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David C. Robacker
South Texas College, dcrobacker@gmail.com

David C. Hawks
University of California - Riverside, hawkscdc@gmail.com

Naidely Castillo
South Texas College

Brianna Miranda
South Texas College

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David C. Robacker

Department of Biology
South Texas College
Weslaco, TX 78596 U.S.A.
dcrobacker@gmail.com

David C. Hawks

Department of Entomology
University of California
Riverside, CA 92521 U.S.A.
hawksc@gmail.com

Naidely Castillo

South Texas College
Weslaco, TX 78596 U.S.A.

Brianna Miranda

South Texas College
Weslaco, TX 78596 U.S.A.

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A new species of *Chrysina* Kirby (Coleoptera: Scarabaeidae: Rutelinae) from the Sierra Madre Occidental of Mexico, with notes on the type locality of *Chrysina adelaida* (Hope, 1841)

David C. Robacker

Department of Biology
South Texas College
Weslaco, TX 78596 U.S.A.
dcrobacker@gmail.com

David C. Hawks

Department of Entomology
University of California
Riverside, CA 92521 U.S.A.
hawksc@gmail.com

Naidely Castillo

South Texas College
Weslaco, TX 78596 U.S.A.

Brianna Miranda

South Texas College
Weslaco, TX 78596 U.S.A.

Abstract. The approximate type locality of *Chrysina adelaida* (Hope, 1841) (Coleoptera: Scarabaeidae: Rutelinae) is fixed in the mountains of southeastern Mexico. *Chrysina occidentalis* Robacker and Hawks is described as a **new species** from the Sierra Madre Occidental in northwestern Mexico based on morphometric comparisons of adults and genital capsules with those of *C. adelaida* from southeastern Mexico and with those of *C. adelaida* (of authors) from neighboring states south of the Sierra Madre Occidental.

Key words. Rutelini, micromorphometric analysis of genitalia, statistical analyses, diagnosing cryptic species.

Resumen. La localidad tipo aproximada de *Chrysina adelaida* (Hope, 1841) (Coleoptera: Scarabaeidae: Rutelinae) se fija en las montañas del sureste de México. *Chrysina occidentalis* Robacker and Hawks se describe como una **nueva especie** de la Sierra Madre Occidental en el noroeste de México con base en comparaciones morfométricas de adultos y cápsulas genitales con las de *C. adelaida* del sureste de México y con las de *C. adelaida* (de los autores) de la vecina estados al sur de la Sierra Madre Occidental.

Palabras clave. Rutelini, análisis micromorfométrico de genitales, análisis estadísticos, diagnóstico de especies crípticas.

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Introduction

The genus *Chrysina* Kirby consists of about 130 species (Monzón-Sierra et al. 2020) ranging from the southwestern United States to Ecuador. Most species are green or metallic silver to gold in color. Conspicuous exceptions are species allied to *C. adelaida* (Hope) in which individuals have various combinations of green, red and white longitudinal stripes on the elytra which are predominately green (green forms) or predominantly red (red forms). Two species are currently recognized, *C. quetzalcoatli* Morón in eastern Chiapas, Guatemala and Honduras (Morón 1990) and *C. adelaida*. Based on distribution records, *C. adelaida* occurs widely in oak-pine forests in the mountains of Mexico (Morón 1990; Moore et al. 2017) where larvae reportedly feed on decaying pine wood

and adults feed on pine needles and oak leaves (Morón 1990). Large series reveal much variation both within and between populations throughout its distribution. To determine if this assemblage of populations is one variable species or a complex of species will require careful and detailed studies.

The objective of this research was to provide evidence that populations from northwestern Mexico represent a species that is distinct from *C. adelaida*. Our method was to demonstrate that these populations differ significantly from *C. adelaida* from the type locality and from *C. adelaida* (of authors) from neighboring states by employing quantitative comparisons of adult external morphology and male genital capsules. Based on these results, we describe the populations in northwestern Mexico as *Chrysina occidentalis* Robacker and Hawks **new species** and place it in the *adelaida* group (sensu Hawks 2001).

Materials and Methods

Determination of type localities of *C. adelaida* and its synonyms. *Pelidnota adelaida* Hope, 1841 was described from Mexico with no further indication of locality (Hope 1841). The species was moved to *Plusiotis* by Burmeister (1844), then to *Chrysina* when Hawks (2001) placed *Plusiotis* as a junior synonym of *Chrysina*. Similarly, *Pelidnota ornatissima* Sturm, 1843 was also described from Mexico with no further indication of locality (Sturm 1843) and later reported from Guatemala (Bates 1888). This taxon was also placed in synonymy with *C. adelaida* (Burmeister 1844; Hawks 2001), although the Guatemalan specimens to which Bates referred undoubtedly represent *C. quetzalcoatl*. Finally, *Plusiotis adelaida pavonacea* Casey, 1915 was described from specimens from Guerrero and later placed in *Chrysina* by Hawks (2001), then placed in synonymy with *C. adelaida* by Moore et al. (2017).

Fixation of the approximate type locality of *C. adelaida* is desirable for two reasons: 1) to ensure that specimens from northwestern Mexico are not topotypical *C. adelaida*; and 2) to compare the northwestern-Mexico population with specimens from the type locality of *C. adelaida*. It was also necessary to determine that *C. ornatissima* was not from northwestern Mexico so we could be confident our study specimens were not applicable to *C. ornatissima*.

To determine the type locality of *C. adelaida*, we acquired photos of the female holotype from the Oxford University Museum of Natural History. For *C. ornatissima* we used the drawing of the dorsum included in the original description (Sturm 1843). Images of both taxa were compared with *C. adelaida* (of authors) specimens from widely distributed localities in Mexico. Further, the length/width ratio was calculated from the dorsal photo of the *P. adelaida* holotype and compared with ratios of specimens from other populations.

Study specimens. Specimens are from the collections of David C. Robacker, David C. Hawks and William C. Warfield. Holotype deposition is provided in the description, and paratypes have been or will be deposited in several public and private collections when appropriate. Type depositories include the following institutions:

- American Museum of Natural History, New York, NY, USA (AMNH)
- California Academy of Sciences, San Francisco, CA, USA (CASC)
- National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM)
- Universidad Nacional Autónoma de México, Colección Nacional de Insectos, Mexico City, Mexico (UNAM)
- University of Nebraska State Museum, Lincoln, NE, USA (UNSM)

Collection localities of specimens used in this work are shown in Figure 1. The map shows one site in Chihuahua and two sites in Sinaloa (represented as one red square) where the study specimens of *C. occidentalis* were collected. Additional specimens designated as *C. occidentalis* were collected at two additional sites in Durango (red square east of the Sinaloa sites). Also shown are two sites near the probable type locality in Veracruz where the study specimens of *C. adelaida* were collected (yellow triangles), and numerous other sites where other specimens of *C. adelaida* (of authors) used for less rigorous comparisons were collected (blue circles).

