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Description of a new genus of North and Central American planthoppers (Hemiptera: Fulgoridae) with fourteen new species

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Abstract

The fulgorid name *Alphina glauca* (Metcalf) has been used erroneously since its inception to refer to a primarily southeastern U.S. species described originally as *Calyptoproctus marmoratus* Spinola. Additionally, at least three undescribed species from the Southwest have been incorrectly identified as *A. glauca*. The holotype of *A. glauca* has not been located. Since *A. glauca* is presently used to refer to multiple species, a neotype is designated which places *A. glauca* into synonymy with *Calyptoproctus marmoratus*. We establish a new genus, *Scaralina*, into which it is placed, giving the new combination *Scaralina marmorata* (Spinola), along with three southwestern, one Texan, and ten Mesoamerican taxa, named here as new species: *S. aethrinsula*, *S. chapina*, *S. cristata*, *S. durango*, *S. gigantea*, *S. hawksi*, *S. metcalfi*, *S. monzoni*, *S. obfusca*, *S. obrienae*, *S. orientalis*, *S. rileyi*, *S. sullivani*, and *S. veracruzensis*. Additionally, one new species of *Scaralis* in a new subgenus, *Scaralis (Alphinoides) inbio*, is described from Costa Rica and Guatemala. The limited information available suggests these insects feed on oaks (*Quercus*). The single defining putative synapomorphy for the subtribe Calyptoproctina is the enlarged apical plate on the female abdomen, which is absent in at least two members of *Scaralina*, and is also present in some genera that belong outside of Poiocerinae, so we reject the recognition of this subtribe. We consider that *Scaralina* is probably more closely related to the genus *Scaralis* Stål than to *Alphina* Stål. Based on morphology, some species originally described in *Scaralis* appear to be more closely related to one another than to the type species of the genus, and are here placed in a new subgenus, *Alphinoides*; *Scaralis fluvialis* Lallemand and *Scaralis nigronotata* Stål, plus three species originally described in *Poiocera*; *Scaralis quadricolor* (Walker) (the type species of *Alphinoides*), *Scaralis semilimpida* (Walker), and *Scaralis spectabilis* (Walker). Diagnoses are given for separation of the genera *Scaralis* and *Scaralina*, as well as the subgenus *Alphinoides*, plus descriptions of and keys to all species of *Scaralina* north of Panama, as well as keys to the genera corresponding to the former subtribe "Calyptoproctina" occurring north of Panama.

Key words: Poiocerinae, Poiocerini, *Alphinoides*, *Calyptoproctus*, *Quercus*, *Scaralina*, *Scaralis*, United States, Mesoamerica, biogeography

Introduction

In the most recent checklist of North American Fulgoridae (Bartlett *et al*., 2014), only 17 species are listed, seven of them in the subtribe Calyptoproctina (tribe Poiocerini, subfamily Poiocerinae), with two of these, *Alphina glauca* (Metcalf, 1923) and *Calyptoproctus marmoratus* Spinola, 1839, being the sole representatives of their respective genera. The former taxon is well-represented in museum collections, from throughout the southeastern United States (North Carolina through Florida and into Texas), but also, in an apparent geographic disjunction,

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abundantly from many of the "Sky Island" mountain regions in southeastern Arizona, particularly the Atascosa, Chiricahua, Huachuca, Patagonia, Peloncillo, Santa Catalina, and Santa Rita mountain ranges. In online resources such as iNaturalist and BugGuide, the southeastern U.S. populations have more often been recently classified as *Calyptoproctus marmoratus*. Despite a lack of published host information, nearly all the known habitats throughout the range appear to include oak (*Quercus* spp.) as a predominant plant, and it is likely that oaks may be the preferred hosts. The overwhelming majority (>99%) of the specimens with collection data are adults attracted to lights at night, reinforcing the idea that they do not feed on herbaceous plants or shrubs, where they would be easily seen and collected by other methods.

Adult males and females collected at many of the "Sky Island" localities were historically considered to comprise three co-occurring "morphs" of *A. glauca*, but upon closer investigation, these three "morphs" are distinct, sympatric species, and none of them are the same as the species from the southeastern U.S. We needed to determine which was the true *A. glauca*, but this was complicated by three factors: (1) the holotype (described as *Crepusia glauca*) was from Brownsville, Texas, (2) the holotype cannot be found, and (3) at least one author (Ball, 1933) had considered *Crepusia glauca* Metcalf to be a junior synonym of *Calyptoproctus marmoratus* Spinola. With access to images of Spinola's type of *Ca. marmoratus* (from "North America"; through the courtesy of Dr. Harald Schillhammer, Naturhistorisches Museum Wien; Fig. 1) for comparison, there is nothing in Metcalf's original description that would invalidate Ball's claim, though Metcalf himself reversed the synonymy (Metcalf, 1947), and considered the use of *Ca. marmoratus* for a species from Mississippi (by Dozier, 1928) to be a misidentification. As such, we accepted Ball's proposed synonymy, meaning that none of the species from Arizona were described, and the name *Calyptoproctus marmoratus* applies to the species that ranges from Texas east to Virginia.

FIGURE 1. Holotype male of *Calyptoproctus marmoratus* Spinola (courtesy Dr. Harald Schillhammer, NMW).

The reality of the synonymy raised another question: this species' name had been associated with various genera by different authors at various times (*Crepusia* Stål 1866, *Alphina* Stål 1863, and *Calyptoproctus* Spinola 1869), creating uncertainty as to which of these genera, if any, represented the correct placement. Metcalf eventually (1938) recognized that *glauca* was not in the genus *Crepusia*, and transferred *glauca* to the genus *Alphina.* Metcalf (1938) also created a new subtribe Calyptoproctina (which he distinguished solely by the elongation of the terminal tergum of the female abdomen into a plate covering the anal region, thus excluding *Crepusia*—exemplified by, e.g., figures 45, 49, 53, and others in Porion, 1994), and placed *Alphina* in the Calyptoproctina. After examination of the type species of *Alphina* (*A. nigrosignata* Stål, 1863) and *Calyptoproctus* (*C. elegans* (Olivier, 1791), and as many additional species in these genera as could be located, it became evident that none of the species at hand, including *Calyptoproctus marmoratus*, belonged to either of these genera.

In the process of examining specimens of New World Poiocerinae for this study, we found additional undescribed taxa, ranging from Mexico to Costa Rica, very closely related to the U.S. species above. While there are strong similarities among certain species within *Alphina* and *Scaralis* Stål, 1863, there are significant differences between the type species of these two taxa and from "*Alphina glauca*" and its relatives. Examination of all the genera of

Poiocerini found in Mesoamerica revealed that *Scaralis* possesses the most similarities, especially of the head and thorax, suggesting that the "*Alphina glauca*" group represents the probable sister taxon to *Scaralis*, though the definition of *Scaralis* is problematic, as the type species shows numerous differences between it and several other species which are presently treated as congeners. The type species of the genus *Jamaicastes* Kirkaldy, 1900 (*J. basistella* (Walker, 1851)), also shares some features and is clearly related to these taxa, though *Jamaicastes* as presently circumscribed is unlikely to be monophyletic, as may be true for *Scaralis*; some older authorities (e.g., Distant, 1887) had placed some of the species of *Scaralis* into *Jamaicastes*, though Metcalf (1938) and others later realigned placements. There are, depending on various criteria, anywhere from 10–15 South American or Mesoamerican genera in Poiocerini, several containing only one or two species, at least a few of which might easily prove close to these two genera (for example, the genus *Matacosa* Distant, 1906, containing the single species *M. miscella* Distant, 1887), but for purposes of this work, we treat the "*Alphina glauca*" group species collectively as a discrete taxonomic entity of equivalent rank, and putative sister taxon, to *Scaralis*. Accordingly, our primary aim, in this work, is to fix the identity of *Crepusia glauca* Metcalf, describe several related species that occur from Panama northward, and provide evidence for placing these in the new genus, *Scaralina* (described below).

Of broader concern is that two of the new species of *Scaralina* lack the elongated supra-anal plate on female tergum 6 that is the defining feature of (and putative synapomorphy for) the subtribe Calyptoproctina, and that an elongated supra-anal plate can also be found in members of genera that are (or have been) outside the Calyptoproctina (e.g., *Birdantis* Stål 1863, *Desudaba* Walker 1858, *Hypaepa* Stål 1862, *Japetus* Stål 1863, *Paralystra* White 1846). We have also seen two undescribed species from the Yucatan peninsula, with several features suggesting affiliation to *Jamaicastes*, that are also lacking a female supra-anal plate. A recent molecular study (Urban & Cryan, 2009) included 11 Poiocerini, 10 of them putatively calyptoproctines, including *Scaralina* (as "*Alphina glauca*") but excluding *Jamaicastes*. These authors were unable to recover Poiocerinae, Poiocerini, or Calyptoproctina as monophyletic, and *Calyptoproctus* was only distantly related to any other calyptoproctines, which appeared at five separate nodes in the phylogeny. The sister taxa to *Birdantis*, *Calyptoproctus*, *Cyrpoptus* Stål 1862, and *Learcha* Stål 1863, were not even in Poiocerini; *Birdantis* (and possibly all the other Old World "calyptoproctine" genera, such as *Desudaba*) appears within Aphaeninae in all analyses, *Paralystra* (Paralystrini) was sister to *Calyptoproctus*, *Amycle* Stål 1861 (Amyclinae) was sister to *Cyrpoptus*, and *Lystra* Fabricius 1803 (Lystrini) was sister to *Learcha*. There was, however, a monophyletic group containing *Scaralis semilimpida* (Walker, 1851), *Matacosa miscella*, and one of the new *Scaralina* species (also some undetermined "*Scaralis*" species). The sister to this clade was *Poblicia* Stål 1866, the sole included member of Poiocerina.

As such, *Calyptoproctus* is possibly not related to any other genera placed in Poiocerini, nor any members of the "Calyptoproctina". The three species determined only as "*Scaralis* sp." Included one from Costa Rica (which might correspond to the new species described herein). It is possible that one or more of these "*Scaralis* sp." may have been *Scaralina* species, as some of them resolved as closely related to the *Scaralina* from Arizona, though relationships differed depending on the analysis (Urban & Cryan, 2009). Given evidence that the female supra-anal plate is subject to variation within existing genera, and can be independently derived or lost (appearing at five places in Urban & Cryan's analysis), it cannot be relied upon to delimit any monophyletic groupings. Poiocerinae, Poiocerini, and Calyptoproctina are not monophyletic as presently defined, and at the very least subtribes within Poiocerini should not be recognized at all, pending much better resolution of the relationships in the subfamily (the genus *Poiocera* Laporte 1832 itself was not included in the study). However, the sister group relationship between *Poblicia* and the "*Scaralis* clade" suggests that the latter lineage does at least belong to Poiocerini, as the morphological similarities of *Poiocera* and *Poblicia* suggest that these genera may indeed be closely related.

It is also worth noting that there are only three described species in the *Scaralis* clade definitively reported from Mesoamerica (*Matacosa miscella*, *Scaralis neotropicalis* (Distant, 1887), and *Scaralis obscura* (Distant, 1887)), two species from the Antilles (*Jamaicastes basistella* and *J. cubana* Dlabola & Zayas, 1980), and one from the U.S. (as *Calyptoproctus marmoratus*); we have seen specimens of all of these except *J. cubana*, and the present work adds numerous additional taxa to the fauna, with no doubt that many more remain to be discovered. We have seen, in museum collections and online images, at least another dozen Mesoamerican poiocerines that represent new taxa, including several new genera, though all but one does not appear affiliated with *Scaralis* and its relatives; placement of the one exception (an apparent *Scaralis*-group relative lacking a supra-anal plate, mentioned above) requires more careful consideration, and it may yet prove to belong in *Jamaicastes*, or represent an intermediate lineage. These observations strongly suggest that the Mesoamerican fulgorid fauna is both undersampled and underdescribed, and

in dire need of more comprehensive revisionary work and molecular analyses; we hope the present study will help stimulate such investigations.

