuahuan distributional record.

Upon closer scrutiny, however, the Cerro San Luis specimen and samples from the Mescalero Sand Dunes differ in several salient morphological respects as follows:

Mescalero Sand Dunes, New Mexico. (15 male topotypes) (Fig. 48). Dorsal integument light yellowish-brown to reddish-brown except head black; anterior clypeal margin moderately reflexed, lateral margins basally convergent; distal maxillary palpomere-4 conical, obtusely tapered at apex, surface coarsely punctate, with only a few randomly scattered golden setae; scutellum narrow, triangular; pronotum widest at basal 1/2, margins strongly explanate, discal setae sparsely to moderately distributed; elytral disc setose or glabrous (abrasion), posterior margins obtusely rounded; protibia bidentate to tridentate;



Figures 48–49. *Polyphylla*. Males. **48)** *Polyphylla mescalerensis* Young [topotype]. Mescalero Sand Dunes, Chaves County, New Mexico. **49)** *Polyphylla* sp. *incertae*. Cerro San Luis, Chihuahua, Mexico.

meta-, mesotibia with two or three acuminate projections; antennae small, slightly to deeply recurved distally; ventral surface of protarsomere-5 smooth, lacking any serration.

Cerro San Luis, Chihuahua, Mexico. (1 male) (Fig. 49). Dorsal integument deep reddish brown except head, lateral pronotal disc, and elytral humeri black; anterior clypeal margin weakly reflexed, lateral margins parallel; distal maxillary palpomere-4 acutely tapered at apex, feebly depressed dorsally, surface finely punctate, with very fine, short pale setae; scutellum transverse; pronotum widest at basal 1/3, margins feebly explanate, discal setae sparsely distributed; elytral disc glabrous, posterior margins recurved inward toward sutural apices; protibia bidentate, lacking any indication of a basal third tooth; meta-, mesotibia devoid of acuminate projections; antennae large, moderately recurved distally; ventral surface of protarsomere-5 with a raised serrated carina.

Given the marked disparity of morphological and ecological factors and the absence of additional specimens confirming its occurrence there, the Chihuahuan record for *P. mescalerensis* is invalidated. Because only a single Cerro San Luis specimen is presently known, definitive taxonomic treatment must await additional material.

Polyphylla rugosipennis Casey

Materials examined. USA, Arizona: Coconino County, Flagstaff, Hwy.180, 15.VII.1991, E.C. and R.C. Mower (1 male, DALC); Mogollon Rim, Hwy 87, 3.3 mi N. of Strawberry, 2000m elev., 1.VIII.1998, MV/BL, R.A. Cunningham, J.D. Beierl (1 male, DALC); **Navajo County**, Show Low, VIII.1975, no collector (1 male, BYUC); East Heber, 12.VII.2003, T.P. Blumer (3 males, BYUC); **Yavapai County**, 17 miles NE Payson, Camp Christopher, at town lights, 6000 ft. el., 1.VIII.1998, R.A. Cunningham Sr./Jr., J.D. Beierl (3 males, DALC).

New Mexico: San Juan County, Jct. of Rd.5577/Rd.5569, 0.5 miles W. of County Rd.350, 36°43.689N / 108° 05.214W, 18.VI.-06.VII. 2006, T.G. Merrion, MVL (2 males, POKC); same locality except labeled 36° 43.682N / 108° 05.231W, various dates between 01.IX.2004-26.VI.2005, P.O. Kaufman, MVL (4 males, POKC).

Utah: Grand County, Sego Canyon, 8 mi N of Thompson Turnoff I-70, Book Cliffs, 13.VII.2006, 6057 ft. elev., T.S. and R.C. Mower (2 males, BYUC); **Iron County**, Kanarraville, 26.VII.2006, K. Miwa (1 male, BYUC); **Kane County**, Grand Staircase-Escalante National Monument, Seaman Spring, off Hwy.89, 37°06'16"N / 112°15'08"W, 29.VI-10.VII.2001, K.A. Clarke, K.C. Greene (3 males, BYUC); **Utah County**, Lake Mt., Saratoga Springs, 23.VIII.2003, D.E. Haider (1 male, DALC).