Quantitative measurements. Length, width and thickness (dorsoventral axis) of adults were measured using a CEN-TECH™ Electronic Digital Caliper (Harbor Freight Tools, Camarillo, CA). Repeated measurements of the same adult specimen indicated that measurement error was ± 0.2 mm. All other quantitative measurements were made using a Leica EZ 4W stereo dissecting microscope (Leica Microsystems (Schweiz) AG, Heerbrugg, Switzerland) set to 8 \times nominal magnification. The microscope was equipped with a built-in Leica HD camera

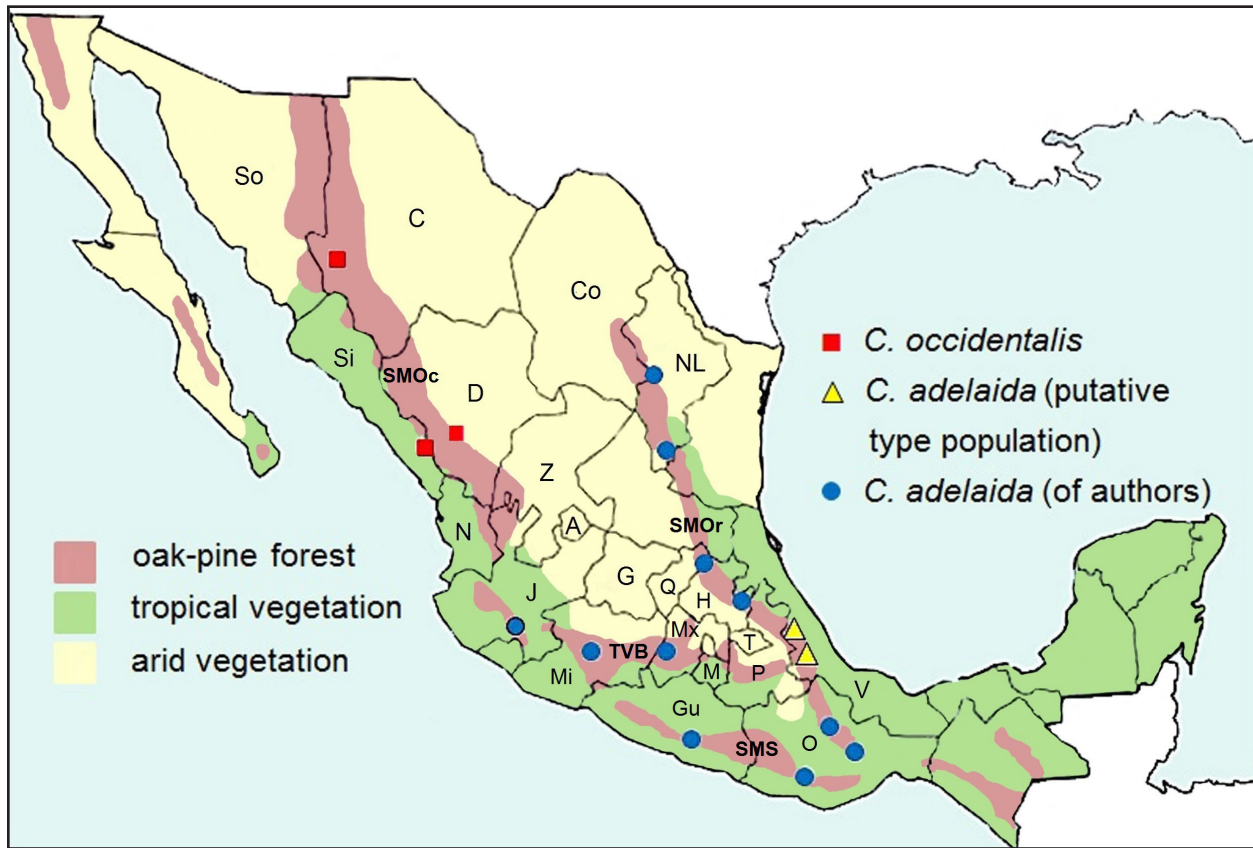


Figure 1. Locations in Mexico of montane oak-pine forests (modified from Guzmán 2008) and of *Chrysina* populations studied in this work. Mountain ranges: SMOc Sierra Madre Occidental, TVB Trans Volcanic Belt, SMOr Sierra Madre Oriental, SMS Sierra Madre del Sur. States discussed in the text: A Aguascalientes, C Chihuahua, Co Coahuila, D Durango, G Guanajuato, Gu Guerrero, H Hidalgo, J Jalisco, Mx Estado de México, Mi Michoacán, M Morelos, N Nayarit, NL Nuevo León, O Oaxaca, P Puebla, Q Querétaro, Si Sinaloa, So Sonora, T Tlaxcala, V Veracruz, Z Zacatecas.

system. The method was to photograph specimens, print the images on paper and measure the structures on the photographs with a plastic ruler. Actual sizes of measured structures were calculated by dividing the ruler measurements on photographs by the observed magnification of 22.2 for the 8× nominal values. These photographic methods result in relatively large errors in sizes of structures (± 0.20 mm) but small errors of size differences between structures (± 0.01 mm), allowing for reliable statistical analyses of size differences. Measurement procedures and discussion of error are described in detail by Robacker et al. (2020).

Parameres curvature. Curvature of the parameres was quantified from photographs of capsules in lateral aspect. Viewed in lateral aspect, parameres generally extend straight out from the base, bend ventrally, and then extend straight to the apex. Curvature was represented by the angle created by two straight lines that intersect between the base and the apex. The first line originated at the base of the parameres and extended distally on the dorsal surface of the parameres, exiting from the parameres where they begin to bend ventrally. The second line originated at the apex of the parameres and extended proximally on the dorsal surface, exiting where they begin to bend toward the base. The angle was measured with a protractor. This procedure was used previously by Robacker et al. (2020).