Material and Methods

Terminology. Veins and wing structures follow Bourgoin *et al*. (2015); the subcosta, Sc (= ScP + R), which delimits the postcostal (or subcostal) cell and runs almost to the wing apex; the first major vein after the subcosta is the medial vein, M (= MP), and the other main vein before the claval vein is CuA; the claval vein (= CuP), which is straight and deeply set in the claval furrow, separating the anal region of the wing (or clavus); the forewing clavus contains the postcubital vein, Pcu, anteriorly, and anal vein, A_1, posteriorly, and these form a fused vein (Pcu + A_1) that reaches the wing margin just basad of the claval vein juncture, diagnostic for the superfamily Fulgoroidea. Fulgorids possess a small but prominent ventral lobe projecting from the basal cell of the forewing, the versteifung, that in *Scaralina* is strongly concave posteriorly and forms a "cap" over the base of the hindwing when at rest, firmly locking the forewings in place.

Male genitalic terms generally correspond to those used by Seidel & Wessel (2013). The descriptions of the various taxa are given in more detail for those common species where it was possible to examine large numbers of specimens, and the rarer taxa in the same species groups are compared and contrasted to these; we expect that a very large proportion of U.S. institutional collections will have specimens of *marmorata*, *aethrinsula*, *cristata*, and possibly *obrienae* to use as standards for comparison, and also feel less comfortable giving detailed descriptions based on only one or two specimens, when some characters may prove to be variable. The genus is intended to be attributed to the senior author, and the species as specified in the text.

Abbreviations. Note that under "Specimens examined" below, if any literal text of labels is given, it is in quotes. Repository codens are:

AMNH—American Museum of Natural History, New York, USA;
ASULOB—Lois O'Brien collection at Arizona State University, Tempe, Arizona, USA;
CAS—California Academy of Sciences, San Francisco, California, USA;
CNC—Canadian National Collection of Insects, Ottawa, Ontario, Canada;
CSCA—California State Collection of Arthropods, Sacramento, California, USA;
EMEC—Essig Museum, University of California, Berkeley, California, USA;
FSAG—University of Liège, Gembloux Agro-Bio Technologies, Gembloux, Belgium;
INHS—Illinois Natural History Survey, Champaign, Illinois, USA;
GGCB—private collection of Geert Goemans;
MNCR-A—Museo Nacional de Costa Rica, San José, Costa Rica (specimens formerly from INBio);
MTEC—Montana State University, Bozeman, Montana, USA;
NCSU—North Carolina State University Insect Collection, Raleigh, North Carolina, USA;
NMW—Naturhistorisches Museum Wien, Wien, Austria;
TAMU—Texas A&M University, College Station, Texas, USA;
TTCC—Texas Tech University, Lubbock, Texas, USA;
UANL—Universidad Autónoma Nuevo León, Linares, Nuevo León, Mexico;
UCR or **UCRC**—University of California, Riverside, California, USA;
UDCC—University of Delaware, Newark, Delaware, USA;
UNAM—Universidad Nacional Autónoma de Mexico, Mexico City, D.F., Mexico;
UNSM—University of Nebraska State Museum, Lincoln, Nebraska, USA;
USNM—National Museum of Natural History, Washington, D.C., USA;
UTIC—University of Texas, Austin;
UVGC—Universidad del Valle de Guatemala, Guatemala City, Guatemala.

Alphanumeric GUIDs, when given, are generally indicative of the repository whose coden corresponds; when they are not, the repository is indicated separately. Abbreviations used here for Mexican states are: CHI (Chihuahua); DUR (Durango); HID (Hidalgo); JAL (Jalisco); NL (Nuevo León); PUE (Puebla); SIN (Sinaloa); SLP (San Luis Potosí); SON (Sonora); TAM (Tamaulipas); VER (Veracruz).

Systematics

Family Fulgoridae Duméril, 1820

Subfamily Poiocerinae Haupt, 1929

Tribe Poiocerini Haupt, 1929 (not Metcalf, 1938)

General information about sexual dimorphism

Sexual dimorphism is minimal in these taxa, as is typical for Fulgoridae, however, nearly all females in genera formerly classified as belonging to Calyptoproctina have abdominal tergum 6 modified and extending backward as a supra-anal plate, generally covering the anal tube and genitalia (though this plate is generally smaller in the genus *Scaralina* than is typical for related genera, and rarely completely conceals the anal tube; in two species, noted below, females lack this plate entirely). Females tend to be slightly larger than males, with a broader anal tube, and often with slightly stronger and/or more extensive dark markings in the forewings. In one species it appears that the base of the hindwing is colored differently in males and females.

Scaralina Yanega, gen. nov.

Type species. *Calyptoproctus marmoratus* Spinola, 1839, by present designation.

Etymology. As these species are intermediate in many features between the related genera *Scaralis* and *Alphina*, the name is a portmanteau of these two generic names. For purposes of gender agreement, the name should be considered feminine.

Diagnosis. Species of this taxon are most similar to those of *Scaralis* Stål, especially in the reduced femoral ridges and mesocoxal spines, as well as numerous minor details of the head and thoracic structure and sculpture, mostly not shared by other genera (other than *Jamaicastes*), such as the pattern of notal carinae, the long rostrum, and the broad lateral lobes of the lower frons. There are, however, several characters that together distinguish all members of *Scaralina* from at least the type species of *Scaralis* (*S. picta* (Germar, 1830)) and many of the other included species we have been able to examine (*S. corallina* (Gerstaecker, 1860), *S. neotropicalis* (Distant), and *S. obscura* (Distant); also see below). Most reliable among these features in *Scaralina* are the following: the second antennomere (small and globose in *Scaralina* versus large and asymmetrically ovoid, larger than the antennal socket in *Scaralis* (Fig. 7)); the more elongate clypeus (usually roughly twice as long as wide, and reaching the apex of the forecoxae); the forewings without an arcuate impressed nodal line at the base of the apical hyaline portion (very well-defined in *Scaralis s.s.*); the distal forewing membrane patterned with irregular maculations and variable venule coloration (membrane hyaline, evenly-tinted, or gradually shading, with venules uniform or very gradually shading in almost all *Scaralis*); a projecting, abbreviated, and concave trapezoidal versteifung with a strongly angulate proximal margin (in *Scaralis* the "versteifung" is lower and sometimes elongated, weakly concave, and more rounded at the proximal end; compare Figs 4–5); the prominent leg markings (contrasting transverse bands on fore- and mid-femora and tibiae); the numerous black granular sublateral pits on the abdominal terga (these pits concolorous with the surrounding cuticle in *Scaralis*, and fewer in number); the male gonostyli more visibly enclosing the aedeagal apex, with a setose bulge at the base of an incurved dorsal surface (in *Scaralis* only the extreme apex of the aedeagal complex is sometimes enclosed dorsally, and the setose bulge is very small and approximates the inner margin of the gonostyle (Figs 8, 9)); the fine but very readily visible pubescence on the dorsal thorax, in particular (the dorsal thorax is usually bare in *Scaralis*, as are the wing veins, or at most with barely visible short, fine setae). Several more variable or occasionally unreliable features can be added to this list, for distinguishing *Scaralina* from *Scaralis* (*Scaralis*): the sub-ocular lobes (nearly absent in most *Scaralina*, versus distinct and rounded or subacute in most *Scaralis*); the well-defined and contiguous carinae of the mesonotum in *Scaralis* (no species of *Scaralina* has all of these carinae well-defined for their entire length; one or more are reduced to low ridges or entirely obsolescent, at least in part); the reduced female supra-anal plate in *Scaralina* (absent or only partially concealing the anal tube versus completely covering it; in genera such as *Scaralis* this

plate is typically at least three times the length of any of the preceding tergites); the deep punctures and/or wrinkles in the dorsal and lateral faces of the pronotum in *Scaralis s.s.*; the red or orange coloration of the hindwing bases (only two *Scaralina* have blue coloration basally, while *Scaralis* typically do); the greatly reduced wax production in *Scaralina* (in *Scaralis*, the face and pleura often have large areas bearing wax pollinosity (Fig. 103), and the spiracles are often entirely occluded by wax, plus a distinct mass of wax on either side of the terminalia in females); the hyaline or weakly infumate anal region of the hind wing (strongly infumated with pale venation in *Scaralis s.s.*); the broadly rounded apical concavity of the male anal tube (generally deeply notched in *Scaralis s.s.*; compare Figs 10–11, 23). Despite some variability, the combined list of such features that differ between the two groups is enough, we believe, to justify a generic-level separation, and we further believe this group as defined here is likely to be monophyletic; nonetheless, it would not be surprising to discover (e.g., if and when a thorough molecular phylogenetic analysis with all of the South American species is performed) that *Scaralina* as here defined render *Scaralis* paraphyletic, or the converse, in which case the two groups may need to be relegated to subgenera within a more inclusive genus *Scaralis*. *Scaralina chapina* and *S. monzoni*, in particular, both described herein, show more intermediate features than any of the other taxa (e.g., these species have the clypeus only slightly longer than broad, have blue hindwing bases, with the forewing basal markings extending to the point where RP deviates from ScP+RA, and lacking translucent basal areas in the forewings; *chapina* also has the male gonostylar hooks short and thickened as in *Scaralis*; compare Fig. 9 and Fig. 83), and were it not for these two species, the separation of the two genera would be far more definitive.

Composition. Included species (15): *Scaralina aethrinsula* Yanega & Van Dam, **sp. nov.**; *S. chapina* Goemans & Yanega, **sp. nov.**; *S. cristata* Yanega & Van Dam, sp. nov; *S. durango* Yanega. **sp. nov.**; *S. gigantea* Yanega, **sp. nov.**; *S. hawksi* Yanega, **sp. nov.**; *S. marmorata* (Spinola, 1839); *S. metcalfi* Yanega & Van Dam, sp. nov; *S. monzoni* Goemans & Yanega, **sp. nov.**; *S. obfusca* Yanega, **sp. nov.**; *S. obrienae* Yanega & Van Dam, sp. nov; *S. orientalis* Yanega, **sp. nov.**; *S. rileyi* Yanega, **sp. nov.**; *S. sullivani* Yanega, **sp. nov.**; *S. veracruzensis* Yanega & Van Dam, **sp. nov.**

Description. ***Head***: Head broader than long, not projecting. Vertex roughly 4 times as wide as long, demarcated on all sides by lamellate rim, produced ventrolaterally into rounded supra-ocular lobes, which are appressed against dorsoposterior eye margin; posterior rim reflexed anteriorly. Sub-ocular lobes absent (or very weak and rounded). Vertex with two pairs of posteromedial spots (e.g, Fig. 47), which may or may not contrast with the surrounding color (so they may not be evident), but of a distinctly differing texture (dull and granular) from the surrounding cuticle to be detectable; the pair nearer the midline are transversely ovoid, and well-defined, outer spots larger, more variable in shape, and irregular, with less definite edges. Frons roughly rectangular (wider than long), broadly flat or very gently convex for most of its surface; typically smoother and sometimes shallowly impressed below upper portion, often very finely rugose below and without well-defined ridges, though a few species (e.g., Figs 31, 39) show a medial ridge and/or converging lateral ridges; the lower margin just above the clypeal suture is sometimes thickened into a low transverse ridge; lateral margins of frons vary from nearly straight and subparallel to slightly concave and divergent below, with lower lobes bearing a depression (sometimes distinctly expanded at corners), which is impressed and often bearing a small translucent window in the depression (e.g., Fig. 34); frons reflexed along upper portion to form an appressed flap, typically at an obtuse angle relative to the plane of the lower frons, delimited above by strong transverse crease, reflexed portion defined laterally by secondary oblique crease a short distance below upper corner of flap, and with the dorsal reflexed portion commonly having distinct, closely-spaced vertical wrinkles; individual specimens sometimes possess small incomplete interstitial ridges (partial flaps) between the upper lateral edge of the transverse frontal crease and the anterior rim of the vertex (these may be remnants of an embryonic frontal sac). Clypeus elongate triangular (distinctly longer than broad, typically at least 1.5 times as long, reaching to apex of forecoxae), nearly straight along sides, surface fairly smoothly convex but often very shallowly concave near midline, with distinct, parallel-sided lateral areas; upper margin varies from almost straight to distinctly dorsally arcuate, sometimes very slightly indented medially. Rostrum with 3 visible segments, middle segment longest, typically extending well beyond metacoxae, the tip of the rostrum reaching almost to the hind femoro-tibial joint or beyond (Fig. 2); in most species, mostly pale except apical segment, and anterior (ventral) ridges also somewhat darkened. Antennae short, base concealed in protruding, pale socket; basal antennal segment often darkened dorsally, otherwise pale; second segment small (diameter approximately equal to antennal socket diameter or very slightly larger), nearly spherical to slightly pyriform, symmetrical (Fig. 32), typically dark, with pale circular to ovoid sensillae; stylus apical, elongate, dark, with a small basal bulbosity,

arising from slight indentation. Eyes prominent, roughly circular in outline; lateral ocelli in angle between frons and lower eye margin, translucent yellowish.

