On the identity of the adventive species of *Eufriesea* Cockerell in the USA: systematics and potential distribution of the *coerulescens* species group (Hymenoptera, Apidae)

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Academic editor: M. Ohl | Received 10 February 2017 | Accepted 8 March 2017 | Published 28 April 2017


Abstract

In the summer of 2010, two male specimens of the neotropical orchid bee genus *Eufriesea* Cockerell were collected in the Guadalupe Mountains of western Texas and southeastern New Mexico, USA. We tentatively identified them as *E. coerulescens* (Lepeletier de Saint Fargeau) because of the uncertainty surrounding the limits of this taxon and hypothesized that they were members of a persistent bee population, rather than long-distance transient vagrants. The goals of this paper are to clarify the identity of these specimens, assess the species limits of *E. coerulescens*, and to evaluate suitability of habitats in the USA for this adventive species. Herein, we revise the species in the *coerulescens* group using morphological features of both sexes and confirm that the specimens of *Eufriesea* from the USA are *E. coerulescens*. We recognize the following six species in the *coerulescens* group: *E. coerulescens*, *E. micheneri* Ayala & Engel, *E. simillima* (Moure & Michener), which is reinstated from synonym with *E. coerulescens*, and three new species from Mexico (*E. barthelli* Gonzalez & Griswold, **sp. n.**, *E. engeli* Gonzalez & Griswold, **sp. n.**, and *E. oliveri* Gonzalez & Griswold, **sp. n.**). To facilitate the identification of these taxa, we present a fully illustrated account of the species, comparative diagnoses, descriptions, and an updated key to all Mexican species of *Eufriesea*. Our analyses using species distribution modelling show an absence of suitable habitat for *E. coerulescens* in western Texas and southeastern New Mexico, thus favoring the long-distance dispersal
hypothesis. The analyses also suggest high suitability of habitats across the Caribbean and some areas in Florida, as well as in other regions in Mexico and Central America. We discuss the implications of these results and compare them with the predicted distribution available for the other two known adventive orchid bee species in the USA.

**Keywords**
Anthophila, Apoidea, Mexico, orchid bees, pollinators

**Introduction**

This paper is the result of investigations into the identity of two male specimens of the neotropical orchid bee genus *Eufriesea* Cockerell (Apidae: Euglossini) collected in the southern United States, and an exploration of whether this represents suitable habitat. Orchid bees are primarily lowland to mid-elevation neotropical bees, but they are occasionally collected outside of their native altitudinal and latitudinal ranges. Most of these records consist of a single or a few individuals, and they are often the product of accidental long-distance dispersal rather than extensions of the natural range of the species. In the Andes, except for the monotypic genus *Aglae* Lepeletier de Saint Fargeau & Serville, specimens of one or two species of the remaining four genera of Euglossini have been collected at elevations above 2500 m (Gonzalez and Engel 2004, Gonzalez et al. 2014, Perger 2015). In the USA, in addition to *Eufriesea*, two other orchid bee species have been documented: *Euglossa dilemma* Bembé & Eltz [as *E. viridissima* (Friese)] in southern Florida and *Eulaema polychroma* (Mocsáry) in southern Arizona and southernmost Texas (Minckley and Reyes 1996, Búrquez 1997, Skov and Wiley 2005, Griswold et al. 2015).

Extralimital records of bees may be the result of large body size and a capacity for long distance flight, allowing individuals to reach higher elevations or latitudes while searching for food. In other cases, bees are accidentally transported by storms or bee nests are transported by humans when moving lumber or plant materials (Minckley and Reyes 1996, Gonzalez and Engel 2004, Michener 2007).

Adventive species may fail to become established if suitable habitats or adequate resources are not available. Using species distribution modelling (SDM), Hinojosa-Díaz et al. (2009) estimated the suitability of habitats in the USA for *E. dilemma* and *E. polychroma*. They found a high suitability of habitat in southern Florida for *E. dilemma*, the area of its accidental introduction and current establishment (Pemberton and Wheeler 2006). In contrast, they found low to complete absence of suitable habitat in southernmost Texas and southern Arizona for *E. polychroma*, thus supporting the idea of a long-distance dispersal event, as Minckley and Reyes (1996) inferred based on the heavily worn wings of the captured specimen. Unlike the specimen of *E. polychroma*, the two males of *Eufriesea* collected in the USA displayed no signs of major wing damage, and thus Griswold et al. (2015) suggested that these specimens might be members
of a persistent bee population, rather than long-distance transient vagrants. If this were correct, a SDM would predict highly suitable habitat for this species of Eufriesea in the southern USA, as in the case of *E. dilemma*.

The identity of the two male specimens of *Eufriesea* collected in the USA during the summer of 2010 in the Guadalupe Mountains of Texas and New Mexico has proved challenging. Griswold et al. (2015) tentatively identified them as *E. coerulescens* (Lepeletier de Saint Fargeau), a rarely collected bee from Mexico whose species limits and true geographical distribution are unclear. The name *E. coerulescens* has been applied to specimens of both sexes with a short tongue (not exceeding the third sternum in repose) and concolorous tagmata, ranging from metallic green or blue to violet. However, while addressing the identity of the USA specimens, Griswold et al. (2015) noted a number of morphological variations including tongue length among the male and female specimens standing in collections under *E. coerulescens* sensu Kimsey (1982), which not only questioned its species limits, but also suggested the existence of undescribed species. Although literature records suggest that *E. coerulescens* is widely distributed in Mexico, possibly occurring south as far as Honduras and Guatemala, records from the last two countries and others from Central America listed by Kimsey (1982), Roubik and Hanson (2004), and Moure et al. (2007) remain unconfirmed (Griswold et al. 2015).

Kimsey (1982) separated *E. coerulescens*, along with the Mesoamerican *E. anisochlora* (Kimsey) and the South American species *E. fragrocara* (Kimsey) and *E. brasiliannorum* (Friese), in the species group “XII” or *caerulescens* group [sic]. However, recent morphological and molecular studies (Faria 2009, Ramírez et al. 2010) have shown that most of Kimsey’s species groups, including the *coerulescens* group, are not monophyletic. In the analysis of Ramírez et al. (2010), *E. coerulescens* and *E. micheneri* Ayala & Engel resulted as sister species whereas *E. anisochlora* and *E. fragrocara* appeared in a clade with species of the groups XI and VI. Thus, herein we consider *E. coerulescens* and *E. micheneri* as the only members of the *coerulescens* group. These results are not surprising because, as noted by Kimsey (1982), the proposed species groups were meant as a tool in species identification and sometimes included species that did not fit all the characters listed for each group. For example, Kimsey (1982) indicated sexually dimorphic coloration as a diagnostic feature of the *coerulescens* group, but it does not occur in *E. micheneri* nor in *E. simillima* (Moure & Michener), a species regarded as a synonym of *E. coerulescens* by Kimsey (1982).

Herein, we revise the species in the *coerulescens* group to assess the species limits of *E. coerulescens* and to clarify the identity of the specimens of *Eufriesea* from the USA. In addition to *E. coerulescens* and *E. micheneri*, we recognize four other species in the *coerulescens* group (one species revalidated from synonym and three described as new). We also confirm that the two male specimens of *Eufriesea* from the USA are *E. coerulescens* and, based on the SDM, suggest that they are likely transient, long-distance vagrants because of the predicted absence of suitable habitat in western Texas and southeastern New Mexico.
Material and methods

Morphology and species descriptions. Morphological terminology follows that of Kimsey (1982) and Michener (2007). Species descriptions are based on the primary type, except for the comparative comments on E. micheneri, which were based on the paratypes available to us. Descriptions emphasize structural characters that are reliable for species identification, such as width of the posterior felty patch of the male mesotibia, presence or absence of setae on the area between the medial margin of this patch and the anterior margin of tibia (Figs 1–6), shape of the subapical projection above the male metatibial spurs (Figs 7–19), punctation of the mesoscutellum and terga (Figs 20–23), and presence of setae on the dorsal lobe of the gonostylus of the male genitalia (Figs 24–26). In the female, punctation and pubescence of the mesoscutellum (Figs 27, 28), terga, and tegula (Figs 29, 30), shape of the posterodistal margin and width of the distal emargination of metatibia (Figs 31–33), as well as width of the metasternal lobes, have proven to be reliable in species recognition. The following common characters are omitted from the descriptions: Male mesotibia with anterior felty patch triangular, about half length of posterior patch, midbasally with sparse ( integument largely visible among setae), short setae, otherwise covered with dense, longer setae obscuring integument. Male metatibia outer surface coarsely, contiguously punctate basally, punctures smaller, fainter, widely scattered on apical one-third. Female metatibia about twice as long as broad, with posterodistal angle broadly rounded. Female metasternal lobes about half of tibial length, with posterodistal margin projected in acute angle. The abbreviations S and T are used for metasternal sternum and tergum, respectively.

Measurements were taken with an ocular micrometer on an Olympus SZX-12 stereomicroscope. Intertegular distance was measured as the shortest distance between the inner margins of tegulae. Forewing length was measured from the posterior margin of tegula to the tip of the wing. We measured the maximum width and length of the posterior patch of the mesotibia and compared the subapical width of this patch with the maximum width of the distance between its medial margin and the anterior margin of the tibia. Photomicrographs were prepared using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens, and were assembled with the CombineZM™ software package.