Remarks. Type locality: "Arizona (Grand Cañon of the Colorado)" Casey (1914).

This species is poorly represented in collections and little is known of its natural history or ecological associations. At present, the known distribution is significantly fragmented being recorded primarily from the Grand Canyon area of northern Arizona and the Sierra San Pedro Martir, Baja California, Mexico (Hardy 1981; Young 1988). The female remains unknown.

The San Juan County, New Mexico, locality is in an area of *Juniperus* sp. and *Atriplex canescens* (Pursh) Nuttall (saltbush: Amaranthaceae), 1675 m elevation, associated with the Chaco Dune Field in northwestern New Mexico (Schultz and Wells 1981). *Polyphylla decemlineata* was sympatric at this locality (P.O. Kaufman, personal communication).

Sego Canyon, Grand County, is in southeast Utah among pinyon-juniper-oak woodlands with scattered to dense stands of *Artemisia* sp. and *Ericameria* sp. growing in sandy alluvial soil.

Seaman Spring, Kane County, is in south central Utah in an area of *Pinus edulis* and *Juniperus osteosperma* at an elevation of 1870 m.

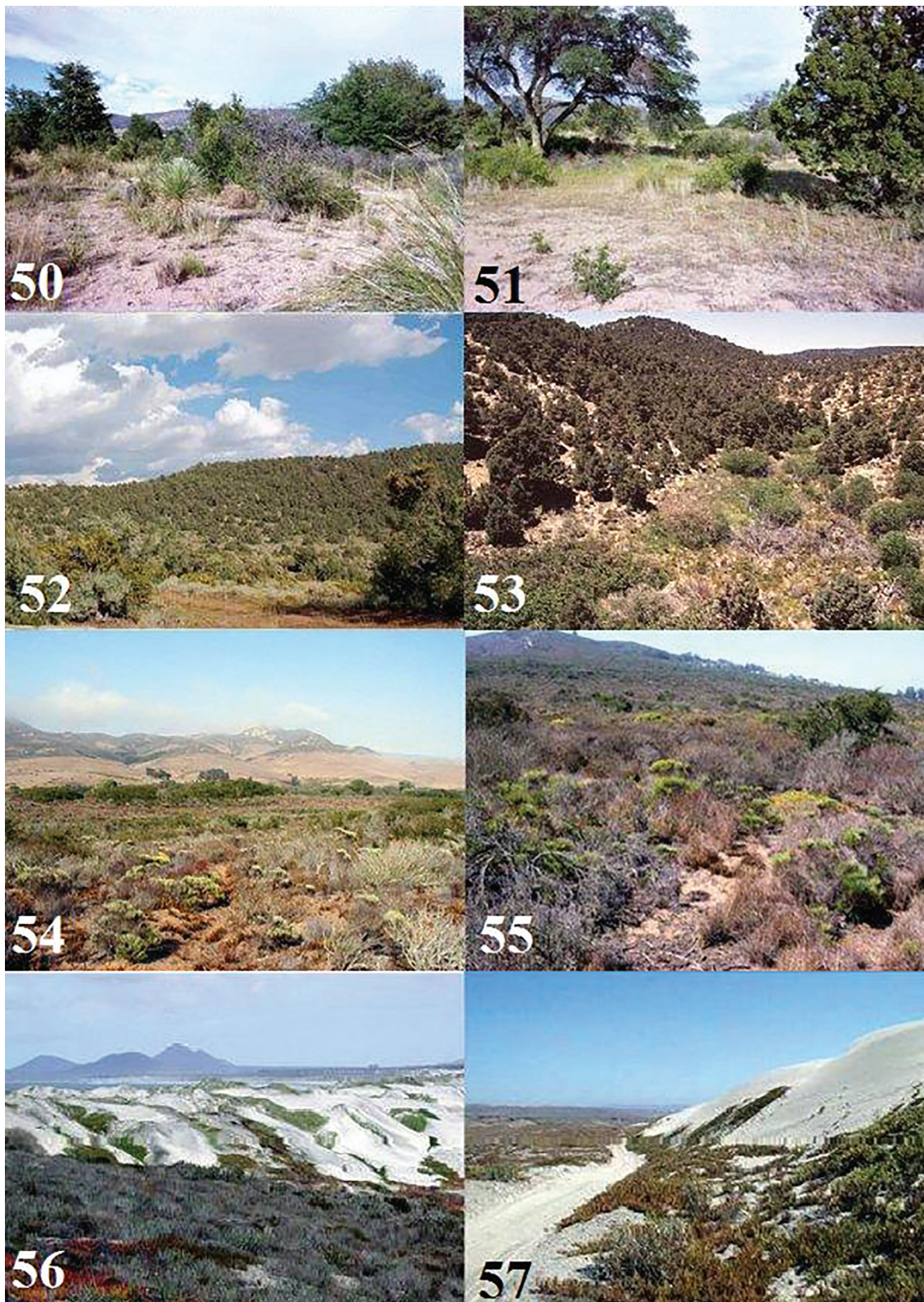
The combination of dark brown to black dorsal integument; presence of head, pronotal, elytral, and pygidial setae; rough-edged, incomplete elytral vittae; parallel lateral clypeal margins; coarsely punctate pronotal disc; comparatively small antennal structure; and bidentate protibia distinguish males of this species from sympatric congeners: *P. arguta*, *P. decemlineata*, *P. diffracta*, and *P. hammondi*. Of these, *P. rugosipennis* is most similar to *P. arguta* with which it shares a brown to black dorsal integument; white squamal vestiture; elytral vittae linear, whether continuous or fragmented, with edges coarsely eroded; and medium to large size (length usually greater than 25 mm). *Polyphylla