***Thorax*.** Dorsal and lateral surfaces with very fine and slightly scattered pale erect pubescence, generally longest on pleura and ventral sclerites. On the notum of nearly all species these setae are longer than the interspaces between setae, and easily seen (especially in *S. rileyi* (Fig. 3)), but the type species, *S. marmorata*, has diagnostically shorter setae; the density is similar to other species, but shorter and slightly recumbent, making them difficult to observe unless viewed from an oblique angle. Pronotum elongate (more than 2x length of vertex along midline), anterior margin concave, following contour of head, disc with a distinct medial carina, sometimes projecting and sub-lamellate; with a sharply carinate lateral anterior rim that starts near the inner eye margin, and continues to near the middle of the tegula, below the eye; there is an oblique carina just ventral to this, continuing onto the ventral posterior lobe of the pronotum, which approximates the forecoxal bases and partly overlaps the anterior face of the mesepisternum; posterior margin of pronotum usually with angulate medial notch, and commonly a low transverse ridge immediately preceding posterior margin. Pronotum with paired, dark granular spots similar to those on vertex; a somewhat pit-like anteromedial pair, and a lateral post-ocular pair (at the indentation immediately behind the outer posterior edge of the eye), and often with fine transverse wrinkles in the posterior half. Mesonotum at midline about equal in length to the vertex and pronotum combined, bearing low longitudinal medial and lateral carinae, the latter sinuate to varying degrees, ending posteriorly at the outer edges of a pair of small dark posterior granular spots (the inner edges of which may sometimes be bordered by a weak inner posterior carina that starts at the terminus of the lateral longitudinal carina), and the inner edges of much larger granular spots (dark at least in part) which are variously elongated anteriorly; the lateral carinae at the extreme anterior edge are strongly angled inward and converge at the midline, but these anterior "arms" are hidden underneath the posterior pronotal margin, and thus seldom visible (they may be exposed if the pronotum is somewhat depressed); there are short transverse-oblique ridges located laterad of the lateral carinae, but these become obscure before attaining the lateral carinae; the medial carina becomes obscure posteriorly, ending in an upward-angled semi-acute lobe that is typically creased or wrinkled transversely at its base. Mesopleuron delimited from mesosternum by a strongly and fairly evenly arcuate ridge running from the upper posterior corner of the procoxal membrane to the upper anterior corner of the mesocoxa; the degree of curvature of the ridge reduces gradually from anterior to posterior. Metacoxa with a prominent dorsoposterior spine, this spine absent or reduced to a minute pointed tubercle on the mesocoxa. Femora weakly convex on anterior face, more strongly so on posterior face, with only two well-defined longitudinal setose ridges, along the anterior dorsal and ventral edges. Fore- and mid-legs virtually identical in color pattern: anterior coxal face typically with two dark spots which may coalesce; femora with at least two black bands, the basal one largest, and sometimes with a very small third apical or subapical band or mark; tibiae with three black bands, the apical one generally largest, often but not always reaching the apex; pro- and mesotarsi black except for pale dorsal mark on third tarsomere; metafemur typically with one black band near apex, metatibia with three dark bands and four or five lateral spines, metatarsi with first two tarsomeres mostly pale except dorsally at base, third tarsomere generally matches those of other legs.

Wings. Forewings without evident nodal line; "versteifung" posteriorly concave, abbreviated and strongly protruding, angulate at least on proximal margin, trapezoidal to almost triangular (Fig. 5); pigmented portion of forewing (excluding postcostal cell) extending over less than half the length (ending near the claval juncture). Distal portion of forewing with membrane faintly to strongly maculated, never entirely hyaline, and venules varying from light to dark, never uniform in color. Nearly all species with the basal forewing markings divided into a paler basal portion and a darker distal portion that forms a band from subcosta to clavus, near the first branch of MP (about 1/3rd of the wing); the gap between MP and CuA is almost always less than the gap between it and ScP+R. Venation relatively coarse, with relatively few branches and relatively few crossveins compared to most poiocerine genera. In most species, the crossveins are simple and define square to rectangular cells, though there are typically some reticulated venules in the radial cell (between the base of MP and ScP+R) and in the anal region (especially between Pcu and A_1); a few species show reticulated venules elsewhere, such as the postcostal cell, which in most species has simple crossveins or may be nearly devoid of crossveins. Hindwings with colored bases, typically red or orange (rarely pale blue), membrane of anal region entirely clear to slightly infumate.

Abdomen. Most species with tergites and pleurites predominantly dark, and sternites predominantly pale; dorsal pale markings, when present, most commonly yellow to orange, though sometimes red, and sometimes grayish-buff. Spiracles large, one pair dorsal at base of abdomen (Fig. 6), others in the dorsal pleurites. Terga 3–6

typically with small, black, pit-like lateral depressions with granular texture; typically arranged in two sets on each side, an anterior set of 3–4 pits and a posterior set of one large pit and one very small pit (Fig. 6). Female tergum 6 often produced into a supra-anal plate, but generally not entirely concealing anal tube; at most twice the length of any of the preceding terga, but unmodified in two species (*aethrinsula* and *durango*), where terga 5 and 6 are nearly identical in length. Wax production evidently limited, typically a faint residue at the base of the genitalia, and traces in spiracular apertures.

Male terminalia. Apico-dorsal portion of the gonostyli very strongly incurved and largely enclosing the apex of the aedeagal apparatus, in most species nearly parallel at the midline for most of the apical half. The outer inflection of the incurved portion marked by a swollen region with numerous sharp, short, bristle-like setae (the "setose bulge"); basal hook of the gonostyle located anterior to this swelling, the hook variably developed but generally small, recurved, and sharply acute, with a well-developed flap-like fold at the base. Inflatable aedeagal elements (in inflated preparations) with sac-like dorsal and ventral lobes on both sides, and medial outcurving horn-like lobes with slightly sclerotized inner basal edges and faintly sclerotized apices. Both sexes with anal tube somewhat heart-shaped in dorsal view, widest near middle (in female) or past middle (in male) and narrowest at base; in female strongly compressed and only very slightly convex on upper and lower surfaces, in male more convex dorsally; margin of apical aperture broadly concave, semicircular, exposing pygofer (Fig. 23, resembling also Fig. 11).

KEY TO THE SPECIES OF THE GENUS *SCARALINA* OCCURRING NORTH OF PANAMA

1. Mottling of dorsal thorax composed primarily of numerous, tiny pale spots on a dark background, each spot with a seta in its center (Figs 42, 44–47)—*cristata* species group **2**
-. Dorsal thoracic markings otherwise, well-defined. **6**
2. Pronotal carina strongly cristate (Fig. 12); spots on thoracic dorsum and vertex mostly well-separated (Fig. 44); abdomen with strong dark bands separating the median and lateral pale markings, which are composed of fused spots (Fig. 15) . . . . . ***cristata*** **Yanega & Van Dam, sp. nov.** (USA: AZ, NM; Mex: CHI, DUR, SON)
-. Pronotal carina sometimes strong, but not compressed into a crest; spots on thoracic dorsum and vertex mostly fused into irregular clusters (Figs 42, 45–47); abdomen with irregular dark markings, median and lateral pale markings largely confluent (Figs 6, 13, 17–18) **3**
3. Abdominal dorsum extensively bright red; hindwing very broadly red at base (Fig. 18); forewing heavily maculated medially with contrasting venation (Fig. 61); large species (well over 20 mm from frons to wing tips) . . . . . .***gigantea*** **Yanega**, **sp. nov.** (Mex: CHI, DUR)
-. Abdominal dorsum yellowish to orange; hindwing basal markings small, orange in color; forewing maculation variable but never as extensive. **4**
4. Hindwing reddish-orange at base; abdominal dorsum mostly orange (Fig. 17); forewings with distinct medial maculation (Fig. 60); lower frons mostly dark (Fig. 30); female lacking elongated supra-anal plate on tergum 6 . . . . . ***durango*** **Yanega**, **sp. nov.** (Mex: DUR)
-. Hindwing pale orange at base; abdominal dorsum yellowish (Figs 6, 13, 19); lower frons at least partially pale with contrasting dark circular spots (Figs 27, 32); forewings with faint spotting medially (Figs 57, 62) **5**
5. Frons with large dark spots (Fig. 27); female lacking elongated supra-anal plate on tergum 6 (Fig. 6) . . . . . ***aethrinsula*** **Yanega & Van Dam, sp. nov.** (USA: AZ, ID, NM, UT; Mex: CHI)
-. Frons mostly pale, with very small dark spots (Fig. 32); female with elongated supra-anal plate (Fig. 19) . . . . . .***hawksi*** **Yanega, sp. nov.** (Mex: DUR)
6. Lower frons without tiny dark spots, upper edge of frons smooth and largely or entirely pale, clypeus only slightly longer than broad (Figs 28, 35); hindwings blue or red at base **7**
-. Lower frons with tiny dark spots (or entirely black), upper edge of frons irregularly maculated and/or with vertical creases, clypeus distinctly longer than broad (Figs 33–34, 36–41); hindwings orange or reddish-orange at base—*marmorata* species group. **8**
7. Frons entirely pale yellowish green (Fig. 28), forewing bases and postcostal cell strongly marked with rose-magenta and green (Figs 14, 58) . . . . . ***chapina*** **Goemans & Yanega, sp. nov.** (Guatemala to Honduras)
-. Frons dark with upper margin pale, and dark intrusion at midline (Fig. 35); forewing bases extensively black, venation highly contrasting, greenish, including in postcostal cell (Figs 21, 65) . . . . . .***monzoni*** **Goemans & Yanega, sp. nov.** (Mex: SIN to Panama)
8. Base of forewing with dark sub-basal band greatly reduced, light markings mostly orange, semi-translucent, remainder of wing almost entirely hyaline, often with unusually large rectangular cells (Figs 26, 70–71). **9**
-. Base of forewing with dark sub-basal band more extensive, light markings and crossveins varying from translucent to opaquely pale ochraceous, remainder of wing with distinct, irregular spotting, cells not especially large. **10**
9. Hindwings light orange at base; basal half of subcostal cell lacking crossveins (Fig. 71); pronotum pale anteromedially (Fig. 56); frons laterally nearly straight, lower lobes not expanded laterally (Fig. 41) . . . . . .***veracruzensis*** **Yanega & Van Dam, sp. nov.** (Mex: VER)

-. Hindwings reddish-orange at base; basal half of postcostal cell with crossveins (Figs 26, 70); pronotum black anteromedially (Figs 26, 55); frons laterally slightly concave, lower lobes expanded laterally (Fig. 40) . . . . . ***sullivani* Yanega, sp. nov.** (Mex: VER)

10. Lateral mesonotal carinae low but distinct, with posterior portion running along inner (medial) side of posterior mesonotal spot, thus appearing strongly recurved (Fig. 49); medial abdominal dorsum broadly orange (Fig. 20). . . . . ***metcalfi* Yanega & Van Dam, sp. nov.** (USA: AZ; Mex: CHI)

-. Lateral mesonotal carinae with posterior portion running distinctly along outer (lateral) side of posterior mesonotal spot, thus gently sinuate (Figs 48, 51–56); medial abdominal dorsum with at most pale marks on terga 2 and 3 and/or a narrow orange midline (Figs 16, 22–26) **11**

11. Frons very slightly convex, with upper inflection gently rounded; lateral margin of frons slightly concave, lower lobes expanded laterally (Figs 36–37); medial abdominal dorsum variable but generally mostly dark (Figs 22–23); basal half of postcostal cell lacking crossveins (Figs 66–67). **12**

-. Frons flat to slightly impressed, upper inflection almost an obtuse angle, and with one to three low medial ridges; lateral margin of frons nearly straight, lower lobes not expanded (Figs 33, 38–39); medial abdominal dorsum typically with pale marks on terga 2 and 3 (Figs 16, 24–25); only basal quarter of postcostal cell without crossveins (Figs 63, 68–69). **13**

12. Hind wings orange at base; pronotum mostly pale with small black markings (Fig. 52) . . . . . ***obrienae* Yanega & Van Dam, sp. nov.** (Mex: JAL to HID, south to Guatemala)

-. Hindwings red at base; pronotum mostly black with limited pale markings (Fig. 51) . . . . . ***obfusca* Yanega, sp. nov.** (Mex: CHI, DUR)

13. Setae on dorsal notum shorter than spaces between them and slightly recumbent; lower frons and clypeus with extensive pale coloration (Fig. 33). . . . . ***marmorata* (Spinola)** (USA: TX to FL, north to OK and VA)

-. Setae on dorsal notum long, erect (Fig. 3); lower frons and clypeus almost entirely dark (Figs 38–39). **14**

14. Base of forewings with crossveins and membrane of pale area orange-tinted (Figs 24, 68); frons weakly impressed at most (Fig. 38). . . . . ***orientalis* Yanega, sp. nov.** (Mex: NL, PUE, SLP, TAM)

-. Base of forewings with crossveins whitish, and membrane hyaline (Figs 25, 69); frons strongly impressed on either side of elevated midline (Fig. 39). . . . . ***rileyi* Yanega, sp. nov.** (USA: TX)

Species occurring in the United States

Scaralina aethrinsula Yanega & Van Dam, sp. nov.