Institutional acronyms used herein are: AMNH, American Museum of Natural History, New York, USA (J. Rozen); BBSL, USDA-ARS, Pollinating Insects Research Unit, Utah State University, Logan, Utah, USA (H. Ikerd); ECOSUR, Colección de Insectos, El Colegio de la Frontera Sur, Division Agroecológica, Tapachula, Chiapas, Mexico (R. Vandame, P. Sagot); EMEC, Essig Museum of Entomology, University of California, Berkeley, USA (C. Barr, R.L. Zuparko); FSCA, Florida State Collection of Arthropods, Florida State University, Gainesville, Florida, USA (C. Whitehill); MNHN, Museo National D’Histoire Naturelle, Paris, France (A. Touret-Alby); SEMC, Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA (Z. Falin, J. Thomas, M.S. Engel); UNAM, Museo de Zoología Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México, México (M.A. Luis, O. Yañez).
Species distribution modelling. We obtained occurrence data from the labels on specimens we examined. We georeferenced each collecting locality using the Global Gazetteer (http://www.fallingrain.com) and Google Earth (Google, Mountain View, CA, USA). We assembled 46 occurrence records to characterize the distribution of the *coerulescens* group, 24 of which are of *E. coerulescens*.

We obtained environmental data from WorldClim (version 1.3, http://www.worldclim.org; Hijmans et al. 2005), which contains climate data (i.e., monthly precipitation, and monthly mean, minimum, and maximum temperatures) at a spatial resolution of 0.1° (ca. 10 × 10 km resolution) that is obtained by interpolation among climate-station records from 1950 to 2000. These data are used to derive biologically meaningful bioclimatic variables representing annual trends, seasonality, and extreme conditions. We excluded 4 of the 19 variables available in WorldClim (mean temperature of wettest quarter, mean temperature of driest quarter, and precipitation of warmest and coldest quarters) due to anomalies and odd discontinuities between neighboring pixels. To reduce dimensionality and collinearity, we conducted a principal component analysis to the matrix of environmental variables using the “princomp” routine in R (v. 3.2.2 Core Team, 2014). This transformation rotates all extracted measures in a new space to capture the most variance, in decreasing order. In each case, models were estimated with the first four principal components of the environmental variables, which accounted for 95% of overall variance in the environmental dataset.

We used Maximum Entropy (MaxEnt 3.3.3.k; Phillips et al. 2006) implemented in the R package ‘dismo’ to estimate the potential distribution. Such an algorithm is considered one of the most reliable methods, especially with few biased samples of occurrence points (Hernandez et al. 2006, Pearson et al. 2007, Wisz et al. 2008). Calibration was done via 10 bootstrap replications, which creates replicates from the original data set by resampling with replacement (Warren and Turreli 2009). Model performance was evaluated using a partial ROC (receiver operating characteristic) area under the curve (AUC, Peterson et al. 2008). Partial ROC is based on the traditional approach, but it considers the extent of coverage of the commission error axis by model predictions. Also, it gives priority to omission error over commission in evaluating model robustness (Peterson et al. 2008). Models were evaluated by calibrating them with a random 50% of occurrences, and comparing the threshold-independent area under the curve (AUC) to null expectations. To compare partial ROC to AUC ratios of each model with null expectations, the dataset was bootstrapped, and probabilities were obtained by direct count, with AUC ratios calculated using a Visual Basic script developed by Narayani Barve (University of Kansas), based on 100 iterations and an $E=10\%$ omission threshold.

The background area used to run the model is of paramount importance, as its geographic extension can determinately influence the results of ecological niche modeling analyses (Barve et al. 2011). Therefore, we used two different extensions of background area as calibration datasets, one to run the models for the group and another one just for *E. coerulescens*, representing their respective area of known distribution. Model results were processed and visualized using the GIS software ArcView and ArcGIS 10.4.
Figures 1–3. Male mesotibia showing anterior (ap) and posterior (pp) felty patches. The presence or absence of setae in the area between the medial margin of the posterior patch and the anterior margin of tibia (aa) distally, is an important feature in species identification. 1 *E. coerulescens* (Mexico: Nuevo León; ECO-TAP-E-104040) 2 *E. oliveri* (holotype) 3 *E. simillima* (holotype).
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Results

Systematics

Coerulescens species group

**Diagnosis.** Species of this group can be recognized by the combination of the following features: head, mesosoma, and metasoma concolorous; body integument metallic blue, purple, or green; tongue in repose not surpassing S2; male labrum sharply pointed in lateral view; male mesotibial brush absent; male gonostylus with dorsal lobe longer than ventral lobe; and male mesotibia with anterior felty patch triangular, about half length of posterior patch.

**Included species.** *E. barthelli* Gonzalez & Griswold, sp. n., *E. coerulescens* (Lepeletier de Saint Fargeau), *E. engeli* Gonzalez & Griswold, sp. n., *E. micheneri* Ayala & Engel, *E. oliveri* Gonzalez & Griswold, sp. n., and *E. simillima* (Moure & Michener). These six species are presently known only from Mexico (except for *E. coerulescens*) and can be arranged into two subgroups based on the shape of the subapical projection of the concavity on the anterior margin of the male metatibia and the pubescence and shape of the dorsal lobe of the male gonostylus (Table 1). In *E. coerulescens*, *E. oliveri* sp. n., and *E. simillima* the subapical projection on the metatibia is positioned posteriorly on the concavity and spine-like when seen in anterior as well as lateral view (Figs 8–13) and the dorsal lobe of the gonostylus is largely asetose, not distinctly broad apically (Fig. 25). In the remaining species the subapical projection consists of a carina that is positioned dorsally and only appears spine-like in lateral view (Figs 14–19) and the dorsal lobe is distinctly setose and apically broad (Fig. 26).

<table>
<thead>
<tr>
<th>Species</th>
<th>Sexual color dimorphism</th>
<th>Subapical projection of ♂ metatibia</th>
<th>Glossa length ♂</th>
<th>Glossa length ♀</th>
<th>♂ Gonostylus (dorsal lobe)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. coerulescens</em> Lepeletier de Saint Fargeau</td>
<td>+</td>
<td>spine-like</td>
<td>mesotrochanter</td>
<td>metatrochanter</td>
<td>Narrow, asetose</td>
</tr>
<tr>
<td><em>E. oliveri</em> Gonzalez &amp; Griswold, sp. n.</td>
<td>+</td>
<td>spine-like</td>
<td>S2</td>
<td>S2</td>
<td>Narrow, asetose</td>
</tr>
<tr>
<td><em>E. simillima</em> (Moure &amp; Michener)</td>
<td>−</td>
<td>spine-like</td>
<td>metatrochanter</td>
<td>metatrochanter</td>
<td>Narrow, asetose</td>
</tr>
<tr>
<td><em>E. barthelli</em> Gonzalez &amp; Griswold, sp. n.</td>
<td>+</td>
<td>carinate</td>
<td>S2</td>
<td>S2</td>
<td>Broad, setose</td>
</tr>
<tr>
<td><em>E. engeli</em> Gonzalez &amp; Griswold, sp. n.</td>
<td>?</td>
<td>carinate</td>
<td>S2</td>
<td>?</td>
<td>Broad, setose</td>
</tr>
<tr>
<td><em>E. micheneri</em> Ayala &amp; Engel</td>
<td>−</td>
<td>carinate</td>
<td>S2</td>
<td>S1</td>
<td>Broad, setose</td>
</tr>
</tbody>
</table>

Table 1. Summary of currently included species in the *coerulescens* group of *Eufriesea* with information on some morphological features. Plus (+) and dash (−) symbols indicate presence and absence, respectively, of a particular feature, ? = unknown.
Figures 7–13. Outer view of the male hind leg (7) and detail of the subapical projection (indicated by an arrow) above the tibial spurs in anterior (8, 10, 12) and lateral views (9, 11, 13) Red box in Fig. 7 indicates detailed area in subsequent figures 7–9 E. coerulescens (Mexico: Nuevo León, ECO-TAP-E-104040) 10, 11 E. oliveri (paratype. Mexico: Guerrero, EMEC 1069134) 12, 13 E. simillima (paratype. Mexico: Chihuahua, KUNHM-ENT 0504566).
Figures 14–19. Detail of the subapical projection (indicated by an arrow) above the spurs of the male metatibia in anterior (14, 16, 18) and lateral views (15, 17, 19). 14, 15 E. barthelli (paratype. Mexico: Jalisco, Ajijic, KUNHM-ENT 0504535); 16, 17 E. engeli (paratype, KUNHM-ENT 0504531) 18, 19 E. micheneri (paratype. Mexico: Jalisco, Talpa, KUNHM-ENT 1121712).
Key to Mexican Species of Eufriesea

(Modified from Ayala and Engel 2008)