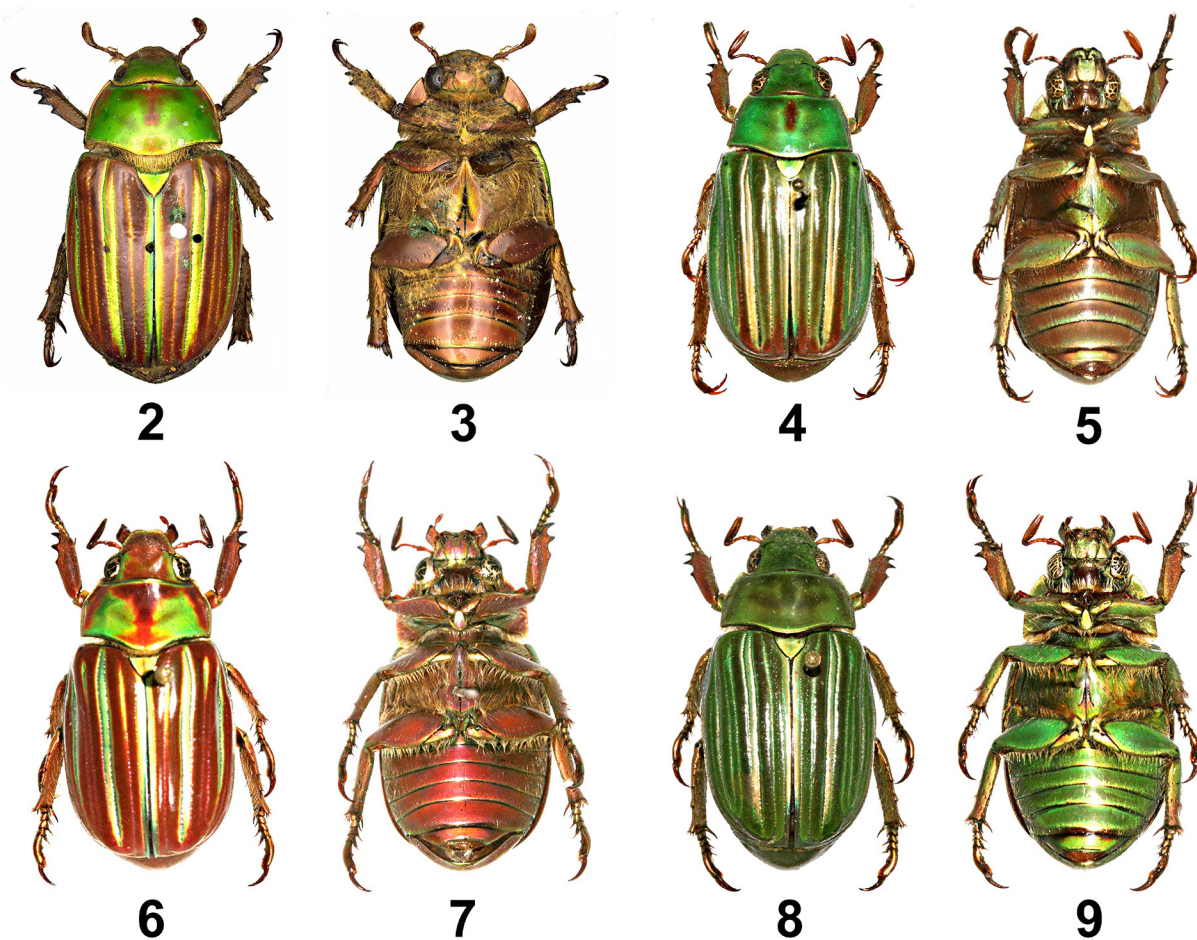
Adult color. Amount of reddish coloration (hereafter red) on the elytra, location of red on the elytra and amount of red on the pronotum were visually quantified. Amount of red on elytra was quantified to the nearest 10% for each specimen. Location of red on elytra was scored as uniformly distributed or distributed mostly on the

posterior half. Amount of red on the pronotum was scored as small (less than 10% of the area) or large (greater than 30%). These assessments were conducted using all study specimens from northwestern Mexico but only red-form specimens from Veracruz. In addition, visual qualitative assessments of color of pygidia, sternites and femora were conducted by comparing study specimens from northwestern Mexico with both red and green forms of specimens from Veracruz.

Statistical analyses. Student's *t*-tests and single-factor (one-way) analyses of variance were conducted to compare quantitative measurements of populations from various regions of Mexico using Microsoft Excel 2010 (Microsoft Corporation, Redmond, WA, USA). Chi-square tests for independence of categories in 2×2 contingency tables, with Yates continuity correction, were conducted to analyze qualitative measurements using GraphPad Quick-Calcs (Motulsky 2018).

Results

Type localities of *C. adelaida* and its synonyms. The type locality of *C. adelaida* within Mexico is unknown. Populations from southeastern, central, and southwestern Mexico including states of Hidalgo, Veracruz (Fig. 6–7), Oaxaca, Estado de Mexico, Morelos, Guerrero, Michoacán and Jalisco contain red-form individuals that closely match the dorsal and ventral images of the holotype of *P. adelaida* (Fig. 2–3). Similarities include colors and patterns on the elytra, pronotum, frons, clypeus, pygidium, sternites and femora. Populations (specimens



Figures 2–9. Dorsal and ventral habitus of adult *Chrysin* specimens. 2–3) *P. adelaida* holotype female (courtesy of Oxford University Museum of Natural History). 4–5) *C. occidentalis* holotype. 6–7) *C. adelaida* red-form from Veracruz, Mexico. 8–9) *C. adelaida* green-form from Veracruz, Mexico.

available to us) from Nuevo León and Querétaro in the northern Sierra Madre Oriental and from Chihuahua, Sinaloa, and Durango in the Sierra Madre Occidental of northwestern Mexico (Fig. 4–5) do not include red-form individuals that look similar to the holotype.

Ratio of adult length to width, measured from the dorsal image of the female *P. adelaida* holotype, was 1.91. Eastern Mexico populations from states including Nuevo León, Hidalgo, Veracruz, Oaxaca, Estado de Mexico, Morelos and Guerrero have a mean length to width ratio of 1.99 ± 0.058 SD. The holotype value of 1.91 falls within the range (1.85–2.16) of these eastern Mexico specimens ($n = 46$). Western Mexico populations from states including Chihuahua, Sinaloa, Durango, Jalisco, and Michoacán have a mean ratio of 2.07 ± 0.057 SD. The holotype does not fall within the range (1.98–2.19) of western Mexico specimens ($n = 47$). Note in Tables 1 and 2 that length to width ratios are the same for males and females.

The analyses above provide strong evidence that the holotype of *P. adelaida* comes from one of the southeastern or southcentral Mexican states. Historical records show that much commerce and insect collecting in Mexico between 1830 and 1840 took place on the main road between the port of Veracruz and Mexico City (Barber 1928). This suggests that the holotype is not from Guerrero which is located far from the old road but is more likely from Veracruz, Hidalgo, northern Oaxaca, Puebla, Tlaxcala, Estado de Mexico or Morelos inasmuch as the road passed through or near these states.