arguta* lacks pronotal and elytral discal setae usually present in *P. rugosipennis*. However, the presence or absence of pronotal setae in *P. rugosipennis* is apparently variable (Casey 1914; Cazier 1938) as is their length either short (Hardy 1981) or long (Young 1988). All of the specimens cited here have short pronotal setae. Although male protibial dentition in *P. rugosipennis* is typically bidentate, one specimen from the Camp Christopher, Yavapai County, Arizona, series is distinctly unidentate without any indication of further dentition or excessive abrasion. Furthermore, the elytral vittae of *P. rugosipennis* may vary from nearly longitudinally complete to significantly fragmented and discontinuous. As a result of erroneous concepts and perfunctory "gestalt" taxonomy, the latter variation is frequently misidentified as *P. diffracta*. This variability in intraspecific morphology may possibly contribute to the species' misidentification and explain its inconsistent distribution.

Polyphylla petiti (Guérin-Méneville)

not *petiti* of authors [ICZN 1999, Article 33.4]

Materials examined. GUATEMALA: Baja Verapaz, 6 km S. Purulhá, 11.X.1985, P. Hubbell, at light (DALC).

HONDURAS: Cortés, Parque Nacional Cusuco, 1600 m, 15°29' N, 88°12' W, 1.III.1995, R. Cordero; 21.VIII.1998, J. Torres; Francisco Morazán, El Zamorano, elev. 850 m, 14°1' N, 87°0' W, 2.V.1988, F. Restrepo; 1.V.-31.VII.1990, Estudiantes EAP [Escuela Agrícola Panamericana]; 6.IX.1990, F. Barahona; 10.VI.1999, M. Avilés and S. Avila; Gracias a Dios, 2.2 km SE Wampusirpi, elev. 60 m, 15°9' N, 84°36' W, 23.IV.2001, R. Cave and R. Cordero; Lempira, Erandique, elev. 1270 m, 14°15' N, 88°27' W, 16.IX.2000, R. Cordero; Montaña de Puca, elev. 1150 m, 14°42' N, 88°34' W, 28.VI.2000, R. Cordero and J. Torres; Olancho, Montaña del Malacate, elev. 800 m, 15°7' N, 85°35' W, 18.IV.1999, R. Cave