Male

1 Head, mesosoma, and metasoma concolorous, usually metallic blue or dark green (Figs 36, 37, 53, 56, 68, 69, 85, 86, 101, 102, 113, 114)..................2
– Head and mesosoma different in coloration from metasoma (typically with T1 dark and T2–T5 with yellow or golden shining pubescence, sometimes with blue or purple iridescence)......................................................7

2(1) Anterior margin of metatibia in inner view with distinct spine-like subapical projection above inner spur in anterior view (Figs 7–13); genitalia with dorsal lobe of gonostylus spatulate, not distinctly broad apically, largely asetose (Figs 24, 25)........................................................................................................3
– Anterior margin of metatibia in inner view without a distinct spine-like subapical projection above inner spur, but upper margin of distinctly depressed area projected medially, thus often appearing spine-like in profile (Figs 14–19); genitalia with dorsal lobe of gonostylus apically broad, distinctly setose on outer surface (Fig. 26)............................................................................5

3(2) Glossa reaching S2 in repose; T2 with punctures on disc separated by at most half a puncture width (Fig. 23), impunctate distal margin very narrow, at most as wide as a puncture width....E. oliveri Gonzalez & Griswold, sp. n.
– Glossa shorter, not surpassing metatrochanter; T2 with punctures sparser on disc, separated by at least half a puncture width (Figs 22, 72), impunctate distal margin usually broader, at least as wide as a puncture width..........4

4(3) Glossa reaching metatrochanter; anterior margin of metatibia in inner view, above tibial spurs, not bordered laterally by an elevated ridge and thus not forming a distinct pocket, subapical projection acute in profile (Figs 12, 13); outer surface of mesotibia with area between the anterior margin and posterior felty patch largely bare distally (Fig. 3); disc of clypeus weakly convex, without a longitudinal median depression; mesepisternum, dorsum of mesosoma and metasoma dark purple (Figs 67–69) (Western slope of the Cordillera of Chihuahua).................................................E. simillima (Moure & Michener)
– Glossa shorter, reaching mesotrochanter; anterior margin of metatibia in inner view, above tibial spurs, laterally bordered by an elevated ridge, forming a distinct pocket, subapical projection stout in profile (Figs 8, 9); outer surface of mesotibia with area between the anterior margin and posterior felty patch pubescent throughout (Fig. 1); disc of clypeus with longitudinal median depression bounded laterally by weak longitudinal ridge (Fig. 35); mesepisternum blue, dorsum of mesosoma and metasoma largely green sometimes with weak purple highlights (Figs 36, 37)....E. coerulescens (Lepeletier de Saint Fargeau)
5(2) T2 with punctures separated by at least a puncture width on disc (Fig. 117); metabasitarsus with posterodistal margin projecting in an acute angle (Fig. 115), inner surface near base strongly protuberant (Figs 18, 19); metatrochanter distinctly projecting ventrally, thus appearing somewhat triangular in ventral view (Fig. 116); outer surface of mesotibia with area between the anterior margin and posterior felty patch largely asetose on apical half, with scattered setae along patch (Fig. 6)..............*E. micheneri* Ayala & Engel

- T2 with punctures contiguous or separated by at most a puncture width on disc (Figs 89, 105); metabasitarsus with posterodistal margin broadly rounded (Figs 87, 103), inner surface near base weakly protuberant (Figs 14–17); metatrochanter not distinctly projecting ventrally; outer surface of mesotibia with area between the anterior margin and posterior felty patch pubescent throughout except on apical third (Figs 4, 5)...........................................6

6(5) Posterior felty patch of mesotibia subapically broader than distance between its medial margin and anterior margin of tibia (Fig. 5) (southern Mexico).... ..............................................................*E. engeli* Gonzalez & Griswold, sp. n.

- Posterior felty patch of mesotibia subapically about as wide as distance between its medial margin and anterior margin of tibia (Fig. 4) (central Mexico).........

....................................................*E. barthelli* Gonzalez & Griswold, sp. n.

7(1) Glossa extending beyond S2 ...............................................................8

- Glossa short, not reaching S2................................................................eken71

8(7) Vertex and anterior half of mesoscutum with pale pubescence (southern Mexico)..............................................................*E. pallida* (Kimsey)

- Vertex with black pubescence, contrasting with brown or pale brown setae on anterior half of mesoscutum..........................................................9

9(8) Forewing medial cell not darker than remainder of wing; S8 produced into a single, elongate apical point in lateral view (Mexico to northern Costa Rica).... .....................................................*E. mexicana* (Mocsáry)

- Forewing medial cell darker than remainder of wing; S8 produced into two apical points in lateral view (Mexico to Brazil)............*E. surinamensis* (Linnaeus)

10(7) Clypeus with strong sublateral ridges; surface of metatibia black, without metallic iridescence.................................................................11

- Clypeus without sublateral ridges; metatibia with exterior surface reddish brown, remainder of tibia black (Mexico to western Panama).................................

.................................................................*E. rugosa* (Friese)

11(10) Clypeus without medial ridge, area between sublateral ridges concave and impunctate; mesotibia with setal brush poorly developed (Mexico to southeastern Brazil).................................................................*E. concava* (Friese)

- Clypeus with medially punctate, with ridge or welt; mesotibia with setal brush well developed (Mexico to southeastern Brazil)......*E. mussitans* (Fabricius)
Figures 20–26. Dorsal views of male mesoscutellum (20, 21) and second metasomal tergum (22, 23), and lateral views of the genital capsule (24) and dorsal (gsd) and ventral lobes (gsv) of the gonostylus (25, 26). Red box in Fig. 24 indicates detailed area in subsequent figures. 20 E. micheneri (paratype. Mexico: Jalisco, Talpa, KUNHM-ENT 1121712) 21, 23–25 E. oliveri (paratype. Mexico: Guerrero, EMEC 1069134, -35) 22 E. coerulescens (lectotype) 26 E. engeli (paratype, KUNHM-ENT 0504531).
Female

(Female of *E. engeli* unknown)

1 Body concolorous, metasoma without contrasting anterior to posterior integument or pubescence (Figs 46–48, 54, 57, 79–81, 96–98, 124–126).....2
  – Body with strongly contrasting colors of the integument and pubescence, pubescence of metasoma with at least T1 dark and posterior terga light......6
2(1) Glossa long, reaching S2 or beyond, two or more times as long as compound eye length ..................................................................................................................3
  – Glossa short, not reaching S2, length less than twice compound eye length
3(2) Mesoscutellum finely, contiguously punctate throughout; medial longitudinal groove distinct, with row of dense pubescence (Fig. 27).................................................................
  – Mesoscutellum with coarser, noncontiguous punctures submedially; medial longitudinal groove weak, lacking distinct row of dense pubescence (Fig. 28)............................................
4(2) Metasoma with dark brown to black setae; labrum with distinct median tubercle basally, sublateral carinae absent (Western slope of the Cordillera of Chihuahua) ......................................................... *E. simillima* (Moure & Michener)
  – Metasoma with apical terga and sterna with white setae at least laterally; labrum with strong, elevated median line and often with distinct sublateral carinae ...... 5
5(4) Mesoscutum and mesoscutellum with pubescence not partially obscuring integument (Fig. 47); mesoscutellum with fine, dense punctures (Fig. 49); tegula densely punctate, punctures separated by a puncture width or less (Fig. 29); metatibia with emargination on distal margin broad, about 0.7–0.8 times width of posterodistal projection; metabasitarsus 1.7–1.8 times longer than broad (Fig. 31); glossa extending to metatrochanter (pine-oak forests of the Sierra Madre Oriental; eastern Mexico from Coahuila to Hidalgo and Querétaro)................................................. *E. coerulescens* (Lepeletier de Saint Fargeau)
  – Metasoma and mesoscutellum with denser pubescence partially obscuring integument (Fig. 126); mesoscutellum with coarser, sparser punctures (Fig. 127); tegula more sparsely punctate, punctures separated by at least a puncture width (Fig. 30); metatibia with emargination on distal margin narrow, about half width of posterodistal projection; metabasitarsus longer, about twice as long as broad (Fig. 32); glossa extending to S1 (west-central Mexico) ................................................................................. *E. micheneri* Ayala & Engel
6(1) Integument of all terga dark, blue or purple greenish (Mexico to western Panama) ...................................................................................................................... *E. rugosa* (Friese)
  – Posterior terga light, bright golden to light yellowish green, often with reddish tinges..............7
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Figures 27–33. Dorsal views of female mesoscutellum (27, 28) and tegula (29, 30), and outer view of hind leg (31–33). 27 *E. barthelli* (paratype. Mexico: Morelos, Tepoztlán, UNAM 01827) 28, 33 *E. oliveri* (paratype. Mexico: Guerrero, EMEC 1069136) 29, 31 *E. coerulescens* (Mexico: San Luis Potosí, ECO-TAP-E-104700; Querétaro, ECO-TAP-E-104753) 30, 32 *E. micheneri* (paratype. Mexico: Jalisco, Mascota, KUNHM-ENT 1121708). Arrows in Fig. 27 indicate the distinct medial longitudinal groove with row of dense pubescence.
7(6) Clypeus with strong, narrow medial ridge, without sublateral ridges; galea long, in repose reaching S2 or beyond, two or more times as long as compound eye length .................................................. 8
– Clypeus with sublateral ridges; galea short, in repose not reaching S2, length less than twice compound eye length .................................................. 9
8(7) Forewing medial cell darker than remainder of wing; mesoscutellum and mesoscutum posteromedially doubly punctate with scattered large punctures among fine ones (Mexico to Brazil) .................. E. surinamensis (Linnaeus)
– Forewing medial cell not darker than remainder of wing; mesoscutellum and mesoscutum posteromedially not distinctly doubly punctate, puncture size somewhat variable but not extreme (Mexico to northern Costa Rica) ............ E. mexicana (Mocsáry)
9(7) Clypeus with sublateral ridges, without medial ridge, area between sublateral ridges concave, impunctate and polished (Mexico to southeastern Brazil) ..... E. concava (Friese)
– Clypeus with sublateral and weak medial ridges (Mexico to southeastern Brazil) .................................................. E. mussitans (Fabricius)