Further evidence concerning the origin of the *P. adelaida* holotype can be gleaned from Hope's (1841) original description. The publication included the original description of *C. victorina* (Hope, 1841) and a supplementary description of *C. auripes* (Gray, 1832). Both of these species occur in northern Oaxaca in cloud forest habitats not far from oak-pine habitat of *C. adelaida* (DCR personal observation) and neither of them occur in states to the west. The oak-pine forest in this region of Oaxaca is contiguous with the oak-pine forests of Veracruz (Fig. 1). Recently, *C. victorina* has also been reported in southeastern Veracruz (Mora-Aguilar et al. 2018), again not far from habitats with *C. adelaida* including some of the specimens studied herein. There are indications that Hope may have acquired the three species together in a collection of Coleoptera from Mexico (Hope 1841: 145). This indication does not mean the three species were collected at the same locality but suggests the possibility that the three species were collected by the same person who may have worked in a particular region of Mexico. Our discussion in this section indicates that the likely type locality of *C. adelaida* is near the old road between the city of Veracruz and Mexico City, probably in the oak-pine forests of the southern Sierra Madre Oriental. This evidence supports our use of specimens from Veracruz as representing nominate *C. adelaida*.

A drawing of the dorsal habitus of *P. ornatissima* in Sturm (1843) is quite similar to the appearance of the holotype of *P. adelaida* (Fig. 2) and red-form individuals from southeastern Mexico (Fig. 6). It is not similar in appearance to specimens from the Sierra Madre Occidental of northwestern Mexico (Fig. 4). Sturm states in his description that the whole underside of the body, antennae, and legs are copper-red. Thus, the underside is also similar to the *P. adelaida* holotype (Fig. 3), red-form individuals from southeastern Mexico (Fig. 7), and similar but not identical to specimens from northwestern Mexico (Fig. 5). Sturm's measurements indicate that the length to width ratio of the holotype is 1.9. This is also similar to the *P. adelaida* holotype and specimens from eastern Mexico. Using the same arguments regarding collecting activity during the early 19th century that we used for *C. adelaida*, the type locality of *C. ornatissima* is also most likely southeastern Mexico. We conclude that placement of *C. ornatissima* as a junior synonym of *C. adelaida* (Burmeister 1844; Hawks 2001) is correct and that the type locality of *C. ornatissima* is not northwestern Mexico.

Comparison of populations from Chihuahua and Sinaloa with populations from Veracruz. For ease of presentation of the results, we refer to the study specimens from Chihuahua and Sinaloa as *C. occidentalis*, and to the study specimens from Veracruz as *C. adelaida*.

C. occidentalis adults differ in appearance from both red-form and green-form *C. adelaida*. *C. occidentalis* adults appear mostly green but all of them have some red on the elytra, mostly posteriorly (Fig. 4). They all have a small red longitudinal stripe on the pronotum, red pygidium, mostly red sternites, and meso- and metafemora variable but never completely green (Fig. 4–5). Red-form *C. adelaida* have much more red on the elytra and it is evenly distributed anterior to posterior (Fig. 2, 6). They have red markings on the pronotum that are usually larger and of various shapes, red pygidium, red sternites and red meso- and metafemora (Fig. 2–3, 6–7). Green-form *C. adelaida* are completely green except for red on the tibia and tarsi and brownish coloration on the pronotum (Fig.

8–9). Tables 1 and 2 (mean % of red on elytra) and Table 3 detail the differences between *C. occidentalis*, and red and green forms of *C. adelaida* for these characters.

Adult males and females of *C. occidentalis* are generally longer relative to their width, and dorso-ventrally thinner, than *C. adelaida* (Tables 1–2). Interocular distance and antennal club length did not differ between the species.

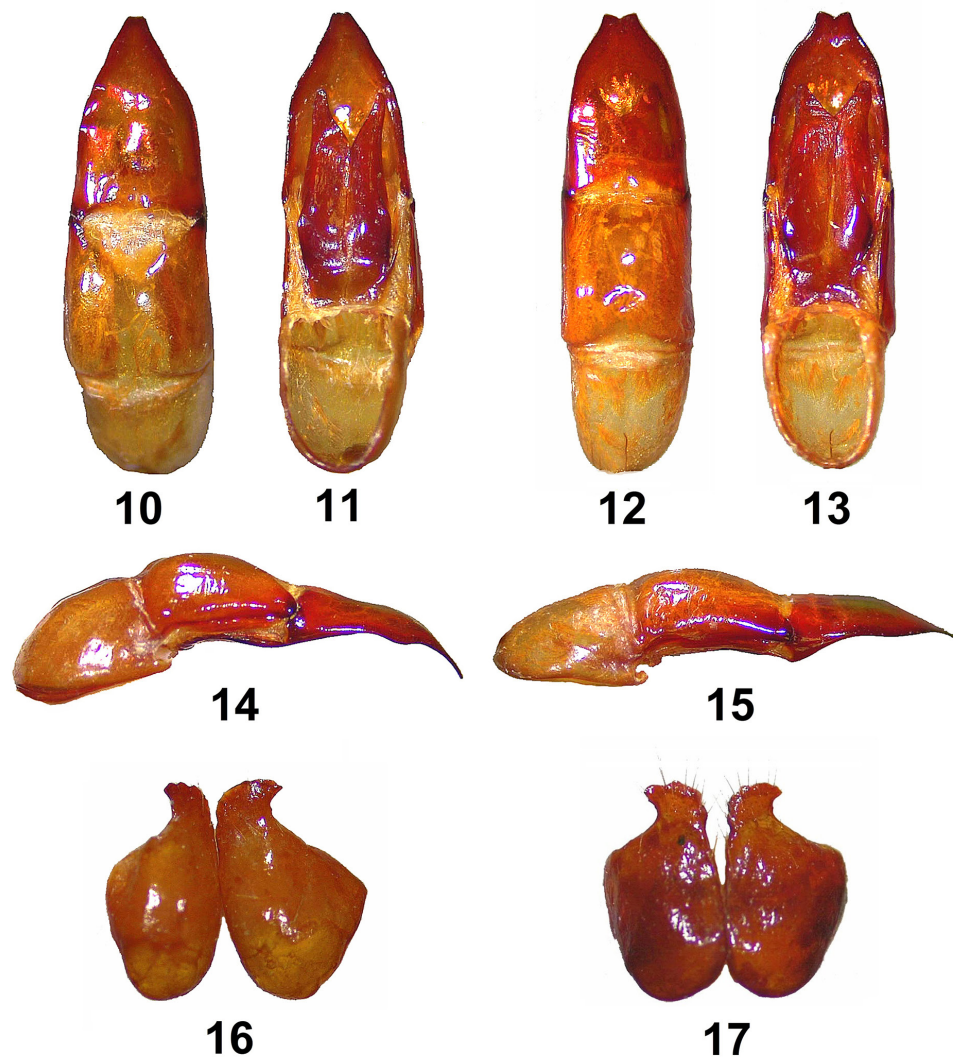
Parameres of male genital capsules of *C. occidentalis* (Fig. 10–11) are narrower, especially toward the apices, than those of *C. adelaida* (Fig. 12–13) (Table 4). Parameres of *C. occidentalis* were not narrower at their widest

Table 1. Adult measurements: males. Data entries are means of measurements. Statistical significance of *t*-tests indicated in last column. Number of specimens examined: *C. occidentalis* 12, *C. adelaida* 10 (except color analysis 4). Significance levels of *t* values: ns, no significant difference at the 5% level; **P* < 0.05; ***P* < 0.01; *****P* < 0.0001.