Figures 50–57. Habitats. **50–51)** *Polyphylla anivallis*. Animas Valley Sand Dunes, Hidalgo Co., NM. **52–53)** *Polyphylla koso*. Coso Mountains, Inyo Co., CA. **52)** Coso Bridge. **53)** Mill Springs Canyon. **54–55)** *Polyphylla morroensis*. Baywood Fine Sands, San Luis Obispo Co., CA. **56–57)** *Polyphylla socorrana*. El Socorro Sand Dunes, Baja California, MX.

and J. Torres; Montaña del Malacate, elev. 900 m, 15°8' N, 85°35' W, 9.IX.1999, R. Cave, J. Torres, and R. Díaz; Yoro, Linda Vista, elev. 1000 m, 15°9' N, 87°38' W, 10.IX.1999, R. Cave, J. Torres and R. Díaz; 8.XII.1999, R. Cordero; Parque Nacional Pico Bonito, El Portillo, elev. 640 m, 15°26' N, 87°8' W, 27.IX.2000, R. Cordero and J. Torres; 26-27.I.2001, R. Reyes (all EAPZ).

NICARAGUA: **Estelí**, Cerro Tomabú, 1295 m, 29.X.2000, J. M. Maes and B. Tellez; **Jinotega**, El Jaguar, 1346 m, 13°14'N 86°09'W, 14-16.IX.2004, J. M. Maes (both JMMC).

Remarks. The southern distributional extent of this species was previously reported from “Nicaragua, Nueva Segovia, 15 km north of Jalapa” (La Rue 1998:32).

The Nicaragua records presently extend the known distribution of the genus and species in the New World approximately 100 km south and below 13° north latitude. The genus has not been encountered in adjacent Costa Rica (A. Solís, *in litt.*).

Checklist of the “Western Clade” species of *Polyphylla*, north of Mexico

The checklist is organized into informal species groups inferred from adult morphological parity (Table 1.), mtDNA analyses (Russell 2000), and hypothesized phylogenetic relationships. Species followed by an asterisk (*) warrant further taxonomic consideration.

Polyphylla Harris 1841

“aeolus” group

Polyphylla aeolus La Rue 1998

Polyphylla koso La Rue, **new species**

“crinita” group

Polyphylla crinita LeConte 1856

syn. *Polyphylla pacifica* Casey 1895

syn. *Polyphylla crinita mystica* Casey 1914

syn. *Polyphylla incolumis* Casey 1914

syn. *Polyphylla ruficollis perversa* Casey 1914*

syn. *Polyphylla ona* von Bloeker 1939

syn. *Polyphylla santarosae* von Bloeker 1939

Polyphylla modulata Casey 1914

Polyphylla nigra Casey 1914*

syn. *Polyphylla incolumis relictata* Casey 1914

syn. *Polyphylla incolumis robustula* Casey 1914

syn. *Polyphylla martini* von Bloeker 1939

syn. *Polyphylla santacruzae* von Bloeker 1939

Polyphylla morroensis La Rue, **new species**

“decemlineata” group

Polyphylla decemlineata (Say) 1824 (as *Melolontha*)