(Figs 6, 13, 27, 42, 57, 73, 82)

Etymology. A compound formed from the Latin noun "*aethra*" (here elided to "*aethr*-" to promote euphony) meaning "sky," and the Latin noun "*insula*" meaning "island." Thus, a direct transliteration of the term "sky island," which is widely used, especially in reference to the Madrean Sky Islands; higher-elevation, pine/oak habitats in Arizona, New Mexico, and adjacent Mexico where this species is most often found, and is to be treated as a noun in apposition.

Diagnosis. This species is broadly sympatric with, and somewhat similar to, *cristata*, but some features separating them, especially the low pronotal carina, the lack of medial wing maculations, and exceptionally reticulate medial crossveins, are visible and consistent. Most specimens of *aethrinsula* are readily distinguished, even at a great viewing distance, by the paler notum and the very dark markings at the apex of the clavus in the forewing, which form a "V" or "Y" when the wings are closed. Additional features are the dark distitarsi, aspects of the frons, and details of the abdominal coloration. However, the variation in this species is such that there are individuals, especially those with medial wing maculations, that require more than a cursory glance to recognize. At the other extreme, some individuals have the wing markings reduced to the point where the basal transverse band is absent (as in Fig. 13), though the "V" is always present. Females differ from *cristata* very obviously by the unmodified tergum 6, and the male gonostyli have a slightly smaller incurved portion near the setose bulge, and a low ridge running to the medial margin, as well as extensive pale marking on tergum 7. The abdomen is actually most similar to that of *durango* and *hawksi*, and this species shares with the former the unmodified tergum 6 of the female.

Description. ***Head*** (Figs 27, 42). Rim of vertex almost entirely dark anteriorly and laterally, with three relatively small pale marks anteriorly (the middle one sometimes nearly absent); supra-ocular lobes narrowly pale apically; posterior rim mostly pale, except darkened adjacent to supra-ocular lobes. Dark granular spots of vertex slightly posterior in position, somewhat obscured amidst general mottling of surface, which is mostly dark except for tiny pale spots (often confluent) at the base of each microscopic seta, the pale apical portion of the supra-ocular lobes, and the slightly raised, generally pale midline. This basic pattern of coloration - dark with each seta in the center of a pale spot - predominates over the entire surface of the thoracic nota and pleura, as well as the tegulae and extreme

lower frons; in the middle frons, if spotting is evident, then the pattern is reversed, with each microseta in a small dark spot. General coloration and structure very similar to *cristata*, but with consistently, though slightly, more extensively confluent pale markings dorsally, and generally darker middle frons and central clypeus. Pale markings at corner of frontal crease near ocellus much larger and more well-defined than in *cristata*, extending the length of the secondary crease that marks the lateral edge of the reflexed upper frons. Reflexed upper frons mostly but not entirely pale. Rostrum typical for genus.

Thorax (Fig. 42). Pronotal spots very weak, dorsal face of pronotum generally much paler than in *cristata*, but quite similar laterally. Mesonotum generally much paler between lateral carinae than in *cristata*, posterior black spots very small and entirely outlined by pale cuticle; lateral carinae slightly sinuate anteriorly, but more abruptly sinuate posteriorly, often entirely pale; inner posterior carinae obscure; posterior mesonotal lobe usually entirely pale. Mesepisternum often relatively pale. Legs as in generic diagnosis, but pro- and metatarsi entirely dark (brownish to black), metafemur almost entirely dark, and metatibial bands relatively poorly-defined due to extensive pale spotting. Dorsal setae relatively short but distinct.

Wings (Figs 13, 57). Forewings with dark markings on basal half of vein Pcu well-developed; other markings somewhat variable, but usually with a small dark transverse patch feebly connecting costa to clavus, at the level of the first branch of M (sometimes absent; compare Figs 13 & 57), and with very prominent, nearly opaque dark spots at the end of the claval furrow (these meeting to form a "V" when the wings are closed); postcostal cell strongly mottled with dark and light. Costal crossveins numerous, close, highly anastomosing, highly reticulate; M with 2–5 main branches (generally 3 or 4), crossveins between them very irregular, generally anastomosing and forming numerous interstitial venules and irregular (non-rectangular) cellules, especially between the more anterior branches; CuA with 2–4 branches (generally 2 or 3), rarely more than 1 of these coming directly off of CuA; greatest distance between Pcu and A_1 veins greatly exceeds greatest distance between A_1 and wing margin (sometimes almost 2x); fused vein posterior to juncture relatively long. Hind wing hyaline except base slightly orange-infused.

Abdomen (Figs 6, 13). Dorsum with very limited black; primarily orange medially, and grayish-buff laterally. Ventral pleurites entirely black, sternites mostly pale but basally dark, the dark markings becoming more extensive on more apical sternites. Female with tergum 6 not modified into supra-anal plate.

Male terminalia (Figs 73, 82). Gonostyle tips black, middle pale. Incurved basal portion near setose bulge moderate in size, and partially separated from apical portion by a low oblique ridge. Lateral hooks of gonostyli small, sharply acute, tapering.

Type material. ***Holotype***, male: **ARIZONA**: **Cochise Co**.: Miller Cyn Rd, 1760m, 31°24'56"N, 110°16'32"W, 21.vii.2004, D. Yanega (UCRC ENT 98275, at UCRC).

Paratypes (123 specimens) as follows: **ARIZONA**: **Apache Co**.: "White Mts.", viii.1930, D.K. Duncan, 1M (AMNH); **Cochise Co**.: 15 mi. SW Rodeo, N.M., 17.vii.1976, M.A. Cazier, O.F. Francke, 1M (TTU-Z 18715); 15 mi. W Rodeo, N.M., 18.vii.1976, M.A. Cazier, O.F. Francke, 1F (TTU-Z 18704); same but 21.vii.1976, 1F (TTU-Z 18698); same but 6.viii.1976, 2M (TTU-Z 18712–13); same but 11.viii.1976, 1F (TTU-Z 18699); same but 17.viii.1976, 1F (TTU-Z 18706); 5 mi. W Portal, Chiricahua Mts, 31.vii.1987, R. Morris, Hg light, 1F (TTU-Z 18717) (all preceding TTCC); 5 mi. W Portal, SWRS, 5400 ft, 12.ix.1955, 1F; same but 17.viii.1955, W.J. Gertsch, 1F; same but 9.vii.1956, C. & M. Cazier, 1M; same but 22.vii.1959, 1F; same but 19.viii.1959, 1F; same but 7.viii.1956, E. Ordway, 1M; same but 25.vii.1957, M. Statham, 1M (all preceding AMNH); 5 mi W. Portal, SWRS, 5400 ft, 21.vii.1988, "Miller family", 1M; same but 23.vii.1988, 1F; same but 31.vii.1988, 1F, 1M; same but 10.viii.1988, 1F (all preceding MTEC); same but 8.viii.1969, L.D. Anderson, 1F; same but 25.viii.1965, 1F; same but 25.viii.1968, 1F; same but 25.viii.1964, 1F; same but 5.viii.1969, 1F (UCR ENT 122007, 122011–12, 122015–16); same but 8.viii.1965, C.A. Saario, 1M (UCR ENT 122018); same but 25.viii.1960, D.C. Rentz, 1M (ASULOB); same but 31°53'00"N, 109°12'22"W, 22.viii.2000, J.C. Schaffner, M.J. Yoder, 1F (TAMU); same but 19–21.viii.2000, M. Yoder, 1F (TAMU); South Fork Campground, South Fork Cave Creek, Coronado National Forest, 9.viii.1972, S.I. & S. L. Frommer, 1F (UCRC ENT 123060); 1 mi E. Portal, 23.viii.1966, L.D. Anderson, 1F (UCR ENT 122003); 2 mi. N Portal, Chiricahua Mts, 5.viii.1986, 1F (MTEC); Portal, 5.ix.1966, W.J. Gertsch, 1F (AMNH); Portal, 5.viii.1972, B. Vogel, M. & W. Durden, T, DePuy, 1M (UTIC); same but 8.viii.1968, J.B. Heppner, 1F (UCR ENT 122005); 4 mi W. Portal, Sunny Flat, 27.viii.1979, C.W. Melton, 1F (UCR ENT 122017); 3.5 mi NW SWRS, 1975m, 31°54'18"N, 109°14'33"W, 3.viii.2019, R. Brown, UV, 3M, 1F (UCRC ENT 531495–98); Paradise, Chiricahua Mts, 1.viii.1966, A.B. Patterson, at light, 1M (CSCA); same but 4.viii.1966, L.D. Anderson, 2M (UCR ENT 122009, 122013); same but 12.viii.1966, 1M (UCR ENT 122010); 3 mi SW Paradise, 1.viii.1967, D.J. Culver, 1F (UCR ENT 122006); 4 mi