Measurement	<i>C. occidentalis</i>	<i>C. adelaida</i>	<i>t</i>
mean % of red on elytra	16.7	75	9.6****
length (L) (mm)	26.9	27.0	0.2 ns
maximum width (W) (mm)	13.0	13.6	2.5*
thickness (T) (mm)	9.0	9.5	3.0**
L/W	2.07	1.99	3.2**
L/T	2.99	2.85	3.5**
W/T	1.45	1.43	0.8 ns
maximum pronotum width (P) (mm)	10.1	10.5	2.1*
interocular distance (I) (mm)	3.9	4.1	1.8 ns
P/I	2.56	2.59	0.9 ns
antennal club length (A) (mm)	2.80	2.85	0.8 ns
A/I	0.71	0.70	0.7 ns

Table 2. Adult measurements: females. Data entries are means of measurements. Statistical significance of *t*-tests indicated in last column. Number of specimens examined: *C. occidentalis* 8, *C. adelaida* 8 (except color analysis 3). Significance levels of *t* values: ns, no significant difference at the 5% level; ****P* < 0.001; *****P* < 0.0001.

Measurement	<i>C. occidentalis</i>	<i>C. adelaida</i>	<i>t</i>
mean % of red on elytra	16.2	80.0	14.4****
length (L) (mm)	29.4	29.1	0.3 ns
maximum width (W) (mm)	14.2	14.8	1.4 ns
thickness (T) (mm)	9.8	10.3	1.5 ns
L/W	2.06	1.97	4.2***
L/T	3.00	2.83	4.1***
W/T	1.46	1.43	0.8 ns
maximum pronotum width (P) (mm)	10.9	11.2	0.9 ns
interocular distance (I) (mm)	4.3	4.3	0.4 ns
P/I	2.53	2.58	1.2 ns
antennal club length (A) (mm)	2.49	2.49	0.0 ns
A/I	0.58	0.57	0.5 ns



Figures 10–17. *Chrysina* spp. genital structures. 10–15) Male genital capsule dorsal (d), ventral (v) and lateral (l) habitus. 10–11) *C. occidentalis* holotype. 10) (d). 11) (v). 12–13) *C. adelaida* from Veracruz, Mexico. 12) (d). 13) (v). 14) *C. occidentalis* holotype (l). 15) *C. adelaida* from Veracruz, Mexico (l). 16–17) Female genital plates. 16) *C. occidentalis* from Sinaloa, Mexico. 17) *C. adelaida* from Veracruz, Mexico.

point near their base. Thus the tapering of the parameres from base to apex is different in the two species. Parameres of *C. occidentalis* (Fig. 14) are more curved ventrally than those of *C. adelaida* (Fig. 15) (Table 4). There was no overlap in the ranges of curvature measurements for *C. occidentalis* (range 38.5–59.5°) and *C. adelaida* (24.0–37.0°).

Comparisons of populations from Chihuahua and Sinaloa with populations from Durango. We refer to specimens from Chihuahua and Sinaloa as *C. occidentalis*. Three male and three female specimens were collected in Durango (Fig. 1). These specimens have the same appearance and length/width ratio (mean 2.06) as *C. occidentalis*. Two males have the same widths of parameres at the apex (0.46, 0.38 mm) and the same parameres curvature (40°, 50°) as *C. occidentalis*, while the third was missing its genital capsule. We conclude that these specimens and probably other populations in Durango represent *C. occidentalis*.

Table 3. Adult appearance: males and females combined. Data entries are proportions of study specimens exhibiting a particular character vs an alternate character. Significance levels of χ^2 values: ns, no significant difference; or $P < 0.001$.

Measurement	<i>C. occidentalis</i>	<i>C. adelaida</i> red form	<i>C. adelaida</i> green form	χ^2
small red stripe on pronotum vs larger red markings	20/20	0/7	na	22
small red stripe on pronotum vs brown markings	20/20	na	0/11	27
red on elytra mostly posterior vs evenly distributed	18/20	0/7	na	15
red vs green pygidium	20/20	7/7	na	ns
red vs green pygidium	20/20	na	0/11	27
sternites mostly red vs completely green	20/20	7/7	na	ns
sternites mostly red vs completely green	20/20	na	0/11	27

Table 4. Male capsule measurements. Data entries are means (n) of measurements. Significance levels of t values: ns, no significant difference at the 5% level; ** $P < 0.01$; **** $P < 0.0001$.

Measurement	<i>C. occidentalis</i>	<i>C. adelaida</i>	t
capsule length (L) (mm)	10.3 (10)	10.1 (9)	1.8 ns
parameres L (mm)	4.2 (10)	4.0 (10)	1.9 ns
parameres maximum width (W) (mm)	2.7 (10)	2.8 (10)	0.9 ns
parameres W at ventral plates apices (mm)	1.8 (10)	2.0 (10)	2.9**
parameres W at apices (mm)	0.42 (7)	0.56 (10)	3.9**
parameres curvature angle (degrees)	47.2 (10)	30.6 (10)	6.5****

Populations from neighboring states. Specimens of *C. adelaida* (of authors) have not been reported from Sonora to the west of Chihuahua, Nayarit to the south of Sinaloa, or Aguascalientes, Guanajuato, or Zacatecas to the southeast of Durango. Populations probably do not occur in the Chihuahuan desert of eastern Chihuahua and western Coahuila. Records from Coahuila probably pertain to the southeastern region where the Sierra Madre Oriental intersects. Populations with the closest proximity to the Sierra Madre Occidental are found in Michoacán and Jalisco which are addressed in the next section.

Comparison of populations from Chihuahua and Sinaloa with populations from Jalisco and Michoacán.

We refer to specimens from Chihuahua and Sinaloa as *C. occidentalis*. Collection sites of specimens from Jalisco and Michoacán are shown in Fig. 1 (two blue circles, each circle representing 2–3 collecting sites). We chose to compare several key characters from our comparisons with *C. adelaida* from the type locality: adult appearance, adult length/width ratio, width of parameres apex, and parameres downward curvature.