syn. *Polyphylla decemlineata laticauda* Casey 1914

syn. *Polyphylla decemlineata parilis* Casey 1914

syn. *Polyphylla decemlineata reducta* Casey 1914

syn. *Polyphylla matrona* Casey 1914

syn. *Polyphylla potosiana* Casey 1914

syn. *Polyphylla ruficollis* Casey 1914

syn. *Polyphylla ruficollis castanea* Casey 1914

syn. *Polyphylla ruficollis oregona* Casey 1914

syn. *Polyphylla squamotecta* Casey 1914

syn. *Polyphylla comstockiana* von Bloeker 1939*

Polyphylla arguta Casey 1914

“devestiva” group

Polyphylla devestiva Young 1966

Polyphylla avittata Hardy and Andrews 1978

syn. *Polyphylla ratcliffei* Young 1986, **new synonymy**

“diffracta” (s.l.) group

Polyphylla diffracta Casey 1891*

syn. *Polyphylla fuscula* Fall 1908*

syn. *Polyphylla adusta* Casey 1914

syn. *Polyphylla laevicauda* Casey 1914

syn. *Polyphylla opposita* Casey 1914

syn. *Polyphylla alleni* Cazier 1939

syn. *Polyphylla diffracta arida* Van Dyke 1947*

Polyphylla uteana Tanner 1928, **reinstated status**

“hirsuta” group

Polyphylla hirsuta Van Dyke 1933

“monahansensis” group

Polyphylla monahansensis Hardy and Andrews 1978

Polyphylla mescalerensis Young 1988*

“stellata” group

Polyphylla stellata Young 1986

Polyphylla anivallis La Rue, **new species**

group incertae

Polyphylla barbata Cazier 1938

Polyphylla nubila Van Dyke 1947

Polyphylla pottsorum Hardy and Andrews 1978*

Polyphylla rugosipennis Casey 1914

syn. *Polyphylla peninsularis* Van Dyke 1943

Polyphylla sobrina Casey 1914

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Table 1. Character matrix for western clade species-groups, north of Mexico, based on male morphology. n/a - character not applicable; or (underlined) - specific character states within group species; or (not underlined) - inclusive variation within group species; ¹ a highly variable, polytypic species, further taxonomic analyses required; ² viewed under white fiber optic illumination and magnification of 10-15x; ³ samples from the Pacific Northwest frequently larger and darker; ⁴ rarely olivaceous; ⁵ some specimens with blackish head and pronotum; ⁶ excluding elytral suture; ⁷ approximate measure rounded to nearest 0.5 based on minimum of six examples; ⁸ linear measurement - length of pedicel (excluding scape) ; length of lamellae (basal constriction to apex in dorsal aspect); ⁹ pronotum transverse in all species groups; ¹⁰ pronotum trivittate in all species groups; ¹¹ rarely nonlinear in *P. aeolus* (note La Rue 1998:35 Fig. 5); ¹² rarely avittate in *P. devestiva*; ¹³ some specimens of *P. anitallis* have short vittal fragments; ¹⁴ present in *P. ruficollis perversa* Casey 1914 (= syn. *P. crinita*, *sensu* Young 1988:59), further taxonomic analyses required.

Species-groups	"aeolus" group	"crinita" group	"decemlineata" group	"devestiva" group	"diffracta" (s.l.) group	"hirsuta" group	"monahansensis" group	"stellata" group
Ecology	stenotopic: psammophilous or montane	facultative	facultative	stenotopic: psammophilous	facultative	stenotopic: montane	stenotopic: psammophilous	stenotopic: psammophilous
² Integument	deep reddish-brown	black, reddish-black, brown or olivaceous-brown	³ yellowish-brown, brown or black	yellowish-brown to reddish-brown	^{4, 5} yellowish-brown, brown or reddish-brown	⁶ light brown to deep reddish-brown	yellowish-brown to reddish-brown	black, reddish-black or deep reddish-brown
⁶ Dorsal setae	white or pale yellowish-brown	yellowish-brown or reddish-brown	n/a	golden to pale yellowish-brown	white or pale yellowish-brown	pale yellowish-brown	pale yellowish-brown	golden to pale yellowish-brown
Dorsal squamae	white or pale yellow	white	white	white or pale yellow	white or pale yellow	n/a	white	white or pale yellow
Interstitial squamae	white or pale yellow	pale yellow to yellowish-brown	white or pale yellow to yellowish-brown	white	pale yellow to yellowish-brown	n/a	white	n/a
Antennal structure	large to moderate, deeply recurved, attaining a right-angle	large, moderately to deeply recurved or small, slightly recurved	variable	moderate, slightly to deeply recurved	variable	small, slightly recurved	large, moderately to deeply recurved	small, slightly recurved
^{7, 8} Antennal pedicel : lamellae ratio	4.5 - 5 : 1	4 - 4.5 : 1	variable	4 - 4.5 : 1	variable	4.5 - 5 : 1	4 - 5 : 1	4 - 4.5 : 1