Genus Eufriesea Cockerell, 1908

Eufriesea coerulescens (Lepeletier de Saint Fargeau, 1841)

Euglossa coerulescens Lepeletier de Saint Fargeau, 1841: 11 (Lectotype: MNHN; ♂, Mexico); Moure, 1967: 407 (lectotype designation)

Diagnosis. The male of this species shares with that of E. oliveri and E. simillima the subapical projection of the anterior margin of the male metatibia, which is formed by the medial portion of the ridge that borders the depressed area and thus located above the inner spur, and the dorsal lobe of the gonostylus, which is apically about as broad as its base and largely bare on its outer surface. It can be separated from E. simillima by the length of the glossa (reaching mesotrochanter in E. coerulescens vs. reaching metatrochanter in E. simillima), presence of a longitudinal median depression on clypeus (absent in E. simillima), outer surface of mesotibia with area between the medial margin of the posterior felty patch and the anterior margin of tibia pubescent throughout except for small area apically (half bare apically in E. simillima), and by the body color (largely metallic green in the male of E. coerulescens vs. dark blue with violet hues in both sexes of E. simillima). In addition, both species are geographically separated: E. simillima is restricted to the western slope of the Cordillera of Chihuahua whereas E. coerulescens is more widely distributed, occurring along the Sierra Madre Oriental and eastern Mexico. From E. oliveri, which shares the same body coloration, it can be separated by the length
of the glossa (reaching S2 in *E. oliveri*), punctuation of T2 (punctures on disc separated by at least half a puncture width in *E. coerulescens*, closer in *E. oliveri*), and posterior felty patch of mesotibia, which is broader medially than apically (about the same width across its length in *E. oliveri*). The female can be recognized by the following combination of features: glossa extending to metatrochanter; dorsum of mesosoma with pubescence not obscuring integument; metasoma with apical terga and sterna with white setae at least laterally; T2 with sparse, coarse punctures; mesoscutellum with fine, dense punctures; and metabasitarsus short, 1.7–1.8 times longer than broad. In *E. simillima* the pubescence of metasoma is black, T2 is more finely punctate, and metabasitarsus is longer (2.2 times longer than broad). In *E. micheneri* the pubescence on the dorsum of mesosoma is denser, partially obscuring the integument, the mesoscutellum is more coarsely and sparsely punctate, and the metabasitarsus is about twice as long as broad.

**Redescription.** Lectotype, ♂: Head width 5.9 mm; intertegular distance 4.9 mm; body length 17.8 mm; forewing length 14.6 mm. Glossa in repose reaching metatrochanter. Anterior margin of metatibia in inner view with elevated ridge bordering depressed, smooth and hairless area above tibial spurs, medial portion above inner spur projecting into a spine; metabasitarsus about twice as long as broad, inner surface near base weakly protuberant in frontal view, posterior margin gently convex, posterodistal margin angled. Dorsal lobe of gonostylus apically about as broad as its base, largely bare on its outer surface.

Mandible black on apical two-thirds, basally blue with weak green hues as on labrum; face green with weak golden hues; vertex and gena blue with weak green and purple hues; antenna black. Mesosoma (excluding legs) predominantly green except mesoscutellum blue, with weak golden hues on mesoscutum anteriorly, weak blue hues on axilla laterally, mesepisternum ventrally, and propodeum basal and laterally. Legs mostly blue-purple except green on pro- and mesotibiae anteriorly and metatibia basally. Wing membrane darkly infuscate, veins dark brown to black. T1–T4 green except distal margins blue to purple; T5–T7 blue with purple marginal zones; sterna mainly green except S6 dark brown, with blue to purple hues on apical sterna.

Head mainly with off-white setae, with gray to black setae on vertex. Mesosoma with black setae except whitish setae on outer surface of mesosasitarsus and off-white on anterior half of mesoscutum, lateral face of mesepisternum anteriorly, and small patch laterally on propodeum. Metasoma with off-white to light brown setae, longer and denser on apical terga and sterna.

Clypeus with longitudinal medial depression, bounded laterally by weak longitudinal ridge. T2 with punctures on disc separated by at least half a puncture width, impunctate distal margin at least as wide as two times a puncture width.

♀️: Head width 5.7–6.0 mm; intertegular distance 4.9–5.0 mm; body length 14.6–16.9 mm; forewing length 13.1–13.8 mm. Metatibia with emargination on distal margin 0.7–0.8 times width of posterodistal angle; metabasitarsus 1.7–1.8 times longer than broad.

Blue-green with purple hues on mandible, labrum, clypeus, vertex, gena, mesoscutellum, legs, discs of sterna, and marginal zones of terga.
Figures 34–39. Male lectotype of *E. coerulescens*. 34 Facial view 35 Detail of clypeus with arrows indicating weak sublateral ridges that form a median longitudinal depression 36 Dorsal habitus 37 Lateral habitus 38 right and left forewings 39 Dorsal view of mesoscutellum.

Pubescence black, except off-white on sides of T3, T4–T6 entirely, sides of S3, entire S4 and S5. Mesoscutellum with poorly defined row of dense pubescence on median longitudinal groove.

Clypeus sometimes with median longitudinal ridge continuing onto supraclypeal area; labrum with basal, longitudinally elongate tubercle, sublateral carinae sometimes weak. Mesoscutellum with fine, dense punctures. T2 with punctures on disc sparser than in the male, separated by at least a puncture width, impunctate distal margin wide, at least three or four times a puncture width.
Material examined. \((n = 46♀, 3♂, )\) 1♂, USA: Texas, Culberson County: Guadalupe Mountains National Park, Pine Springs, N31.8955 W104.6317, 1551m, 22 Jul 2010, J.D. Herndon, A. Druk, H. Ikerd, pantrap, GUMO27853 (BBSL); 1♂, New Mexico, Eddy County: Longview Spring, 0.7km E, N32.1007 W104.6317, 1551m, 22 Jul 2010, J.D. Herndon, Cirsium sp., CAVE20415 (BBSL); Mexico: 2♀, Chihuahua, General Trias, August 20, 1991, J. Rozen/N. Pember, SM0307820, -21, KUNHM-ENT (SEMC); 1♀, Coahuila, Cuesta la Muralla, 12-76/ J.A. Chemera, J. Powell, A.&M Michelbach-er collectors/ EMEC1069129 (EMEC); 8♀, Durango, Dgo., Mex., 8200ft. Aug. 14, 1947 / D. Rockefeller, Exp. Gertsch / SM0504556, -59–65 KUNHM-ENT (SEMC); 1♂, idem (FSCA); 1♀, idem / BBSL849648 (BBSL); 1♀, idem / D. Rockefeller, Exp. Spieth / SM0504557, KUNHM-ENT (SEMC); 1♀, idem / D. Rockefeller, Exp. Cazier / SM0504558, KUNHM-ENT (SEMC); 1♀, ECO-TAP-E-105054, Mex., Hgo. [Hidalgo], La Misión, Puerto de Piedra, 1678 m, 21,05076N, 99,11475W, 19/8/2013, 09:10, Col. Jorge Mérida; 3♀, Mexico: Hidalgo, 24km NW Cardonal (Barranco del Tulanlan-go), 1590m / 13 July 1990, R.L. Minckley, ex., Cassia / SM0504551–53, KUNHM-ENT (SEMC); 1♀, Mexico: Hidalgo, 3.5km W Canyon of Tolantongo / NE of Ixmiquilipan, 1590 m, 13 July 1990, I. Yarom, on Cassia? / SM0504576, KUNHM-ENT (SEMC); 1♀, Mexico: Hidalgo, 31 km S Jacala, 1050m, 12 July 1990, W.J. Bell #2/ SM0504579, KUNHM-ENT (SEMC); 1♀, Mexico: Hidalgo, Santorun, Atotonlico el Grande, 13 Sept. 1997, L. Godinez, #736, ex. Senecio salignus / SM0504580, KUNHM-ENT (SEMC); 1♂, ECO-TAP-E-104040, NL [Nuevo León], Arañazaí, P. de Anteojitos, 2041 m, 24,21185N, 99,88922W, 8/8/2013, 09:05, Col. Jorge Mérida (ECOSUR); 2♀, ECO-TAP-E-104736, -53, Mex., Qro. [Querétaro], La Loma, 1830 m, 21,36714N, 99,76277W, 16/8/2013, 10:35, Col. Jorge Mérida, Erika Esquivel; 1♀, Mexico: Querétaro, 27km W San Luis Potosi, 1270 m, 8 July 1990, W.J. Bell #1 / SM0504577, KUNHM-ENT (SEMC); 2♀, idem, 26.5 km W San Luis Potosi / borde ron Hwy. 120, 1270 m, 9 July 1990, R.L. Minckley / SM0504523–70, KUNHM-ENT (SEMC); 1♀, Mexico: Querétaro, 27km W San Luis Potosi, 1270 m, 8 July 1990, W.J. Bell #2/ SM0504579, KUNHM-ENT (SEMC); 1♀, Mexico: Querétaro, 27km W San Luis Potosi / 17 mi. E Cd. Maiz, 3200', 23 July 1965, U.Kans. Mex. Expedition/ SM05045, KUNHM-ENT (SEMC); 1♀, Mexico, San Luis Potosi, 15 mi. E Cd. Maiz, 3200', 23 July 1965, U.Kans. Mex. Exped. / SM0504569, KUNHM-ENT (SEMC); 1♀, idem, 15 mi. E Cd. Maiz, 3000' / SM0504528, KUNHM-ENT (SEMC); 2♀, idem, 5 mi. E Ciudad del Maiz, S.L.P., Mex. 4700 feet, vii-22, 23-1954/ SM0504554, -55, KUNHM-ENT (SEMC); 1♀, Mexico: San Luis Potosi, 15 mi. W, Xilitla, 1350m, viii-15-1977, E.I. Schlinger/ on plant #8, Cassia sp. / EMEC1069131 (EMEC); 1♀, Villagran, Tamaulipas, Mex, ix-8-1966, D.H. Janzen, Thevetia/AMNH_BEE 00164041 (AMNH); 1♀, Mex: Tamaulipas, 15 mi. SW Cd. Victoria, 5000', ix-
**Figures 40–45.** Male terminalia of *E. coerulescens* (Mexico: Nuevo León, ECO-TAP-E-104040).  
40 Seventh metasomal sternum in ventral view 41, 42 Eighth metasomal sternum in ventral and lateral views 43–45 Genital capsule in dorsal, ventral, and lateral views.