Appearance of adults from Jalisco and Michoacán is not similar to *C. occidentalis*. Adults have green and red color forms. Green-form adults are nearly identical to green-form adults of *C. adelaida* from the type locality in Veracruz. They do not have red on the elytra, pronotum, sternites, pygidium or femora as described for *C. occidentalis*. Red-form adults are also similar to *C. adelaida* (type locality) but with smaller red markings on the

pronotum. They differ from *C. occidentalis* in having much more red on the elytra and in having the red evenly distributed on the elytra.

Comparisons of morphological characters are shown in Table 5. Specimens from Jalisco and Michoacán have nearly identical length/width ratios, numerically larger but not significantly different widths of parameres at the apex, and significantly less downward curvature of the parameres compared with *C. occidentalis*. As with the comparisons of *C. occidentalis* and *C. adelaida* from the type locality (previous section), there was no overlap in the ranges of curvature measurements for *C. occidentalis* (range 38.5–59.5°) and *C. adelaida* from Jalisco and Michoacán (22–33°). Based on adult appearance and parameres curvature, these data indicate that specimens from Jalisco and Michoacán are not *C. occidentalis*. These specimens are similar in most respects to topotypical *C. adelaida*, and we currently refer to them as *C. adelaida* (of authors) pending further study.

Clinal morphological change between Veracruz and northwestern Mexico. Results from the previous sections show that specimens from Chihuahua and Sinaloa in northwestern Mexico differ from *C. adelaida* from Veracruz (type locality) and from *C. adelaida* (of authors) from Jalisco and Michoacán in various characters. This section investigates whether these differences vary as a continuous cline or discontinuous stepped cline from Veracruz across the Trans Volcanic Belt to Jalisco and Michoacán and northward into Sinaloa and Chihuahua in the Sierra Madre Occidental (Fig. 1).

Table 5 shows the three characters that were investigated. Adult length/width ratio was the same for northwestern Mexico and the western states of Jalisco and Michoacán but significantly smaller for Veracruz in eastern Mexico. The clinal nature of this character is uninformative for our purposes. Width of parameres at the apex decreases from Veracruz to Jalisco and Michoacán and decreases further in northwestern Mexico. This is consistent with a continuous cline suggesting the possibility of gene flow across Mexico. Curvature of the parameres was constant from Veracruz to Jalisco and Michoacán, but increased abruptly from Jalisco and Michoacán to northwestern Mexico. As stated previously, the data ranges for the two regions did not overlap. This discontinuous stepped clinal pattern indicates gene flow was not occurring between the populations in the two regions.

In addition to the quantitative characters in Table 5, appearance of the adults also fits a discontinuous stepped cline as indicated in the previous section. Appearance of adults changed little from Veracruz to Jalisco and Michoacán, but changed abruptly from Jalisco and Michoacán to northwestern Mexico. Again, this indicates no gene flow between the two regions.

Speciation in *C. adelaida* populations. The fact that *C. adelaida* has not been divided into several species may be more a product of bias than reality. In this section we challenge this bias by reviewing speciation in other taxa in the Mexican highlands, widely regarded as biodiversity hotspots (Mittermeier et al. 2005; González-Elizondo et al. 2013) due to prolific speciation between adjacent mountain ranges.

Howden (1966) stated that most of the North American genera of Scarabaeidae were established by at least the Miocene. It seems reasonable to assume that the origin of *Chrysina* falls in this time frame. As such, ongoing orogenesis (Ferrusquia-Villafranca et al 2005), radiation of *Pinus* (Rundel 2019), and climatic cycling during the Neogene and Pleistocene (Baker 2008) probably all played roles in distribution, vicariance and possibly speciation

Table 5. Comparisons of *C. adelaida* (of authors) from Jalisco and Michoacán with *C. adelaida* from Veracruz and *C. occidentalis*. Data entries are means (*n*) of measurements. Means in the same row followed by the same letter are not significantly different from each other by Fisher's Protected LSD ($P < 0.05$). *F* values and statistical significance of *F* tests are indicated in the last column: ** $P < 0.01$; **** $P < 0.0001$.

Measurement	<i>C. occidentalis</i>	<i>C. adelaida</i> Jalisco	<i>C. adelaida</i> Michoacán	<i>C. adelaida</i> Veracruz	<i>F</i>
adult length/width ratio	2.07 (20) b	2.08 (11) b	2.08 (10) b	1.98 (18) a	10****
parameres W at apices (mm)	0.42 (7) a	0.50 (8) ab	0.51 (6) ab	0.56 (10) b	5.6**
parameres curvature angle (degrees)	47.2 (10) b	26.8 (8) a	28.2 (7) a	30.6 (10) a	34****

of *C. adelaida*. In fact, numerous studies have implicated events of the late Neogene, including orogenesis of the Trans Volcanic Belt, as agents of speciation (Mulcahy and Mendelson 2000; Hulseley et al. 2004; McCormack et al. 2008; Bryson et al 2011; Rundel 2019).

A molecular study of rattlesnakes in the *Crotalus intermedius* species complex (Viperidae) is particularly relevant because the snakes' habitat is oak-pine forest above 1900 m (Bryson et al. 2011), almost cohabiting with *C. adelaida* in much of Mexico. The work showed that speciation of these snakes probably occurred during the late Miocene through the Pliocene. The first speciation event initiated from a population split between the southern Sierra Madre Occidental and the Trans Volcanic Belt. Two additional speciations followed in the Trans Volcanic Belt and in the southern Sierra Madre Oriental resulting in four species now recognized in Mexico. Orogenesis of the Trans Volcanic Belt was cited as the likely agent of speciation. The data also show that the distribution of the snakes into the northern Sierra Madre Oriental and the Sierra Madre del Sur probably occurred during glacial periods of the Pleistocene when the oak-pine forests moved downslope forming connections among several of the mountain ranges. According to Bryson et al. (2011), *Crotalus* populations on the four mountain ranges currently are not in contact due to intervening xeric habitat that isolates the populations on each range.

Based on speciation rates of other taxa in the Mexican highlands during the late Cenozoic, it seems likely that the same forces would have been acting on *C. adelaida*.

Reproductive isolation between neighboring states. We showed previously a lack of gene flow between populations from the Sierra Madre Occidental in northwestern Mexico and populations in Jalisco and Michoacán. However, lack of gene flow could be due to geographic isolation rather than reproductive isolation. Reproductive isolating mechanisms usually develop when sibling species resulting from geographic isolation come back into contact. If speciation did occur during the Neogene, then those sibling species probably were brought back into contact during the glacial periods of the Pleistocene, perhaps as recently as the last glacial maximum about 20,000 years ago when oak-pine forests connected the Sierra Madre Occidental and the Trans Volcanic Belt (Bryson et al. 2011). Without reproductive isolation, homogenization of adult appearance and parameres curvature would be expected. This did not occur. Current populations exhibit distinctly different adult appearance and non-overlapping ranges of parameres curvature suggesting development of reproductive isolating mechanisms. This indicates that populations in northwestern Mexico are reproductively isolated from populations in Jalisco and Michoacán.