N. Paradise, 5.viii.1967, F.G. Andrews, 2F (UCR ENT 122008, 122014); Cave Creek Canyon, 5000 ft, 30.vii.1988, M.M. Hooten, 1F, 1M (MTEC); same but C.E. Seibert, 1M (MTEC); same but 5100 ft, K. Philips, 2M (MTEC); Cave Creek Canyon nr. Portal, 5150 ft, UV light, 31°52'59"N, 109°10'49"W, 5.viii.2003, E.G. Riley, 1F (TAMU); East Turkey Creek, W Portal, 7.viii.1988, N.K. and R.S. Miller, BLT, 1F (MTEC); same but 1830m, 31°54'49"N, 109°14'19"W, 28.vii.2005, J. & E. Adams, 2M (UCRC ENT 128977–78, UCRC); same but 1960m, 31°54'32"N, 109°15'6"W, 27.vii.2019, J.R. Jones, MV, 2F (UCRC ENT 562008, 562675); ~5 mi SE Parker Canyon Lake, 18.viii.2001, N. Moorhatch, 1F (UCR ENT 122004); "Chiricahua N.F. vic. campgrd - Idlewilde", 7.vii.1991, S. & S. Frommer, 1M (UCR ENT 122019); Peloncillo Mts, 17.vii.1973, S. McCleve, light, 1M (AMNH); Miller Canyon, Huachuca Mts, 31°24.952'N, 110°16.539'W, 1750m, 3.viii.2007, J. Mottern, MV, 1M (UCRC ENT 323690); same but 1.viii.2021, R. Velten & S. McElfresh, at UV, 2M, 1F (UCRC ENT 561188–90); same but 1760m, 31°24'56"N, 110°16'32"W, 21.vii.2004, D. Yanega, 2F, 2M (UCRC ENT 98270–74); same but 6000 ft, 28.vii.1989, W.B. Warner, UV light, 1M (ASULOB); Carr Canyon, Huachuca Mts, 1.viii.1952, M. Cazier, W. Gertsch, R. Schrammel, 3F (AMNH); Ash Canyon, 18.viii.1982, A. Reifschneider, 1M (UNSM); Ramsey Canyon, Huachuca Mts, 1685m, 27.viii.2022, D. Yanega, 1F (UCRC ENT 559488); Garden Canyon, Huachuca Mts, 31°28'20"N, 110°21'8"W, 1640m, 27.viii.2011, D. Yanega, MV, 2F (UCRC ENT 308517–18); Copper Canyon, Huachuca Mts, 31°21'45"N, 110°18'01"W, 1850m, 8.vii.2010, D. Yanega, 1F (UCRC ENT 276159); **Coconino Co**.: 3.5 mi. S Sedona on Rt. 179, 4200 ft, T17N R6E Sec 30, 15.vi.1983, R.T. Schuh, M.D. Schwartz, HG vapor, 1M (AMNH); **Gila Co**.: Sycamore Forest Camp, 7 mi. N Payson, 4600 ft, 13.viii.1950, T. Cohn, P. Boone, M. Cazier, 1F (AMNH); **Maricopa Co**.: 2 mi E Tortilla Flat, Superstition Mts, 23.viii.1982 S.H. Lin, 1F (UCRC ENT 126008); **Pima Co.**: Santa Rita Mts, N. end, Rosemont area, "Barrel Cn. r Sec. 28," 31°48–53'N, 110°42–47'W, UV light, 10.ix.1975, J. Busacca, C. Olson, 1F (INHS 96445); Madera Canyon, Santa Rita Mts, 8.viii.1986, M.A. Ivie, at light, 1F (MTEC); same but 23.viii.1971, E.A. Kane, C.E. Langston, 1M (CSCA); same but 13.viii.1952, M. Cazier, R. Schrammel, C. & P. Vaurie, 2F, 2M (AMNH); same but 19–20.vii.1978, D.C. Hawks, 1F (UCR ENT 122020); **Santa Cruz Co.**: Madera Canyon, Santa Rita Mts, 14.viii.1968, R.L. Westcott, 1F (UDCC); same but 4600–5600 ft, 4.viii.1975, 1M (INHS 96443); same but 5600 ft, 31.vii.1968, D.N. Harrington, 1M (CSCA); same but 4880 ft, 18.vi.1965, 1F (CSCA); same but 2.ix.1960, F.G. Andrews, 1M (TAMU); same but 5.viii–3.ix.1978, L.L. Lampert. Jr., 1M (ASULOB; dissected); Santa Rita Canyon, 1870m, 31°42'06"N, 110°48'58"W, 31.vii.2002, D. Yanega, 3M (UCRC ENT 72839–41); same but 30.vii.2003, 4M (UCRC ENT 86125–28); same but 20.vii.2004, 3M (UCRC ENT 98474–76); Upper Madera Canyon, 31°42'47"N, 110°52'27"W, 7.vii.2010, D. Yanega, 2M (UCRC ENT 276019–20); Upper White Rocks Campground, Peña Blanca Lake, 1200m, 29.vii.2003, A.L. Park, Hg vapor light, 3M (UDCC); 13 mi S Patagonia, 2–3.ix.1997, Wappes & Turnbow, 1F (ASULOB); **IDAHO**: **Owyhee Co**.: Bruneau Sand Dunes, 15.vi–10.ix.1982. L. Lampert, 1M (ASULOB); **NEW MEXICO**: **Otero Co**.: Pine Camp, 2 mi. NE Cloudcroft, 8600 ft, 3.vii.1964, F., P., & M. Rindge, 1M (AMNH); Fresnal Canyon, Sacramento Mts, 1785m, UV light, 32°56'50"N, 105°52'29"W, 10.viii.2003, E. Riley, 1F (TAMU); **Socorro Co**.: 0.8 mi S Kelly, 2265m, 34°04'25"N 107°12'18"W, 25.vii.2017, J.K. Adams, 1F, 3M (UCRC ENT 525197–200); **UTAH**: **Washington Co**.: Oak Creek, Zion National Park, 22.vii.1981, C.R. Nelson, 1M (ASULOB); **MEXICO**: **Chihuahua**: Cuiteco, 1.viii.1969, T.A. Sears, R.C. Gardner, C.S. Glaser, 1M (CSCA); same but 3.viii.1969, 1F (CSCA); 8 mi. W Matachic, 7200 ft, 8.vii.1947, "D. Rockefeller Exp.", Cazier, 1M (AMNH).

Distribution. This species has the widest latitudinal distribution of any member of the genus, ranging from Chihuahua to Idaho (over 1700 km), and the widest altitudinal gradient (from 750 to over 2600 meters); it and *orientalis* are the only species other than *marmorata* known from any locations below 900 meters, though each has only one record below 1200 meters. It has been found from the southern edge of the Mogollon Rim to the Atascosa, Chiricahua, Huachuca, Patagonia, Peloncillo, Santa Rita, and Superstition ranges (all part of the Sky Islands), also extending well east of the Continental Divide (the Magdalena and Sacramento Mountains of New Mexico), north and west into Utah and Idaho, and south into the northern Sierra Madre Occidental at least as far as Matachic, Chihuahua. Given that there are so many locations at which this species and *cristata* can be collected together (sometimes along with *metcalfi*), it is possible that each species has a preferred host oak, and are sympatric where the hosts are sympatric, but further field investigation is required (i.e., forced rearing of this species on *Quercus arizonica* may not reflect choices in the wild; Gómez-Marco *et al*., 2023).

FIGURE 2. Ventrolateral view of rostral apex, *Scaralina cristata*; note that tip of last rostral segment extends beyond the femorotibial joint of the hind legs when the hind legs are pointed straight back.

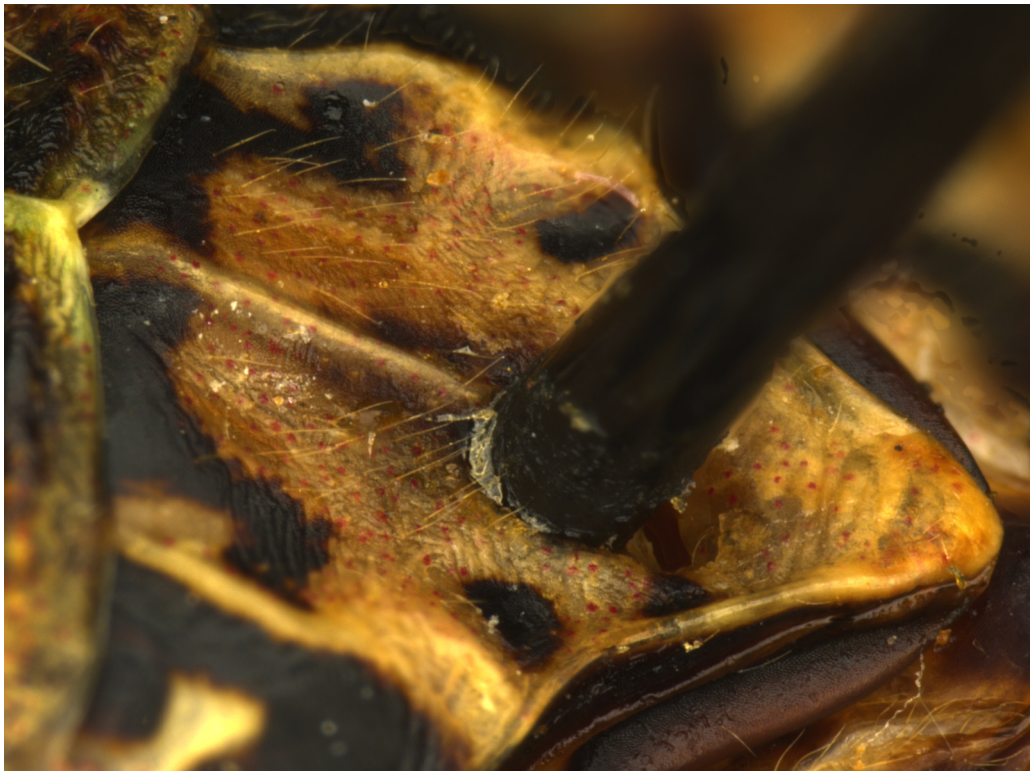
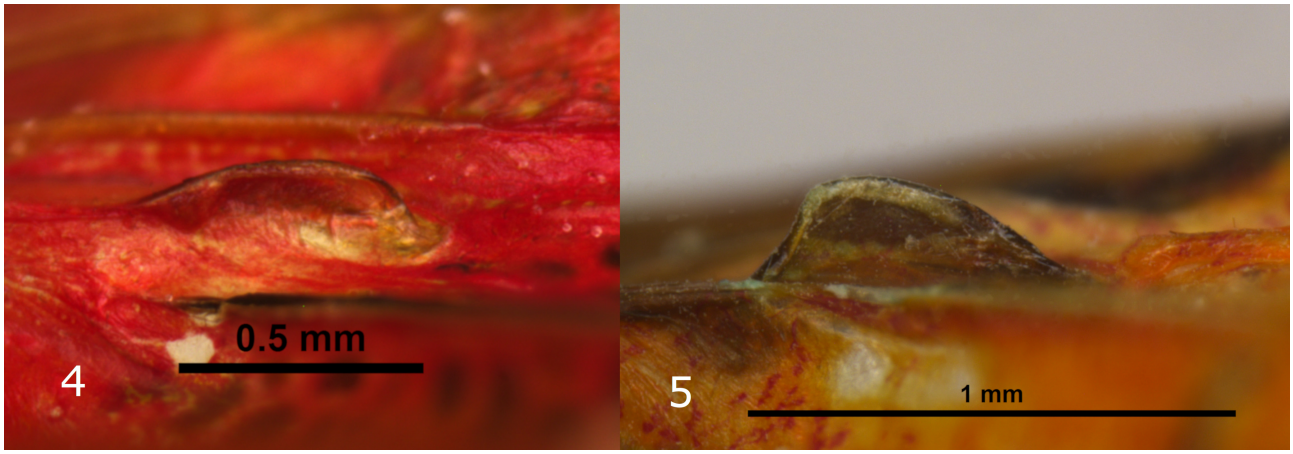


FIGURE 3. Mesonotum of *Scaralina rileyi* showing long dorsal pubescence.



FIGURES 4–5. Versteifung, underside of left forewing, viewed from posteroventral angle in both photos, so wing base is to the left; (4) *Scaralis* (*Alphinoides*) *semilimpida*; (5) *Scaralina obrienae*.

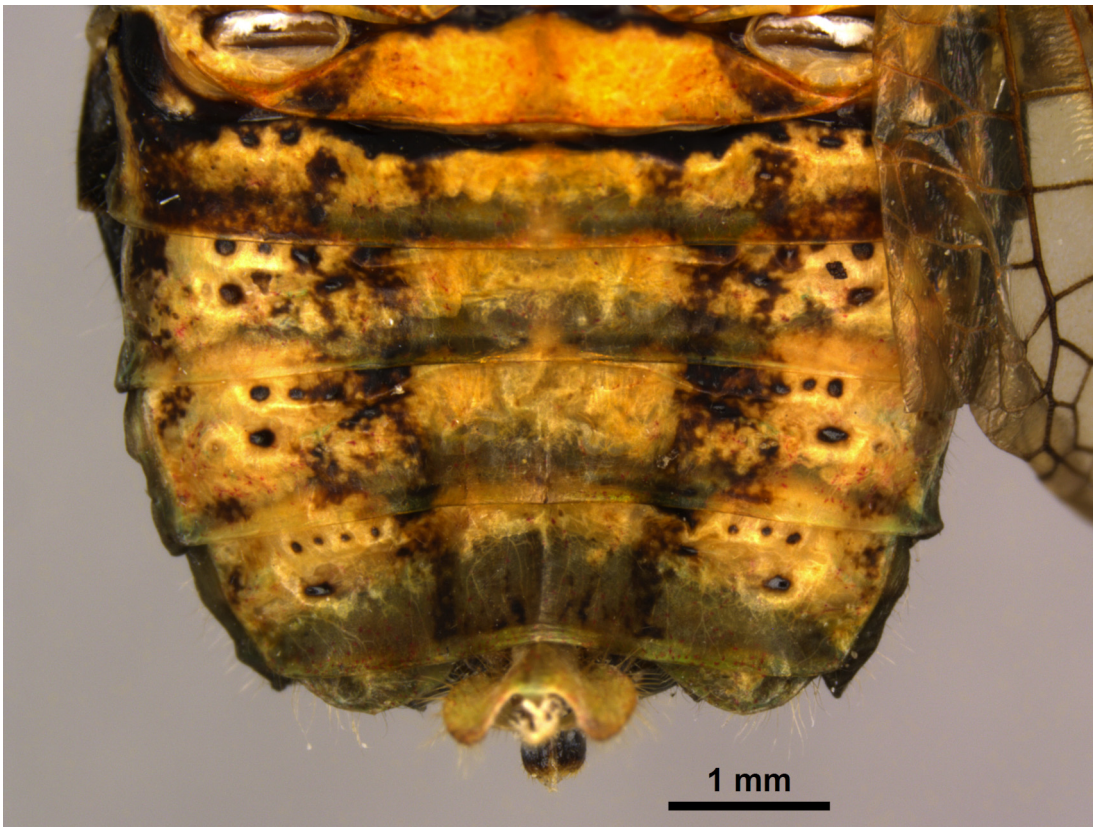


FIGURE 6. Dorsum of abdomen (terga 2–7) of female *Scaralina aethrinsula*, showing dark granular sublateral pits and unmodified tergum 6. Anal tube in this specimen is angled upwards and foreshortened.