**Distribution.** (Fig. 128) Mexico: Chihuahua, Coahuila, Durango, Hidalgo, Nuevo León, Querétaro, San Luis Potosí, Tamaulipas. USA (accidental?, see results and discussion): Texas, New Mexico.

**Floral records.** Females have been collected on flowers of *Cassia* sp. (Fabaceae), *Solanum* sp. (Solanaceae), *Senecio salignus* (Kunth) H.E. Robins. & Brett (Asteraceae), and *Thevetia* sp. (Apocynaceae). One of the two males captured in the US was visiting flowers of *Cirsium* sp. (Asteraceae).
Figures 46–50. Female of *E. coerulescens* (Mexico: San Luis Potosí, ECO-TAP-E-104161; Querétaro, ECO-TAP-E-104753 [Fig. 46]). 46 Facial view 47 Dorsal habitus 48 Lateral habitus 49 Dorsal view of mesoscutellum 50 Second metasomal tergum.

Comments. The male lectotype is in poor condition (Figs 34–39). Both forewings are detached from the specimen and the left leg, right antenna and most of the left flagellum are missing. In addition, the left mesepisternum, right sides of S1, S2, S5, S6, T5–T7, and part of genital capsule appeared to have been eaten by dermestid beetles. Because the right mesotibia is very close to the body and the genitalia is partly destroyed, the following measurements and photographs were taken from the specimen collected in Nuevo León, Mexico: mesotibia with area between medial margin of
posterior patch and anterior margin of tibia setose throughout except by small apical area; posterior patch about four times longer than broad, subapically broader than distance between its medial margin and anterior margin of tibia. Hidden sterna and genitalia as in Figs 40–45.

Female specimens vary considerably in the presence of green hues, from nearly absent to very distinct on face, mesoscutum and terga. The identity of the male from “Durango, Dgo., Mex., 6200ft. Aug. 14, 1947 / D. Rockefeller, Exp. Gertsch” is questionable, made more difficult because the two hind legs that are glued to the body are from different species; this male lacks the blue mesepisternum considered diagnostic for E. coerulescens.

Eufriesea oliveri Gonzalez & Griswold, sp. n.
http://zoobank.org/049C4796-6175-4614-B502-C96DADD79DF0
Male, Figs 2, 10, 11, 21, 23–25, 51, 53, 55, 56, 58–62; Female, Figs 28, 33, 52, 54, 57, 63

**Diagnosis.** Both sexes of this species are most similar to *E. coerulescens*, from which it can be separated easily by the longer glossa and more densely punctate disc of T2. The female of *E. oliveri* can be recognized from that of *E. barthelli* by the mesoscutellum coarsely and non-contiguously punctate submedially, with a weak medial groove lacking a distinct row of setae (finely, contiguously punctate with stronger medial groove having a distinct row of setae in *E. barthelli*), and by the T2, which is more densely punctate on disc, with punctures separate by at most a puncture width (punctures separated by 1.0–2.0 times a puncture width in *E. barthelli*).

**Description.** Holotype, ♀: As described for *E. coerulescens* except as follows: Head width 5.7 mm; intertegular distance 4.6 mm; body length 15.4 mm; forewing length 13.5 mm. Glossa in repose reaching S2; metabasitarsus with posterodistal margin more rounded, not as acute as in *E. coerulescens*. Hidden sterna and genitalia as in Figs 58–62.

Vertex and gena green with weak blue and purple hues. Mesosoma (excluding legs) predominantly green except mesoscutellum green with weak blue and golden hues; metatibia basally mostly green with golden hues; wing membrane infuscate, lighter than in *E. coerulescens*. Metasoma green with distal margins of terga and sterna (excluding S6) weakly blue to purple.

Head with whitish setae, with scattered gray to black setae on vertex. Mesotibia with area between medial margin of posterior patch and anterior margin of tibia setose on basal half, distal half asetose; posterior patch 5.7 times longer than broad, subapically narrower than distance between its medial margin and anterior margin of tibia.

T2 with punctures on disc separated by at most half a puncture width, impunctate distal margin very narrow, at most as wide as a puncture width.

♀: Head width 6.3 mm; intertegular distance 4.9 mm; body length 18.4 mm; forewing length 13.5 mm. Metatibia with emargination on distal margin about half width of posterodistal angle; metabasitarsus twice as long as broad.
On the identity of the adventive species of Eufriesa Cockerell in the USA...

Figures 51–57. Male holotype (except paratype in Fig. 55, EMEC 1069134) and female paratype (Mexico: Guerrero, EMEC 1069136) of E. oliveri. 51, 52 Facial view 53, 54 Lateral habitus 55 Outer view of hind leg 56, 57 Dorsal habitus 51, 53, 55, 56 Male 52, 54, 57 Female.
Blue with purple hues on mandible basally, labrum, frons, vertex, gena, dorsum of mesosoma, mesepisternum, propodeum, legs, discs of sterna, and marginal zones of terga.

Pubescence black, except off-white on sides of T2, T3–T6, sides of S2 and S3, entire S4 and S5, and S6 basally. Mesoscutellum without row of dense setae on weak medial longitudinal groove.

Clypeus with median longitudinal ridge continuing onto supracylpeal area; labrum with distinct median and sublateral carinae. Mesoscutellum with coarse, non-contiguous punctures submedially. T2 with punctures sparser than in the male, separated by a puncture width or less.

**Holotype.** ♂, Mexico: Guerrero, 3 km N Chilpancingo, VI-4-12-91, JA Chemsak / EMEC 1069133 (barcode label). Deposited in EMEC.

**Paratypes.** \( n = 9♀, 2♂ \) Two males and two females with the same data as the holotype but with barcode label numbers 1069132, 1069134–1069136 (EMEC); C. [Clowesia] thylaciochila, La Joya, Morelos, Mex [Mexico], Ernesto Aguirre, 3-22-1977 (FSCA); remaining paratypes deposited in the UNAM with the following label data: 2♂, Mor. [Morelos] La Joya, 1450 m.s.n.m / # 10442; 1♂, Mich. [Michoacán], La Zauda, 1100 m.s.n.m / #10443; 1♂, Arrollo las Damas, Mex., Guerrero, Tetipac. 8-⅚-1986, 1800 m. Luis A. / # 10446; 1♂, idem, Llorente J. / #10445; 1♂, Km 19.5, Autopista Mexico-Cuautla, Tepoztlán; Morelos. 16/06/1996. I. Hinojosa HD-737, 14:10 H, 1350 m, 18°56’17”N, 99°02’18”W, selva baja caducifolia, atraida por esencia (mezcal) / # 00366.