Conclusion

The Hennigian species concept defines species as “reproductively isolated natural populations or groups of natural populations” (Meier and Willmann 2000). Characteristics of individuals and populations delineate species boundaries but do not define species.

In previous sections, we showed that our study specimens from northwestern Mexico: 1. differed significantly from specimens from the probable type locality in Veracruz in adult appearance and morphology and perhaps most importantly in genital capsule morphology, and 2. differed abruptly from specimens from neighboring states of Jalisco and Michoacán in appearance and capsule morphology. We also reviewed evidence that animals living in oak-pine forests of Mexico's mountains underwent speciation during the Neogene and proposed that *C. adelaida* would likely have undergone similar speciation events. Finally, we provided evidence that *C. adelaida* (of authors) populations in northwestern Mexico are reproductively isolated from their neighbors in Jalisco and Michoacán.

We conclude that the populations in northwestern Mexico represent an undescribed species and propose to elevate these populations to new species status as *C. occidentalis*.

Chrysina occidentalis Robacker and Hawks, new species

Figures 4–5, 10–11, 14, 16

Type data. Holotype ♂ (deposited at UNAM) labeled: a) “México: Sinaloa / El Palmito, elev. 7140' / N 23° 35.116, W 105° 51.863 / 16 August 2007 / D. C. Robacker”; b) “Sin 7”; c) on red paper, “*Chrysina occidentalis* ♂ / Robacker & Hawks, 2022 / HOLOTYPE”. Paratype (1 ♂) labeled: a) as holotype; b) “Sin 9”. Paratypes (2 ♂, 1 ♀) labeled: a) “México: Sinaloa / El Palmito logging road / elev. 6690' / 14–22 July, 2007 / D. C. Robacker”; b) males “Sin 8” or “Sin 10”. Paratypes (3 ♂, 3 ♀) labeled: a) handwritten “Mex: Sinaloa / Loberas / VI 1983”; b) males “Sin 1” or “Sin

2” or “Sin 6”, females “Sin 12” or “Sin 15” or “Sin 17”. Paratype (1 ♂) labeled: a) handwritten “Loberas / 12 July 86 / #1”; b) “Sin 4”. Paratype (1 ♀) labeled: a) as previous except “6. July 86 / #2”; b) “Sin 13”. Paratype (1 ♀) labeled: a) as previous except “#3”; b) “Sin 14”. Paratype (1 ♂) labeled: a) handwritten “Mex. Sinaloa / Mpio. Concordia / Loberas, 1975 m / 12 July 86 / E. Welling”; b) “Sin 3”. Paratype (1 ♂) labeled: a) handwritten “México: Sinaloa / Loberas / July 1994”; b) “Sin 11”. Paratypes (1 ♂, 1 ♀) labeled: a) handwritten “México, Sinaloa / Loberas / Aug 3 1983 / E. Giesbert, Coll.”; b) handwritten “*Plusiotis* / *adelaida* / det. E. Giesbert”; c) male “Sin 5”, female “Sin 16”. Paratypes (1 ♂, 1 ♀) labeled: a) “México: Chihuahua / Tomachic / elev. 2000 m / 11 August, 2004 / D. Robacker”; b) male “Chi 1”, female “Chi 12”. Paratype (1 ♀) labeled: a) “México: Chihuahua. / Basaseachic / dead on ground / 23. viii. 2001 A. K. Owen”; b) “Chi 11”. Paratype (1 ♂) labeled: a) “6 miles N. E. / El Salto, Dgo. Dist / Dgo. Mex. 8500 ft. / Aug. 10, 1947”; b) handwritten “AMNH”; c) “D. Rockefeller / Exp. Gertsch”; d) handwritten “*Plusiotis* / *adelaida* Hope / M. A. Morón, det. 1985”; e) “Dur 1”. Paratypes (2 ♂, 2 ♀) labeled: a) handwritten “Mex: Durango / Buenos Aires / July 1994”; b) males “Dur 2” or “Dur 3”. All paratypes (14 ♂, 11 ♀) labeled on yellow paper, “*Chrysinia occidentalis* ♂ or ♀ / Robacker and Hawks, 2022 / PARATYPE”.

Description, holotype male (Fig. 4–5). Length 27.2 mm, maximum width 13.4 mm, maximum dorso-ventro thickness 9.1 mm. Frons mottled light and dark green; clypeus dark green with lighter green toward margins, clypeus margins green and black; pronotum mottled light and dark green with central reddish brown shallow longitudinal depression, margins golden green. Scutellum green. Elytral inner margin black; elytra with 8 striae containing punctures and 9 interstriae with shallow punctures visible under magnification; elytral structure and color, from inner elytral margin outward, 1st interstria narrow and dull brown-green except marginal area cream colored, shallow cream stria, 2nd interstria narrow and brown-green becoming reddish brown at posterior end, deep black and cream stria, 3rd interstria wide and brown-green becoming reddish brown at posterior end, deep black and cream stria, 4th interstria narrow and cream, deep black and cream stria fusing anteriorly with previous stria, 5th interstria narrow and brown-green becoming reddish brown posterior 1/3 of length, shallow cream stria, 6th interstria narrow and bright green, shallow cream stria, 7th interstria narrow and bright green, deep golden-cream stria (appears black from above) inside meso-anterior depression, 8th interstria wide and bright green, shallow cream stria, 9th interstria wide and bright green becoming reddish brown at posterior end; epipleuron green, outer elytral margin golden posterior to epipleuron; calli not apparent. Last abdominal tergite, visible beyond the terminus of the elytra, golden. Pygidium cupreous with green and gold reflections laterally. Ocular canthi green; antennal scape light brown, remainder of antenna darker brown. Ventral thoracic surfaces mainly brown, prosternal plate light green, mesosternal process gold, medial areas of metasternum green. Abdominal sternites mostly reddish brown with green posterior edging. All femora with outer (ventral) surfaces green with a reddish brown streak extending along the anterior edge and another extending laterally in the disc; inner surfaces of profemora like the outer surface, inner surfaces of the meso- and metafemora mainly brown; posterior surfaces of all femora golden. Tibia colored about the same as femora. Tarsi metallic bronze with greenish reflections. Mentum, mandibles and labrum light green; mandibles with black anterior edging; stipes bronze and green.