Scaralina cristata Yanega & Van Dam, sp. nov.

(Figs 2, 12, 15, 29, 44, 59, 75, 84)

Etymology. From the Latin adjective "*cristatus*," meaning "crested," in reference to the characteristically strong pronotal carina.

Diagnosis. This species and *aethrinsula* broadly co-occur and have dorsal thoracic markings composed primarily of microscopic pale dots centered on setae. They both have relatively small cells in the forewings, but consistently different coloration, with *cristata* having numerous strongly pigmented cells in the medial portion of the wing, and in *cristata*, the overall venation is such that the wing generally has more longitudinal veins, more closely spaced,

than any other species; it also has considerably less reticulation of the crossveins than in *aethrinsula*. In addition to its crested pronotum, the thorax is generally darker than in *aethrinsula*, the rostrum darker, and the lateral mesonotal carinae more strongly sinuate. Females have tergum 6 elongated, and males have tergum 7 almost entirely dark, and the incurved dorsal part of the gonostyli has a broad medial portion without distinct ridges and nearly meeting at the midline. Among species for which we have seen males, the gonosytli of *cristata* more completely conceal the aedeagal apparatus than any other species, exposing only a small basal aperture (concealed by the anal tube). The abdominal markings seem to be composed of tiny colored dots, fused to various degrees, a condition not seen to such a degree even in other species in the *cristata* group (*aethrinsula*, *durango*, *gigantea*, and *hawksi*). The abdominal markings are typically orange-yellowish medially, and paler laterally, as is true also of some other species, but it shows strongest structural affinities to *gigantea*, with a strong, complete mediolateral notal carina in addition to a strong medial pronotal carina; it also shares with *durango* and *gigantea* the strongly pigmented cells in the medial forewing. Mexican specimens of *cristata* from Chihuahua and Durango have abdominal and thoracic markings very distinctly orange, and there is no trace of a ridge dorsally on the gonostyli. Specimens of *cristata* from the Magdalena Mountains of east-central New Mexico are also atypical, and show coloration more similar to *aethrinsula*, which is sympatric there; the thoracic markings are paler and more often fused, and the pale abdominal bands are broader and paler, and also more fused. These same specimens have a weak but distinct ridge separating the medial from the apical portion of the dorsal gonostyli, and therefore intermediate between the state seen in *aethrinsula* versus other populations of *cristata*, where this ridge is very faint (Arizona populations) or absent altogether (Chihuahua and Durango populations). Given the morphological differences and large geographic separation from other populations, this New Mexican population (and maybe the Chihuahua and Durango populations) might be worthy of recognition as a subspecies, but we leave that for future work that can take genetic data into account. Biogeographically, specimens from the Magdalena Mountains, Chihuahua, and Durango, are from the eastern side of the Continental Divide, so it would perhaps not be surprising to find significant genetic differences from the other populations, although *S. aethrinsula* can also be found in some of the same locations and we see no external differences in *aethrinsula* populations from the eastern side of the Divide. Note also that it is this species that is figured in Porion (1999) as "*Alphina glauca*", and most of the scattered specimens from Arizona we have located that were identified by Metcalf himself as "*Crepusia glauca*" are of this species.

Description. ***Head*** (Figs 29, 44). Structure and coloration fairly similar to *aethrinsula*, but with pale spots on reflexed portion of frons; on the mid and lower frons, the ground color is pale and each microseta is in a small dark spot (occasionally the spots at the extreme lower margin of frons are ocellate, with a pale center and dark outer circle). Clypeus mostly dark (except quite pale at extreme upper and lower corners), with variously-developed pale spotting; spots near upper center of clypeus often obliquely elongated. Rostrum mostly dark except at extreme base (Fig. 2).

Thorax (Fig. 44). Pronotum medial carina strongly developed, distinctly cristate in lateral view, most prominent posteriorly (Fig. 12). Pronotal spots obscured by mottling of pronotum, which is fairly uniform but quite variable; often distinctly paler just behind eyes, and often darker in a variously-defined "V" shaped mark extending from the lateral edges of the vertex to meet at the posterior apex of the crest. Central carina of mesonotum well-defined but rarely well-marked; lateral carinae abruptly sinuate (recurved or nearly so) anteriorly, and also posteriorly, often entirely pale; posterior granular spots larger than in *aethrinsula*, and inner posterior carina sometimes elevated along anterior margin of spots; posterior mesonotal lobe almost always with some black, at least at apex. Dorsal setae relatively short but distinct. Legs as in generic diagnosis, but metafemur extensively dark, metatibial bands somewhat disrupted by tiny pale dots.

Wings (Figs 15, 59). Forewings with dark markings on basal half of vein Pcu well-developed; other markings somewhat variable, but with a dark transverse band from costa to clavus, at the level of the first branch of M (varying from weak to strong), and with a long prominent row of nearly opaque dark spots in the center of the wing membrane starting near the 1st or 2nd branch of CuA; postcostal cell dark but with large pale spots, often mostly pale. Costal crossveins numerous, close, often sinuous or slightly anastomosing, but not as highly reticulate as in *aethrinsula*; M with 3–5 main branches (generally 4 or 5), crossveins between them closely spaced, often sinuous, making irregularly polygonal cells, but not generally anastomosing or forming interstitial venules or cellules in this region of the wing; sometimes one of the posterior branches of M fuses with CuA; CuA with 3–5 branches, rarely fewer than 2 of these come directly off of CuA; greatest distance between Pcu and A_1 veins equals or slightly exceeds greatest distance between A_1 and wing margin; fused vein posterior to juncture relatively short. Hind wing hyaline except base, which is slightly orange-infused.

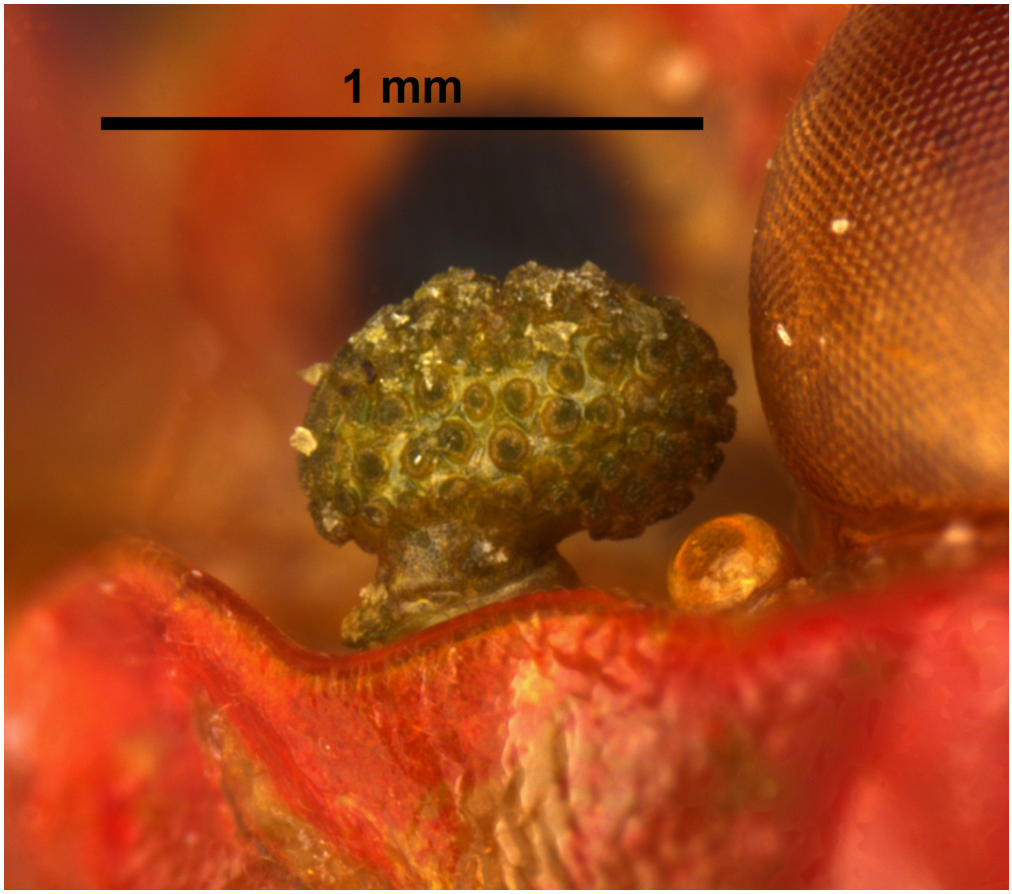
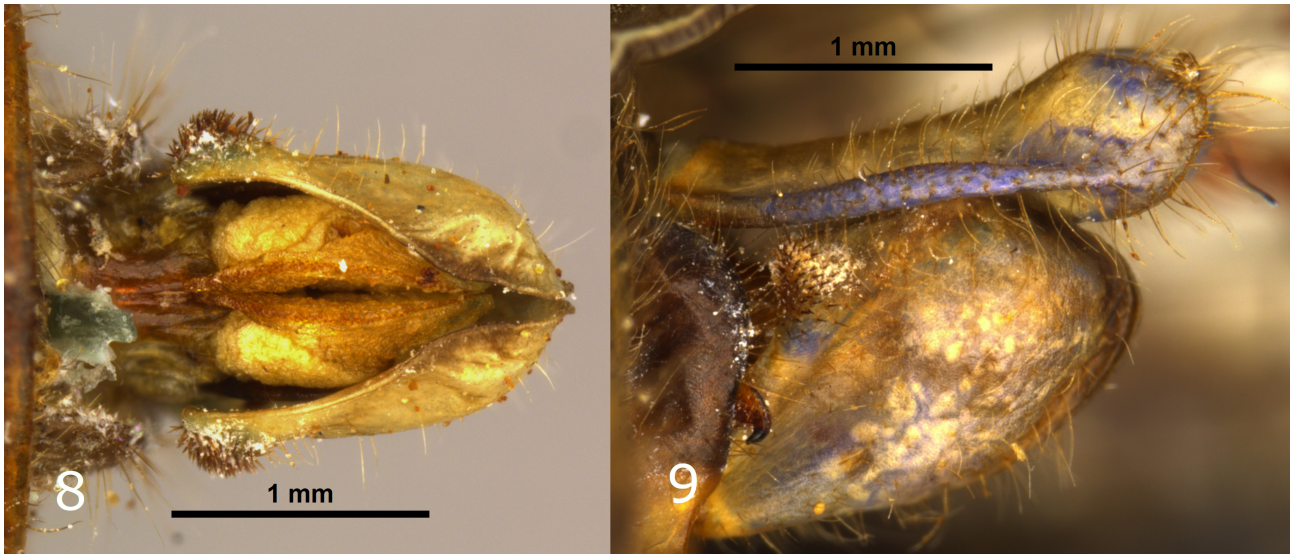
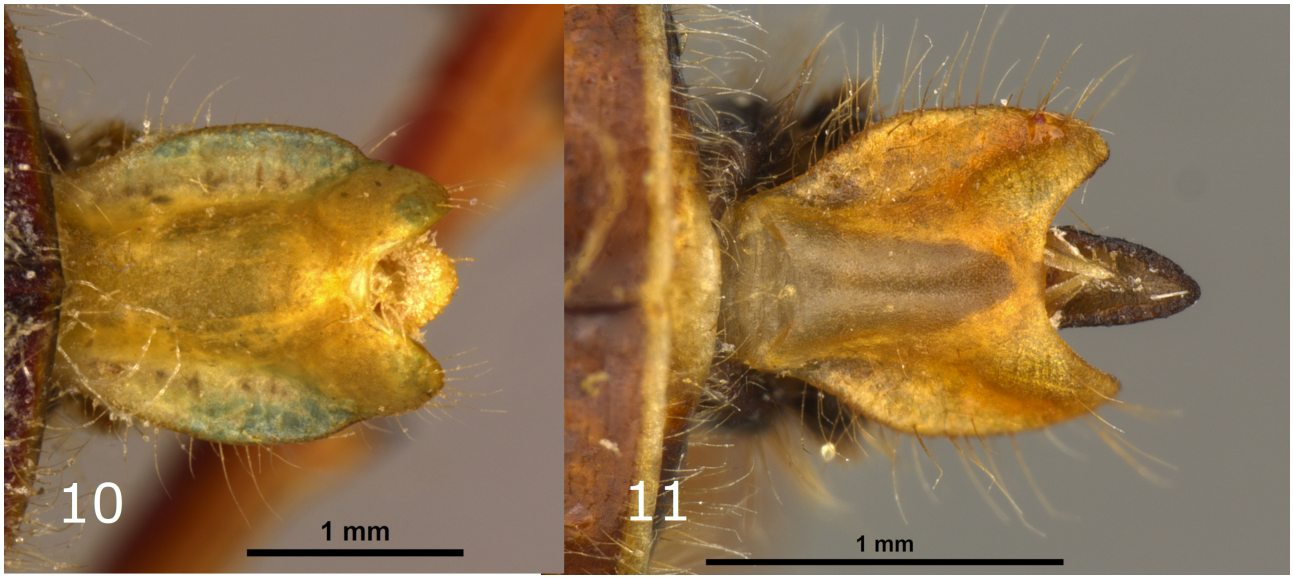