**Additional material.** \( n = 5♀, 12♂ \), not designated as paratypes) 3♀, Mexico: Morelos, 4 mi SW Yautepec, 2 July 1961, 3800’, C.D. Michener/ on flowers of Cassia sp./ KUNHM-ENT 504573, 504526, 504529 (KU); 1♀, Caño de Lobos, Mor. [Morelos], 16-xi-83, R y G. Ayala / #10447 (UNAM); 1♂, Ocuilan, @ Stanhopea hernandezii, 2001, M.A. Soto (FSCA); 3♀, Mex [Mexico], Oaxaca, Tehuantepec, 56 mi N.W., vii-27-63/W.A. Foster collectors/ AMNH_BEE 00265723 (AMNH); 2♀, Mexico, Puebla, 12 mi NW Tehuitzingo, 4050 ft, 29 June 1961, U. Kans. Mex. Exped. / KUNHM-ENT 504524, 504572 (KU); Mexico, Jalisco, Estacion de Biologia Chamela, 5-viii-86 / M. Sánchez/ / KUNHM-ENT 730197; 1♀, idem, 10/14 Jul 1989, T. Griswold/ BBSL861169 (BBSL); 1♀, idem, 4-vii-1984/ R. Ayala/ #10448 (UNAM); 1♂, Tzararacua, near Uruapan, Mich. [Michoacán], Mexico, 28 June 68 [1968], N.H. Williams, Eugenol, 276 (FSCA); 1♂, Mexico, Mich. [Michoacán], Tzararacua, nr. Uruapan, 29 VI 1968, N.H. Williams, 276, Eugenol (FSCA); 1♂, Mexico, Mich. [Michoacán], Tzararacua, nr. Uruapan, 6 VII 1968, N.H. Williams, 276, Eugenol (FSCA); C. [Clowesia] glaucoglossa, La Huacana, Mich. [Michoacán], Mex [Mexico], Ernesto Aguirre, 3-22-1977 (FSCA).

**Etymology.** This species is named after Oliver Mitchell Betancourt, son of the first author (March 11, 2015), who daily brings love and joy.

**Distribution.** (Fig. 128) Mexico: Guerrero, Jalisco, Michoacán, Morelos, Oaxaca, Puebla.
Floral records. Females have been collected on flowers of *Cassia* sp. (Fabaceae). Males have been collected on *Clowesia glaucoglossa* (Rchb.f.) Dodson, *C. thylaciochila* (Lem.) Dodson, and *Stanhopea hernandezii* (Kunth) Schltr. (Orchidaceae).

Comments. The two female paratypes as well as some female specimens from Morelos and Oaxaca have a distinctly large impunctate area just anterior to the median ocellus, but in specimens from Jalisco and Puebla this area is very reduced to nearly absent. Also, in some female specimens from these two states and Oaxaca, the punctures on the disc of T2 are sparser (1.0–2.0 times a puncture width) than in the female paratypes, and the sublateral carinae of the labrum are weak.

Eufriesea simillima (Moure & Michener, 1965) stat. n.
Male, Figs 3, 12, 13, 67–78; Female, Figs 64, 79–83

Euplusia simillima Moure & Michener in Moure, 1965: 275 (Holotype: SEMC; ♂, Mexico: Chihuahua, Maguarichi)

Diagnosis. Both sexes of this species can be easily recognized by their body color, which is predominantly dark purple, thus resembling E. micheneri. However, they can be easily separated from that species by the shorter glossa (not surpassing metatrochanter in E. simillima and reaching S1 in E. micheneri), shape of the subapical projection on the anterior surface of the male metatibia, male gonostylus, and metasoma with dark brown to black pubescence (apical terga and sterna with white setae at least laterally in E. micheneri). (See comparative diagnosis for E. micheneri)

Redescription. Holotype, ♂: As described for E. coerulescens except as follows: Head width 6.0 mm; intertegular distance 4.9 mm; body length 15.4 mm; forewing length 14.3 mm. Glossa in repose reaching metatrochanter. Anterior margin of metatibia in inner view, above tibial spurs, not bordered laterally by an elevated ridge and thus not forming a distinct pocket, subapical projection above inner spur acute in profile; metabasitarsus about 2.2 times longer than broad. Hidden sterna and genitalia as in Figs 73–78.

Mandible black on apical two-thirds, basally purple as on labrum; face largely green, remainder of body purple with weak bluish-green hues on tegula and mesoscutum.
Gena with gray to black setae as on vertex. Mesosoma with black setae except whitish setae on outer surface of mesobasitarsus and off-white on anterior half of mesoscutum. Mesotibia with area between medial margin of posterior patch and anterior margin of tibia setose on apical third; posterior patch 4.5 times longer than broad, subapically about as broad as distance between its medial margin and anterior margin of tibia.

♀: Head width 6.2 mm; intertegular distance 5.2 mm; body length 14.6 mm; forewing length 13.5 mm. Metatibia with emargination on distal margin about half width of posterodistal angle; metabasitarsus 2.2 times longer than broad.

Coloration as in male but face blue with weak green hues, mesoscutum and tegula lacking green hues.

Pubescence black including on legs and metasoma.
Clypeus sometimes with median longitudinal ridge continuing onto supraclypeal area; labrum with basal, longitudinally elongate tubercle, sublateral carinae sometimes weak. Mesoscutellum with fine, contiguous punctures submedially, median longitudinal groove weak, lacking distinct row of dense pubescence. T2 with punctures on disc sparser than in the male, separated by at least a puncture width, impunctate distal margin wide, at least three or four times a puncture width.

**Distribution.** (Fig. 128) This species is known only from the western slope of the Cordillera of Chihuahua, Mexico.

**Comments.** This species is reinstated from synonymy with *E. coerulescens*. As indicated in the key to species and the diagnosis, both sexes of this species are morphologically distinct as well as geographically separated from *E. coerulescens*. Moure (1965: 275)
indicated that the length of the interocellar distance is greater than the ocellocular distance in the male of *E. coerulescens* whereas such a distance was subequal in the male of *E. simillima*; however, such a difference was not observed in the lectotype of *E. coerulescens*, thus suggesting that Moure’s observation may have not been based on the type specimen. We were only able to examine the holotype and paratypes from Maguarichi and Barranca del Cobre, Chihuahua, all deposited in SEMC and FSCA.

**Eufriesea barthelli** Gonzalez & Griswold, sp. n.
http://zoobank.org/65E0C67C-D1CF-4F66-8CD5-F82F1971769D
Male, Figs 4, 14, 15, 84–95; Female, Figs 27, 65, 96–99

**Diagnosis.** This species shares with *E. micheneri* and *E. engeli* the subapical projection of the anterior margin of the male metatibia, which is formed by the upper ridge that borders the depressed area, and the dorsal lobe of the gonostylus, which is apically
Figures 84–89. Male holotype of *E. barthelli* (except paratype in Fig. 87, KUNHM-ENT 0504535). 84 Facial view 85 Dorsal habitus 86 Lateral habitus 87 Outer view of hind leg 88 Dorsal view of mesoscutellum 89 Second metasomal tergum.

broad and covered by setae on its outer surface. It is most similar to *E. engeli* from southern Mexico. It can be separated from that species by the posterior felty patch of the mesotibia, which is subapically about as wide as the distance between its medial margin and the anterior margin of the tibia (broader in *E. engeli*), the finer and slightly sparser punctures on disc of T2, and its geographical distribution (*E. barthelli* occurs in central Mexico). The female of *E. barthelli* is similar to that of *E. oliveri* in

the long glossa, reaching at least to S2. However, they can be separated primarily by the punctation of the mesoscutellum. In *E. barthelli* it is finely, contiguously punctate throughout, with a distinct medial longitudinal groove that bears a row of dense setae. In *E. oliveri*, the mesoscutellum is coarsely, non-contiguously punctate, and with a weak medial longitudinal groove lacking a distinct row of dense pubescence.

**Description.** Holotype, ♀: Head width 6.0 mm; intertegular distance 5.0 mm; body length 18.9 mm; forewing length 15.0 mm. Glossa in repose reaching S2. Anterior margin of metatibia in inner view with elevated ridge bordering depressed, smooth and hairless area above tibial spurs, upper margin of ridge medially projected, appear-
ing as a spine in profile; metabasitarsus about twice as long as broad, inner surface near base weakly protuberant in frontal view, posterior margin gently convex, posterodistal margin broadly rounded. Hidden sterna and genitalia as in Figs 90–95; dorsal lobe of gonostylus broader apically than basally, distinctly setose on outer surface.

Mandible black on apical two-thirds, basally blue; labrum blue with weak green hues; remainder areas of head green with weak golden hues on face and bluish hues around ocelli and gena; antenna black. Mesosoma excluding legs predominantly green, with weak golden hues on mesoscutum anteriorly, disc of tegula and mesepisternum dorsally; weak bluish hues on axilla laterally, mesoscutellum, and propodeum basal and laterally. Legs mostly blue-purple except green on pro- and mesotibiae anteriorly and most of metatibia. Wing membrane infuscate, veins dark brown to black. T1–T4

green except distal margins blue to purple; T5–T7 blue-purple; sterna mainly green with weak blue-purple hues except S6 dark brown, with blue-purple hues barely visible basolaterally.