Head. Form trapezoidal, about as wide as long. Frons with sparse fine punctures, becoming rugopunctate in an anterior semicircular depression and on the clypeus. Clypeus slightly convex, anteriorly reflexed, semitrapezoidal in dorsal view, slightly notched in center of anterior margin.

Anterior border of labrum emarginated and deeply notched at center. Mandibles symmetrical, anterior and medial edges straight and meeting at right angle, visible in dorsal view. Mentum nearly quadrate but rounded laterally, with a depression in the anterior half; surface rugose with lateral setae, anterior margin widely sinuate. Eye size large with ratio of width of pronotum at base to interocular distance 2.6. Ratio of interocular distance to antennal club length 1.4.

Thorax. Pronotum with a slight central anteroposterior depression in the anterior half, basal margin entire; punctures sparse and very fine (only visible under magnification). Mesosternal process rounded at apex and extending beyond mesofemoral base. Prosternal plate narrow and subtriangular, pointed anteriorly and rounded posteriorly. Epipleural fold terminating near metacoxae. Protibia tridentate. Venter mostly setigerously punctate, less on medial area of metasternum, femora and tibia.

Abdomen. Sternites with sparse setose punctures medially, becoming more abundant laterally; last abdominal tergite abundantly punctate with fine terminal setae. Pygidium surface rugose leathery proximally, rugose punctate distally with setae at margin. **Genitalia:** Genital capsule length 9.3 mm (linear measurement) or 10.3 mm (basal piece of capsule + phallobase + parameres). Parameres fused, almost symmetrical, but the right paramere (viewed dorsally) bulges laterally slightly at the tip of the ventral plates and bends downward slightly more than the left paramere. Parameres length 4.0 mm; maximum width 2.7 mm in dorsal view, parameres length/parameres maximum width ratio 1.5, parameres narrowing slightly during the first two thirds of their length then more abruptly during the final third to 0.37 mm at apices; slightly notched at apices; downward curvature of parameres from base to apex 40°. Ventral plates fused at their bases, splitting into two wide structures that narrow medially into pointed projections during the terminal quarter of their length.

Male variation. Color variation mostly in the amount of reddish-brown suffusion, especially on the elytra and femora; replacement of green with beige on the sternites; the amount of black in the deep striae; and replacement of gold with bronze or green on various structures such as the mesosternal process and the edges of the tibia. Variation in degree of punctation on the venter, the interstriae, and the pygidium, the pygidium sometimes completely rugose punctate; abundance of setae varying in proportion with punctation. Some specimens with protibia appearing bidentate.

Means of adult male measurements are shown in Table 1. Ranges in measurements of males ($n = 12$): length 24.9–28.5 mm, maximum width 12.0–13.5 mm, length/maximum width ratio 2.0–2.2, pronotum width 9.4–10.9 mm, interocular distance 3.7–4.2 mm, pronotum width/interocular distance ratio 2.4–2.8, antennal club length 2.6–3.0 mm, and interocular distance/antennal club length ratio 1.3–1.5.

Means of genital capsule measurements are shown in Table 4. Ranges in measurements of capsules: capsule length 9.5–10.9 mm ($n = 10$), parameres length 3.6–4.4 mm (10), parameres maximum width 2.6–2.9 mm (10), parameres length/parameres maximum width ratio 1.3–1.6 (10), parameres width at ventral plates apices 1.5–2.1 mm (10), parameres width at apices 0.37–0.46 mm (7), and parameres curvature 38.5–59.5° (10).

Female morphology and variation. Females similar to males in coloration and morphology. Females generally longer and wider than males but with smaller antennal club length.

Means of adult female measurements are shown in Table 2. Ranges in measurements of females ($n = 8$): length 26.6–31.3 mm, maximum width 13.1–15.2 mm, length/maximum width ratio 2.0–2.1, pronotum width 9.3–11.9 mm, interocular distance 3.8–4.6 mm, pronotum width/interocular distance ratio 2.4–2.6, antennal club length 2.3–2.7 mm, and interocular distance/antennal club length ratio 1.6–1.8.

Inferior genital plates are teardrop shaped with narrowed apices projecting laterally to a point. No consistent differences with *C. adelaida* were observed among the eight females of each species examined (Fig. 16–17).

Diagnosis. *Chrysina occidentalis* is distinguished from both red and green forms of *C. adelaida* by its narrower body shape (length/width range 1.98–2.19 vs 1.89–2.09 for *C. adelaida*), generally green color with red on the posterior of the elytra and small longitudinal red stripe on the pronotum (Fig. 4 vs Fig. 2, 6, 8 for *C. adelaida*), reddish pygidium and reddish brown sternites in combination with overall green coloration of the elytra (Fig. 4–5 vs Fig. 2–3, 6–9 for *C. adelaida*), green on the femora of most specimens in combination with reddish brown sternites (Fig. 5 vs Fig. 3, 7, 9 for *C. adelaida*), narrower parameres especially at the apices (Fig. 10–11 vs Fig. 12–13 for *C. adelaida*; parameres width at apices range 0.37–0.46 mm vs 0.44–0.73 mm for *C. adelaida*), and parameres more strongly curved ventrally (Fig. 14 vs Fig. 15 for *C. adelaida*; curvature angle range 38.5–59.5° vs 24.0–37.0° for *C. adelaida*).

Distribution of *C. occidentalis*. Populations we studied from the Sierra Madre Occidental in the states of Chihuahua, Sinaloa, and Durango represent *C. occidentalis*. Populations from Jalisco and Michoacán, located in the Trans Volcanic Belt, match neither *C. occidentalis* nor *C. adelaida*. Pending further study, we refer to these as *C. adelaida* (of authors). These populations likely are isolated from *C. occidentalis* by lowland tropical forest or xeric shrublands (Fig. 1). We know of no specimens of *C. occidentalis* or *C. adelaida* (of authors) from Sonora, eastern Chihuahua, eastern Durango, western Coahuila, Zacatecas, Aguascalientes, or Guanajuato. *Chrysina occidentalis* would be expected in Sonora, western Zacatecas, northern Jalisco, and eastern Nayarit where oak-pine forests occur. McCormack et al. (2008) stated that populations of Mexican jays in the Transvolcanic Belt are geographically isolated from populations to the north by the Aguascalientes Graben and the Bajío Depression. Also, the

Chihuahuan desert covers much of Chihuahua and Coahuila, and some of eastern Durango. As such, populations of neither *C. occidentalis* nor *C. adelaida* (of authors) would be expected in eastern Chihuahua, western Coahuila, eastern Durango, eastern Zacatecas, Aguascalientes, or Guanajuato.

Etymology. This new species is named for its home in the Sierra Madre Occidental in western Mexico.

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