FIGURE 7. Antenna of *Scaralis* (*Alphinoides*) nr. *semilimpida*; arista not visible.



FIGURES 8–9. Male genitalia of *Scaralis* (*Scaralis*) sp.; (8) dorsal view, anal tube removed; (Fig. 9) lateral view.

Abdomen (Fig. 15). Dorsal pale bands typically somewhat poorly-defined, and composed of tiny confluent dots, orange-yellow in medial band, typically slightly more buff-yellowish laterally, with scattered spots in between. Ventral pleurites and sternites usually mostly dark, the light portions composed of tiny pale tan dots. Male with tergum 7 almost entirely dark, only a few scattered pale spots. Female supra-anal plate large, marked similar to preceding terga but over half again as long.



FIGURES 10–11. Male anal tubes, dorsal view; (10) *Scaralis* (*Scaralis*) sp.; (11) *Scaralis* (*Alphinoides*) *inbio*.

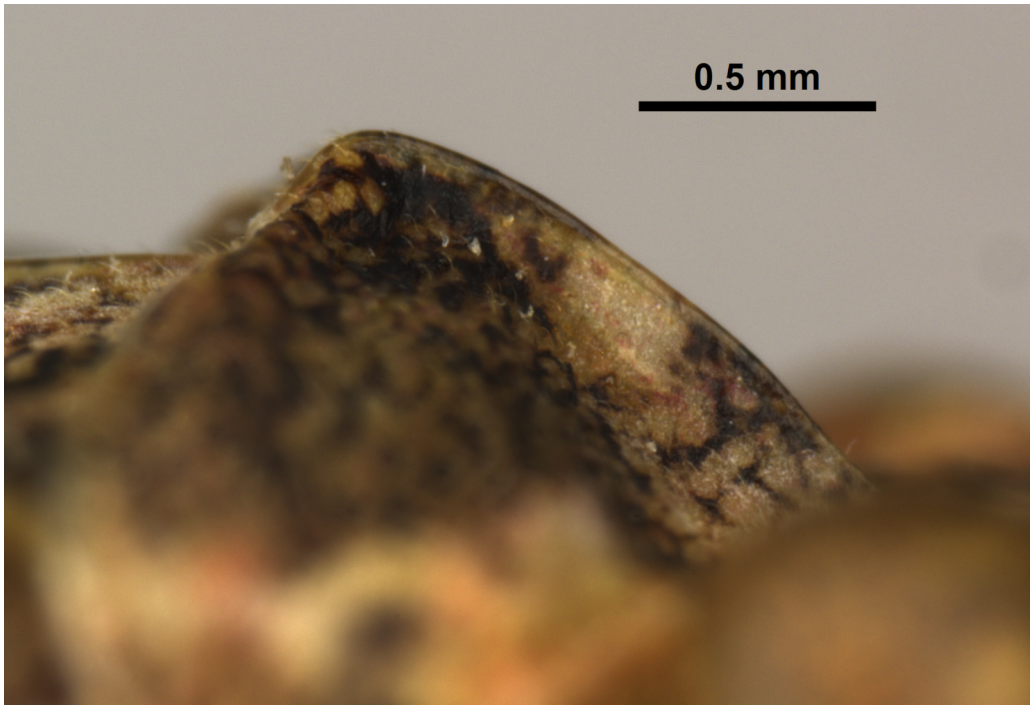


FIGURE 12. lateral view of prothorax of *Scaralina cristata*, showing crest-like medial carina (head is to the right).

Male terminalia. (Figs 75, 84). Gonostyli with apical half dark. Incurved portion near setose bulge very large, with inner corner at right angle nearly meeting at midline, and broadly confluent with apical portion, with medial portion very slightly impressed and only a trace of a ridge between this and the apical portion. Lateral hooks small, sharply acute, tapering.

Type material. ***Holotype***. male: **ARIZONA**: Cochise Co.: "Miller Cyn Rd, 1760m, 31°24'56"N 110°16'32"W, 21.vii.2004, D. Yanega" (UCRC ENT 98278, at UCRC).

Paratypes (204 specimens) as follows: **ARIZONA**: **Cochise Co**.: 15 mi. SW Rodeo, N.M., 27.vii.1977, M.A. Cazier, 1M (TTU-Z 18714); 15 mi. W Rodeo, N.M., 17.vii.1976, M.A. Cazier, O.F. Francke, 1F, 4M (TTU-Z 18694–96, 18700, 18703); same but 18.vii.1976, 1M (TTU-Z 18707); same but 21.vii.1976, 1M (TTU-Z 18697); same but 4.viii.1976, 1M (TTU-Z 18702); same but 5.viii.1976, 2M (TTU-Z 18701, 18708); same but 7.viii.1976,

1M (TTU-Z 18711); same but 14.viii.1976, 1M (TTU-Z 18705); same but 15.viii.1976, 1M (TTU-Z 18710); 5 mi. SW Portal, 28.vii.1977, M.A. Cazier, O.F. Francke, 1M (TTU-Z 18716); Chiricahua Mts, SWRS, 5700 ft, 26.viii.1968, J.B. Heppner, blacklight, 1F (TTU-Z 18718); Cochise Stronghold, 4600 ft, 6.ix.1965, L. & C.W. O'Brien, blacklight, 1M (TTU-Z 18692) (all preceding TTCC); 5 mi. W Portal, SWRS, 5400 ft, 22.vi.1955, M. Statham, 6M; same but 2.vii.1957, 1M; same but 8.vii.1959, 1M; same but 16.vii.1955, W.J. Gertsch, 2M; same but 17.vi.1956, E. Ordway, 1M; same but 9.vii.1956, 1M; same but 12.vii.1956, C. & M. Cazier, 1M; same but 2.viii.1957, M.A. Cazier, 1M; same but 28.vi.1958, 1M; same but 10.vii.1963, J.G. Rozen, D.K. Oliver, A.R. Moldenke, J.A. Woods, 1M; Painted Canyon Ranch, Chiricahua Mts, 1.vii.1954, M. Cazier, 13M; Carr Canyon, Huachuca Mts, 1.viii.1952, M. Cazier, W. Gertsch, R. Schrammel, 2M; Lower Carr Canyon, Huachuca Mts, 21.vii.1955, E. Ordway, W.J. Gertsch, 1M; Ramsey Canyon, Huachuca Mts, 10–15.vii.1941, A.B. Klots, 1M; Texas Canyon, Dragoon Mts, 5300 ft, 12.viii.1974 S. McCleve, black light, 1F; Dragoon, 20.vii.1917, "PARATYPE Crepusia glauca Metc.", 1M (all preceding AMNH); nr. Portal, nr. SWRS, 5500 ft, UV light, 31°52'55"N, 109°13'04"W, 4.viii.2003, E. Riley, 1M (TAMU); SWRS, 25.vi.1970, B. & C. Durden, 1M (UTIC); same but 3.viii.1969, L.D. Anderson, 1M (UCR ENT 122031); same but 8.viii.1969, 1M (UCR ENT 122038); same but 15.viii.1970, 1M (UCR ENT 122030); same but 21.viii.1970, 1F (UCR ENT 122029); 5 mi W. Portal, SWRS, S. & S. Frommer, at light, 1M (UCR ENT 122032); Chiricahua Mts, Cave Creek Canyon, 5100 ft, vii.1988 K. Philips, 1F (MTEC); same but 1.viii.1988, M.A. Ivie, 1M (MTEC); Cave Creek Canyon nr. SWRS, 21–26.vii.1971, 1M (TAMU); same but 5650 ft, 31°53'38"N, 109°12'53"W, 6.viii.2003, E.G. Riley, UV light, 4M (TAMU); Cave Creek Canyon nr. Portal, 5150 ft, 31°52'59"N, 109°10'49"W, 5.viii.2003, E.G. Riley, UV light, 1M, 1F (TAMU); Cave Creek, 5 mi W. Portal, 27.vii.1955 Timberlake, 1M (UCR ENT 122021); Cave Creek Ranch, 1.viii.1965, 5000 ft, G.W. Forister, 1M (UCR ENT 122035); 1 mi E. Portal, 23.viii.1966, L.D. Anderson, 1M (UCR ENT 122034); Paradise, 7.viii.1966, L.D. Anderson, 1M (UCR ENT 122023–25); same but 4.viii.1966, 1F (UCR ENT 122027); Huachuca Mts, Oslar, 17.viii.1903, 1M; same but 23.viii.1903, 1M (NCSU; both labeled by Z.P. Metcalf as "Crepusia glauca"); Guadalupe Canyon, Peloncillo Mts, 1.vii.1975, S. McCleve, light, 1M (ASULOB); same but 1.vii.1976, 1M (ASULOB); Cochise Stronghold, 4600 ft, 6.ix.1965, L. & C.W. O'Brien, blacklight trap, 1M (ASULOB); Ash Canyon, 7 mi W Palominas, Huachuca Mts, 5100 ft, 1.viii.1995, Cate & Quinn, UV light, 2M, 2F (TAMU); Ash Canyon, "Lassie-Placer Claim", 5115 ft., 23.vii.1979, N. McFarland, at UV, 1M (UCR ENT 122033); Ramsey Canyon, Huachuca Mts, 1685m, 27.viii.2022, D. Yanega, 1F (UCRC ENT 559489); Miller Canyon, Huachuca Mts, 1.viii.2021, R. Velten & S. McElfresh, at UV, 2M (UCRC ENT 561186–87); same but 31°24.952'N, 110°16.539'W, 1750m, 3.viii.2007, J. Mottern, MV, 1M (UCRC ENT 323689); same but 31°24'56"N 110°16'32"W, 1760m, 21.vii.2004, D. Yanega, 3M (UCRC ENT 98276–77, 98279); 10 mi S Apache, 7.viii.1972, B. Vogel, 1F (UTIC); 12 mi. S Sierra Vista, 8–10.viii.1977, R.P. Allen, G.C. Duffy, at black light trap, 2M (CSCA); **Gila Co**.: Globe, Pinal Mts, light, 1.vii.1932, 1M; same but Z.P. Metcalf, 1M (NCSU; both labeled by Z.P. Metcalf as "Crepusia glauca"); **Graham Co**.: High Creek, Galiuro Mts, 1600m, 20.vii.1978, S. McCleve, light, 1M (ASULOB); E end Aravaipa Canyon, 12.viii.1975, S. McCleve, light, 1M (AMNH); Noon Creek, Pinaleño Mts, Coronado N.F., blacklight, 19.vii.2001, A. Cognato, J. Usener, 1M (TAMU); Fort Grant, Pinaleño Mts, 15–17.vii.1917, "C.U. Biol. Exped.", 1M (NCSU); **Greenlee Co**.: Blue River, 5600 ft, Apache N.F., 25.vii.1973, M. Schwartz, UV, 1M (AMNH): **Maricopa Co.**: 2 mi E Tortilla Flat, Superstition Mts., 23.viii.1982, S.H. Lin, 1F (UCRC ENT 126008); **Pima Co**.: Tucson, Mt. Lemmon, Santa Catalina Mts, "PPRSAUCE", 4.ix.1965, J.H. Hessel, 1M; Browns Canyon, Baboquivari Mts, 5.viii.1952, M. Cazier, R. Schrammel, 1F, 2M; Kitt Peak, Rincon, Baboquivari Mts, 1–4.viii.1916, 31°57'N 111°33'W, "about 4050 ft.", 1F, 14M; Sabino Basin, Santa Catalina Mts, 15–21.viii.1916, 32°22'N 110°46.5' W, "about 3800 ft.", 2M; Madera Canyon, Santa Rita Mts, 14. viii.1955, Gertsch & Ordway, 1M (all preceding AMNH); same but 19–20.vii.1978, D.C. Hawks, 1M (UCR ENT 122022); Bog Springs Campground, Madera Canyon, 16.viii.1971, T. Halstead, 1M (ASULOB); same but 10.viii.1978, at black light, 1F (MTEC); Santa Rita Experimental Range, 4.viii.1988, S. Lajeunesse, 1M (MTEC); same but T.K. Philips, 2M (MTEC); same but 5.viii.1988, at light, C.E. Seibert, 1M (MTEC); Molino Basin, Santa Catalina Mts, 4600 ft, 3.ix.1965, L. & C.W. O'Brien, blacklight trap, 1M (ASULOB); Box Canyon, Santa Rita Mts, 20.vii.1985, D.C. Hawks, 1M (UCRC ENT 102068); same but 21.vii.1998, J. George, 1M (UCRC ENT 324032); **Pinal Co**.: Jct. Devil's Canyon & U.S. Hwy 60, Pinal Mts, 26.vii.1989, W.B. Warner, UV light, 2M (ASULOB); **Santa Cruz Co.**: 0.6 mi S of Duquesne, 3.viii.1996, W.B. & B.C. Warner, "UVBL," 1M (ASULOB); Sonoita River, Patagonia, 18.vii.1948, C. & P. Vaurie, 3M (AMNH); Madera Canyon, Santa Rita Mts, 13.viii.1966, R.L. Westcott, 1F (UDCC); same but 1.vii.1972, A.J. Gilbert, 1M (CSCA); same but UV light, 31.vii.1965, G. Ballmer, K. Brown, 1M (TAMU); same but 18.viii.1965, C.A. Saario, 1F, 1M (UCR ENT 122028, 122037); Upper Madera Canyon,