Head mainly with off-white setae, with gray to black setae on vertex. Mesosoma with gray to black setae except: whitish setae on posterior margin of meso- and metatibiae, outer surfaces of mesobasitarsus and metatibia; off-white on anterior half of mesoscutum, and lateral face of mesepisternum. Mesotibia with area between medial margin of posterior patch and anterior margin of tibia setose except on apical one-fourth; posterior patch 4.5 times longer than broad, subapically about as wide as distance between its medial margin and anterior margin of tibia. Metasoma with off-white to light brown setae, longer and denser on apical terga and sterna.

Clypeus without longitudinal medial depression. T2 with fine punctures on disc separated by at most a puncture width, distal margin narrow, about twice a puncture width.

♀: Head width 6.3–6.5 mm; body length 16.5–17.8 mm; forewing length 15.0 mm. Metatibia with emargination on distal margin about half width of posterodistal angle; metabasitarsus twice as long as broad.

Blue with purple hues on mandible basally, labrum, dorsum of mesosoma, mesepisternum ventrally, propodeum, legs, discs of sterna, and marginal zones of terga.

Pubescence black, except off-white on sides of T2, T3–T6, S1–S5, and S6 basally. Pubescence denser on mesosoma, not obscuring integument.

Clypeus with median longitudinal ridge continuing onto supraclypeal area; labrum with basal, longitudinally elongate tubercle, sublateral carinae sometimes weak. Mesoscutellum with fine, contiguous punctures submedially, median longitudinal groove well defined, with distinct row of dense pubescence. T2 with punctures on disc sparser than in the male, separated by at least a puncture width, impunctate distal margin wide, at least three or four times a puncture width.

Holotype. ♂, Chalchijapa, Santa Maria, Chimalapa; Oaxaca, 28-v-1995. J.L. Salina, 100 m, Selva Alta Perennifolia, al vuelo JL-265. Red Ornitológica 09:00 h// Museo de Zoología, Hymenoptera 11086. Deposited in UNAM.

Paratypes. (n = 5♂, 2♀), Mexico: 1♂, km. 12, Autopista México-Cuautla, Tepoztlán; Morelos. 30/06/1996, I. Hinojosa, HD-755. 13:00 H, 1650 m. 18°58’24”N, 99°04’57”W, Cultivo de temporal, s/Podranea ricasoliana / # 02290 (UNAM); idem, 1♂, 13/07/1996, O. Yáñez, OY-752, 13:30 H / # 02310 (UNAM); idem, 1♀, 10/11/1996, H. Hinojosa, HD-1343, 12:55 H, s/Tithonia tubaeiformis / # 02709 (UNAM); idem, 1♀, 08/10/1995, O. Yáñez, OY-169, 12:10 H, atraida por esencia (mezcla) / # 01827 (UNAM); 1♂, mts. N. Ajijic, JAL [Jalisco]., MEX. to 5300’, 23 July, 1964, WLNutting & sons, scrub forest // BBSL849647 (BBSL); 1♂, idem (FSCA); 1♂, Canyon N. Ajijic, JAL. MEX. to 5400’, 22 July 1964, WLNutting & sons, scrub forest / SM0504535, KUNHM-ENT (SEMC).

Additional material. (n = 6♀, not designated as paratypes) 1♀, ECO-TAP-E-95712, Mex., Jal., [Jalisco], Tamazula, Agua Zarca, 1829 m, 19.82484N, 103.27449W, 31/10/2012, 10:00, Col. Jorge Mérida (ECOSUR); 1♀, Mexico:

Variation. The blue-purple coloration is strong in both males from Morelos and one of the males from Jalisco. In particular, one of the males from Morelos (UNAM, #02290) has extensive blue hues on all tagmata.

Etymology. This species is dedicated to our friend and colleague Dr. John Barthell (University of Central Oklahoma) for his contributions to bee ecology and efforts to promote undergraduate research on bees.

Distribution. Central Mexico: Jalisco, Michoacán, Morelos, Nayarit, Oaxaca.

_Eufriesea engeli_ Gonzalez & Griswold, sp. n.  
http://zoobank.org/0339D195-AC0A-4F3B-8F74-28C033F2AFA6  
Male, Figs 5, 16, 17, 26, 100–111

Diagnosis. This species is known only from the male sex. It along with _E. micheneri_ and _E. barthelli_ belong to a group of species that differs from other concolorous metallic blue to dark green Mexican _Eufriesea_ by the anterior margin of metatibia in inner view without a distinct spine-like subapical projection above inner spur, but upper margin of distinctly depressed area projected medially, thus often appearing spine-like in profile (Figs 14–19) and the genitalia with dorsal lobe of gonostylus apically broad, distinctly setose on outer surface (Fig. 26). It can be separated from _E. micheneri_ by the metabasitarsus broadly rounded posterodistally (angled in _E. micheneri_), T2 with punctures separated by at most a puncture width on disc (punctures separated by 1–2 times a puncture width in _E. micheneri_), and by the body color (largely metallic green in the male of _E. engeli_ vs. dark blue with violet hues in both sexes of _E. micheneri_). From _E. barthelli_ it can be separated by the posterior felty patch of mesotibia, which is subapically broader than the distance between its medial margin and anterior margin of tibia (narrower in _E. barthelli_), punctuation of T2 (punctures coarser and nearly contiguous in _E. engeli_, finer and slightly sparser in _E. barthelli_), and its geographical distribution (_E. engeli_ occurs in southern Mexico whereas _E. barthelli_ in central Mexico).

Description. Holotype, ♂: As described for _E. barthelli_ except as follows: Head width 5.9 mm; body length 16.7 mm; intertegular distance 4.6 mm; forewing length 14.4 mm. Glossa in repose reaching S2. Hidden sterna and genitalia as in Figs 106–111.

Gena mostly green. Mesosoma excluding legs predominantly green, with weak golden hues on mesoscutum anteriorly, disc of tegula and mesepisternum dorsally; weak bluish hues on axilla laterally, mesepisternum ventrally, and propodeum basal
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and laterally. Legs mostly blue-purple except green on pro- and mesotibiae anteriorly and metatibia basally. T1–T4 green except distal margins blue to purple; T5–T7 blue
with purple marginal zones; sterna mainly green except S6 dark brown, with blue to purple hues on apical sterna.

Mesosoma with mostly off-white setae except gray to black setae on pronotum, posterior half of mesoscutum, mesoscutellum, mesepisternum ventrally, metepisternum, and propodeum. Legs with off-white setae, except gray to dark brown setae on inner surfaces of tibiae, basitarsi, and tarsi of all legs. Mesotibia with posterior patch subapically broader than distance between its medial margin and anterior margin of tibia.

Disc of T2 with coarser and denser punctures on disc than in *E. barthelli*, punctures separated by less than a puncture width to nearly contiguous.

Female. Unknown.


Paratypes. Eight males with the same data as the holotype and also deposited in SEMC, but with the following barcode label numbers: SM0504513–15, -17, -18, -20, -31, and 0748219.

Additional material. (n = 7♂, not designated as paratypes) 1♂, Mexico: Chiapas, L.[Lago] Montebello, 20 v 1970, 1410, R.L. Dressler (FSCA); 5♂, Tuxtla Gutierrez, Chiapas, Mexico, C. Dodson, 7-21-1968, No. 310, Cineole (FSCA); 1♂, Mexico: Chis [Chiapas], Tuxtla Gutierrez, Cineole, C.H. Dodson, 310, 19-23 VII 1968 (FSCA).

Etymology. This species is dedicated to our friend and colleague Dr. Michael S. Engel (University of Kansas), in recognition of his significant contributions to systematic melittology.

Distribution. (Fig. 128) This species is known only from Chiapas, southern Mexico, but can be expected to be found in Guatemala since Lago Montebello is on the border with Guatemala.

Comments. In some paratypes the golden hues are more conspicuous on the face and mesoscutum and the subapical projection of the anterior surface of the metatibia is more acutely projected than the holotype. The tongue has been pulled out in all specimens, including the holotype, and thus it appears to surpass the apex of metasoma. The tongue length provided in the description is based on measuring the galea alone and confirmed by the Lago Montebello specimen where the tongue is in repose.

_Eufriesea micheneri_ Ayala & Engel, 2008

Male, Figs 6, 18, 19, 20, 112–123; Female, Figs 30, 32, 66, 124–127

_Eufriesea micheneri_ Ayala & Engel, 2008: 228 (Holotype: UNAM; ♂, Mexico: Jalisco, Mascota)

Diagnosis. Superficially this species resembles _E. simillima_ in that both sexes are primarily blue with purple hues. In addition to their geographical separation (_E. simillima_ occurs in the Sierra Madre de Occidental whereas _E. micheneri_ occupies western parts of the Transverse Volcanic Belt), it can be separated by the length of the tongue (reaching S2 in _E. micheneri_ and only the metatrochanter in _E. simillima_), the subapical projection of the anterior margin of the male metatibia (formed by the upper portion of the ridge that borders the depressed area in _E. micheneri_ and by the medial portion of the ridge, and thus located above the inner spur, in _E. simillima_), and by the dorsal lobe of gonostylus (apically about as broad as its base and largely bare on its outer surface in _E. simillima_ and apically broad and setose on outer surface in _E. micheneri_). From _E. barthelli_ and _E. engeli_ it can be separated by T2 with sparser punctures on disc (contiguous or separated by at most a puncture width in _E. barthelli_ and _E. engeli_),
metabasitarsus with posterodistal margin angled (broadly rounded in *E. barthelli* and *E. engeli*) and pubescence of mesotibia, between the medial margin of posterior felty
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patch and anterior margin of tibia (presence on basal half in *E. micheneri* and basal two-thirds in *E. barthelli* and *E. engeli*).