Anterior clypeal margin	emarginate to sinuate	emarginate to bisinuate	variable	bisinuate	subarcuate	bisinuate	emarginate to bisinuate
Surface of clypeal disc	rugopunctate	rugopunctate	punctate to rugopunctate	coarsely punctate	shallowly punctate to rugo-punctate	punctate to rugopunctate	shallowly punctate
^{7,9} Pronotal width : length ratio Pronotum	2 : 1	2 – 2.5 : 1	variable	1.5 : 1	1.5 – 2 : 1	1.5 – 2 : 1	1.5 – 2 : 1
Pronotal anterolateral margins	serrate, explanate, setigerous	serrate, explanate, setigerous	variable	widely serrate, explanate, setigerous	weakly serrate, explanate, setigerous	widely serrate, explanate, setigerous	widely serrate, explanate, setigerous
¹⁰ Pronotal vittae	complete or with lateral vittae glomerate posteriorly	complete	complete or fragmented or with lateral vittae glomerate posteriorly	complete or fragmented with lateral vittae glomerate posteriorly	complete or fragmented	complete or fragmented	fragmented
Pronotal discal setae	present	present or absent	absent	present	present	present	present
Scutellum	transverse, angles broadly rounded	transverse, angles broadly rounded	oblong to transverse, angles variable	transverse, angles broadly rounded	transverse, angles broadly rounded	transverse, angles broadly rounded	transverse, sub-triangular, angles acutely rounded
Elytral vittae	¹¹ linear, fragmented, edges coarsely eroded	linear, continuous, edges uneven to coarsely eroded	linear, continuous, edges smooth or fragmented, edges coarsely eroded	¹² nonlinear, an erratic pattern of squamae	n/a	linear, continuous, edges uneven or fragmented, edges coarsely eroded	¹³ avittate n/a
Sutural vittae	complete or fragmented	complete	complete	absent or fragmented	n/a	absent or fragmented	n/a

Subhumeral vittae	absent	present	present	absent	present or absent	n/a	present or absent	n/a
Submarginal vittae	present	present or absent	present	present or absent	present or absent	n/a	present or absent	n/a
Interstitial squamae contiguous with vittae	intermittent	divided	divided	n/a	variable	n/a	divided or intermittent	n/a
Parallel glabrous band	absent	present	present or absent	absent	present or absent	n/a	present or absent	n/a
^e Elytral discal setae	present or absent (abrasion)	¹⁴ absent	absent	present	present or absent	present	present or absent (abrasion)	present or absent (abrasion)
Pygidium	subtriangular, angles obtusely rounded	subtriangular, angles obtusely rounded	variable	narrowly oblong to subtriangular, angles variable	variable	sub-triangular, angles variable	narrowly oblong to subtriangular, angles variable	sub-triangular, angles obtusely rounded
Discal setae	present	present	present or absent	present	present or absent	present	present	present or absent
Profibial dentition	bidentate	bidentate	unidentate, bidentate or tridentate	bidentate to tridentate	unidentate, bidentate or tridentate	bidentate	bidentate to tridentate	bidentate or tridentate to tridentate