**Morphology.** ♂, As described for *E. engeli* except as follows: Head width 6.3 mm; body length 17.8 mm; forewing length 16.3 mm. Metabasitarsus with inner surface near base strongly protuberant in frontal view, posterodistal margin angled. Hidden sterna and genitalia as in Figs 118–123.

Mandible black with green, blue, and purple hues on basal third as on labrum; face green with golden and blue hues; vertex and gena blue with purple hues. Meso- and metasoma blue with green hues on anterior two-thirds of mesoscutum and disc of

**Figures 118–123.** Male terminalia of *E. micheneri* (paratype. Mexico: Jalisco, Talpa, KUNHM-ENT 1121712). 118 Seventh metasomal sternum in ventral view 119, 120 Eighth metasomal sternum in ventral and lateral views 121–123 Genital capsule in dorsal, ventral, and lateral views.
tegula, weak purple hues on remainder areas of mesosoma and marginal zones of terga and sterna.

Face with off-white setae, vertex and gena with gray to black setae. Mesosoma with gray to black setae except on outer surfaces of mesobasitarsi and distitarsi. Mesotibia with area between medial margin of posterior patch and anterior margin of tibia bare on distal half; posterior patch subapically about as broad as distance between its medial margin and anterior margin of tibia. Metasoma with gray setae on terga, white or off-white on S3–S5.

Disc of T2 with finer and sparser punctures than on *E. barthelli*, punctures separated by at least a puncture width.

♀: Head width 6.0 mm; body length 17.5 mm; forewing length 14.7 mm. Coloration as in the female of *E. barthelli* but with stronger purple hues. Pubescence black, with whitish on sides of T4 and T5 and discs of S4 and S5 in some specimens. Mesos-
cutellum with poorly defined row of dense pubescence on median longitudinal groove. T2 with finer, sparser punctures than on E. barthelli.

**Distribution.** (Fig. 128) Mexico: Durango, Jalisco, Michoacán, Nayarit. This species appears to be restricted to mid elevation oak and pine forests in the western parts of the Transverse Volcanic Belt.

**Material examined.** In addition to the paratypes deposited in SEMC (five males and one female from Mascota, Jalisco, and one male from Santa Teresa, Nayarit), we also examined the following two females deposited in ECOSUR: 1 ♀, ECO-TAPE-118160, Méx., Dgo. [Durango], San Dimas, 1760 m, 24°32′10″N, 105°8′13″W, 2/10/2013, 10:00, Col. Liliana Tlapaya; 1 ♀, ECO-TAP-E-102831, Mex., Mich. [Michoacán], Morelia, J. del Monte, 2172 m, 19°6′39″5N, 101°14′6″44W, 4/7/2013, 10:05, Col. Oscar Martínez López.

**Floral records.** Females have been collected on flowers of Salvia sp. (Lamiaceae).
Figure 129. Potential distribution for all species of *Eufriesa* of the *coerulescens* group combined (top map) and for *E. coerulescens* alone (bottom map) with collection localities.

**Comments.** Some of the specimens listed under this species by Ayala and Engel (2008) in the section “additional material examined” correspond to *E. barthelli*. These two species partially overlap in distribution.

**Known and potential distribution**

All examined specimens of the *coerulescens* species group are from Mexico, except for the two males of *E. coerulescens* collected in the USA, over 420 km north of the northernmost known locality for this species (Chihuahua, General Trias). Except for *E. coerulescens*, which occurs along pine-oak forests of the Sierra Madre Oriental from Coa-
huila to Hidalgo, as well as in Durango and Chihuahua, all species of the *coerulescens* group appear to be geographically localized (Fig. 128). *Eufriesea olivieri* and *E. barthelli* appear to be restricted to the Sierra Madre del Sur, *E. simillima* to the northern Sierra Madre de Occidental, *E. micheneri* to western areas of the Transverse Volcanic Belt, and *E. engeli* to deciduous rain forests in southern Mexico.

The potential distribution maps obtained for *E. coerulescens* as well as for all occurrence records of all species combined were largely similar in their general predictions (Fig. 129). Model evaluation showed high scores of performance for both models (*coerulescens* species group: AUC $\bar{x} = 0.828, 0.787–0.854$; ROC $\bar{x} = 1.262, 1.009–1.918$. *Eufriesea coerulescens*: AUC $\bar{x} = 0.908, 0.874–0.954$; ROC $\bar{x} = 1.553, 0.964–1.916$). In both models, the two localities in the USA where *E. coerulescens* was collected show a complete absence of habitat suitability. However, high suitability of habitats (>0.3) in the USA for *E. coerulescens* occurs in some locations in Florida while inclusion of all species in the group expands suitable habitat to much of the southeastern USA. The models also suggest high suitability of habitats across the Caribbean as well as in other regions in Mexico and Central America.

**Discussion**

Herein we circumscribe the species in the *coerulescens* group and confirm that the two male specimens of *Eufriesea* from the USA are *E. coerulescens*. We also provide a fully illustrated account of the species, comparative diagnoses, and an updated key to the Mexican species of *Eufriesea* to facilitate their identification. Both sexes of the three new species described here are superficially almost identical to either *E. coerulescens* or *E. micheneri*, and were discovered while examining specimens standing under these names. They can reliably be distinguished by differences in the length of the glossa, punctation of the male second tergum and female mesoscutellum, and the shape of the posterior felty patch of the male mesotibia. The dark female specimens from Islas Marias of Nayarit State, located 112 km from the coast, mentioned by Ayala and Engel (2008), might also correspond to another undescribed species. However, these specimens were not available for study. Kimsey (1982) was aware of variations among the specimens she examined and determined as *E. coerulescens*, but considering the small number of specimens available, she appropriately regarded them as variants. For example, in addition to mentioning the differences in the integumental coloration, she also pointed out differences in the length and width as well as the distance between the apical lobes of the male S7 of *E. coerulescens* (e.g., Figs 40 and 90). Such differences among the material she examined correspond to the species newly defined herein.

Species distribution modeling (SDM) based on observed occurrences are good tools for predicting the potential distribution of exotic species including bees (e.g., Hinnojosa-Díaz et al. 2005, 2009, Gonzalez et al. 2010, Silva et al. 2014). Incorporating biotic interactions in these models, such as plant-bee relationships, is expected to have a major influence on the modeled distribution. However, host plant associations are not always available or reliable for bees, and available studies suggest that they do not
significantly improve the algorithm’s ability to predict the distribution (e.g., Silva et al. 2014). A few plant records are available for the species of the *coerulescens* group, but most are determined to the genus level and do not distinguish between bees collecting pollen versus nectar. Thus, these records may not represent pollen host associations.

Our models had high AUC and ROC values, which indicate high performance and quality. According to our analyses, the males of *E. coerulescens* collected in the Guadalupe Mountains of western Texas and southeastern New Mexico, USA, are likely long-distance transient vagrants, as suggested by the complete absence of predicted suitable habitat for stable populations of this species to persist in that area. The model using the occurrence records of *E. coerulescens* alone (Fig. 129) predicts habitat suitability (0.169–0.298) in some areas in western Texas and across the state of Coahuila with a similar value to that of the northernmost known locality for this species (Chihuahua, General Trias). Such areas ought to be sampled to determine if populations of the species exist there. The same should be done in western Chihuahua and southeastern Sonora, where conditions appear to be suitable for this species. The model also predicts some areas of southern New Mexico, Arizona, and Florida with high values of habitat suitability, which suggests that the species has the potential to occupy these areas if it eventually reaches there (Fig. 129).

Our model also indicates high habitat suitability (>0.425) for *E. coerulescens* in western and southern Mexico, as well as in Guatemala, El Salvador, Honduras, Nicaragua, northwestern Costa Rica, and part of Panama. This suggests the possibility of a broader overlap in its distribution with the other species of the group in Mexico than currently known and opens up the possibility that some of the literature records for this species from Central America might be correct. Interestingly, our analyses also show the presence of suitable habitats for *E. coerulescens* in the Caribbean, similar to the potential distribution models developed for the other two adventive species of orchid bees in the USA (Hinojosa-Díaz et al. 2009). Except for one species of *Euglossa* from Jamaica, orchid bees are otherwise absent from the modern melittological fauna of the Caribbean, although two fossil species (one of *Euglossa* and one of *Eufriesea*) have been recorded from the island of Hispaniola (Engel 1999).

**Acknowledgements**

We thank David Roubik for comments and suggestions that helped us improved this work, and the curators, collection managers, and staff personnel of the collections from which we borrowed specimens. Agnièle Touret-Alby (Muséum National d’Histoire Naturelle, France) kindly arranged the loan of the type of *Eufriesea coerulescens*. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.
References