31°42’47”N, 110°52’27”W, 7.vii.2010, D. Yanega, 2M (UCRC ENT 276017–18); Upper Madera Canyon, 31°42’46”N, 110°52’25”W, 1660m, 3.ix.2011, D. Yanega, 1F (UCRC ENT 309053); Nogales, Oslar, 25.vi.1903, 2M; same but 1.vii.1903, 1M; same but 17.vii.1903, 2M; same but 29.vii.1903, 1M; same but 23.vii.1903, 1M; same but additional label “Cornell U. Lot 256 Sub.”, 1M (NCSU; all labeled by Z.P. Metcalf as “Crepusia glauca”); Nogales, 15.viii.1972, 1M (CSCA); Mt. Washington, 4300 ft, Patagonia Mts, 13.viii.1991, L.G. Bezark, R.A. Cunningham, D.E. Russell, Hg vapor and UV light, 3M (CSCA); Peña Blanca Lake, 31.viii.1966, F.G. Andrews, 1M (UCR ENT 122026); Upper White Rocks Campground, Peña Blanca Lake, 1200m, 29.vii.2003, A.L. Park, Hg vapor light, 9M (UDCC); same but 31°23’16”N, 111°06’41”W, 1200m, 20.vii.2000, D. Yanega, MV, 2M (UCRC ENT 40854–55); same but 30.vii.2002, 1M (UCRC ENT 72344); same but 29.vii.2003, 5M (UCRC ENT 86118–22); same but 31°23.081’N, 111°5.615’W, 1172m, 24.vii.2009, J. Mottern, MV, 1F, 3M (UCRC ENT 323604–07); S Peña Blanca Lake, 31°24’4”N, 111°5’29”W, 1180m, 1.viii.2005, J. Adams, UV, 5M (UCRC ENT 562489–93); nr. Peña Blanca Lake, UV light, 31°22’58”N, 111°05’30”W, 7.viii.2003, E. Riley, 4M (TAMU); Ruby Road, 1270m, UV light, 31°23’25”N, 111°7’24”W, 1.viii.2005, J. Adams, 7M (UCRC ENT 129044–46, 562595–98); Sycamore Canyon, 1220m, 31°25’53”N 111°11’21”W, 19–20.viii.2004, D. Yanega, 1M (UCRC ENT 100055); 5 mi S. Canelo, 20.viii.1965 K. Brown, 1M (UCR ENT 122036); **Yavapai Co**.: Kirkland, Peeples Valley, 4500 ft, 22–24.viii.1927, “Cornell U. Lot 542 Sub. 333”, 1M (NCSU); Cherry, 1.viii.1970, D.B. Carver, blacklight, 1M (ASULOB; dissected); **NEW MEXICO**: **Hidalgo Co**.: Clanton Draw, 41 mi E Geronimo Pass, Peloncillo Mts, T31S R21W sec 16, 5400 ft, 22.vii.1972, M.E. Toliver, 1M (ASULOB); **MEXICO**: **Sonora**: “8 mi W Tepoca, 3000 ft, 28.30–109.17” (erroneous GPS coordinates, should be 28.46, -109.33), 6.viii.1986, V. Roth, 1M (AMNH; dissected); “Sierra de los Ajos, head of Cañon de Evans”, 4550 ft, 15.vii.1970, V. Roth, 3M (AMNH).

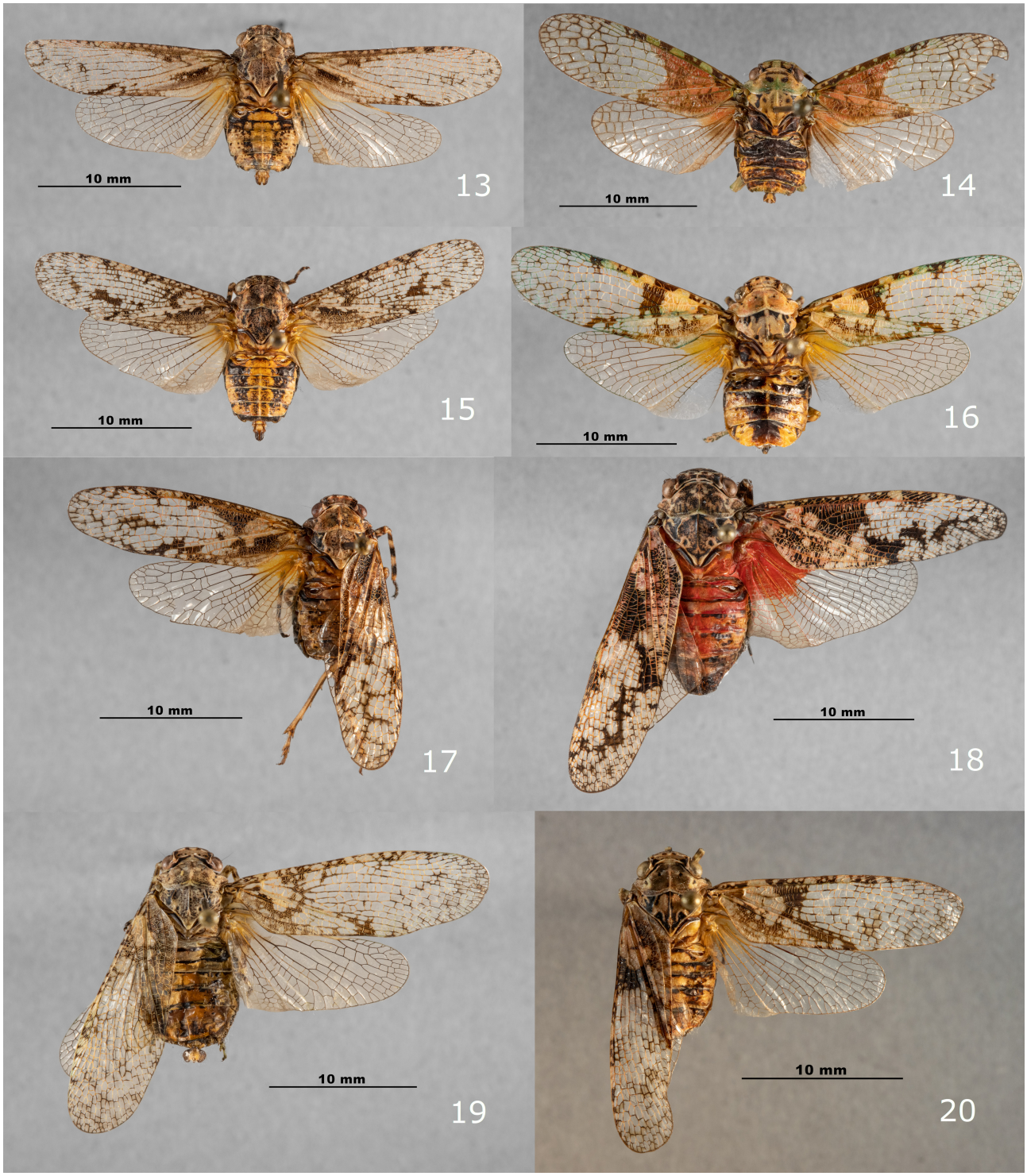
Other material examined. **NEW MEXICO**: **Socorro Co**.: 0.8 mi S Kelly, 2265m, 34°04’25”N 107°12’18”W, 25.vii.2017, J.K. Adams, 3M (UCRC ENT 525194–96); **MEXICO**: **Chihuahua**: Santa Barbara, 6300 ft, 18.vii.1942, “D. Rockefeller Exp.”, Cazier, 1F; Arroyo Catarinas, 15 mi S Matamoros, 14.ix.1950, R.F. Smith, 1F; Catarinas, 5800 ft, 25.vii.1947, “D. Rockefeller Exp.”, Schramel, 1F, 1M; 8 mi W Matachic, 6400 ft, 8.vii.1947, “D. Rockefeller Exp.”, Schramel, 1F; same but 7200 ft, Cazier, 1M (all preceding AMNH); “Villa Matamoros (1715)”, 16.vi.1972, J. Mateu, 1M (ASULOB);13 mi E Cuauhtemoc, 6600 ft, UV & white light, 11.vii.1964, J.A. Chemsak, J. Powell, 1M (EMEC); 15 mi E Cuauhtemoc, white light, 11.vii.1964, J. Chemsak, J. Powell, 1M (EMEC); **Durango**: Encino, 6200 ft, 27.vii.1947, “D. Rockefeller Exp.”, Schramel, 1F (AMNH); **Sonora**: Rancho Las Tierras, Sierra Murrieta near Bacanora, 1380m, 28.90110, -109.51360, 15.ix.2022, S. Carnahan, 1F (photo record).

Distribution. This species has been reported from a very large number of mountain ranges, mostly within the broader system known as the Madrean Sky Islands. As noted above, the typical form is found west of the Continental Divide, from the southern edge of the Mogollon Rim to the Atascosa, Baboquivari, Chiricahua, Dragoon, Galiuro, Huachuca, Pajarito, Patagonia, Peloncillo, Pinal, Pinaleño, Santa Catalina, Santa Rita, and Superstition ranges (all part of the Sky Islands), also extending west as far as the Bradshaw Mountains and south into the northern Sierra Madre Occidental at least as far as Yécora, Sonora. Populations from the US and Mexico from east of the Continental Divide are provisionally included in this species, but we designate no such specimens as paratypes. In total, this is a larger number of known occurrences than for *aethrinsula*, but *aethrinsula* ranges more widely to the east, west, and north. Records are from between 1100 and 2200 meters in elevation, with one record from 950 meters.

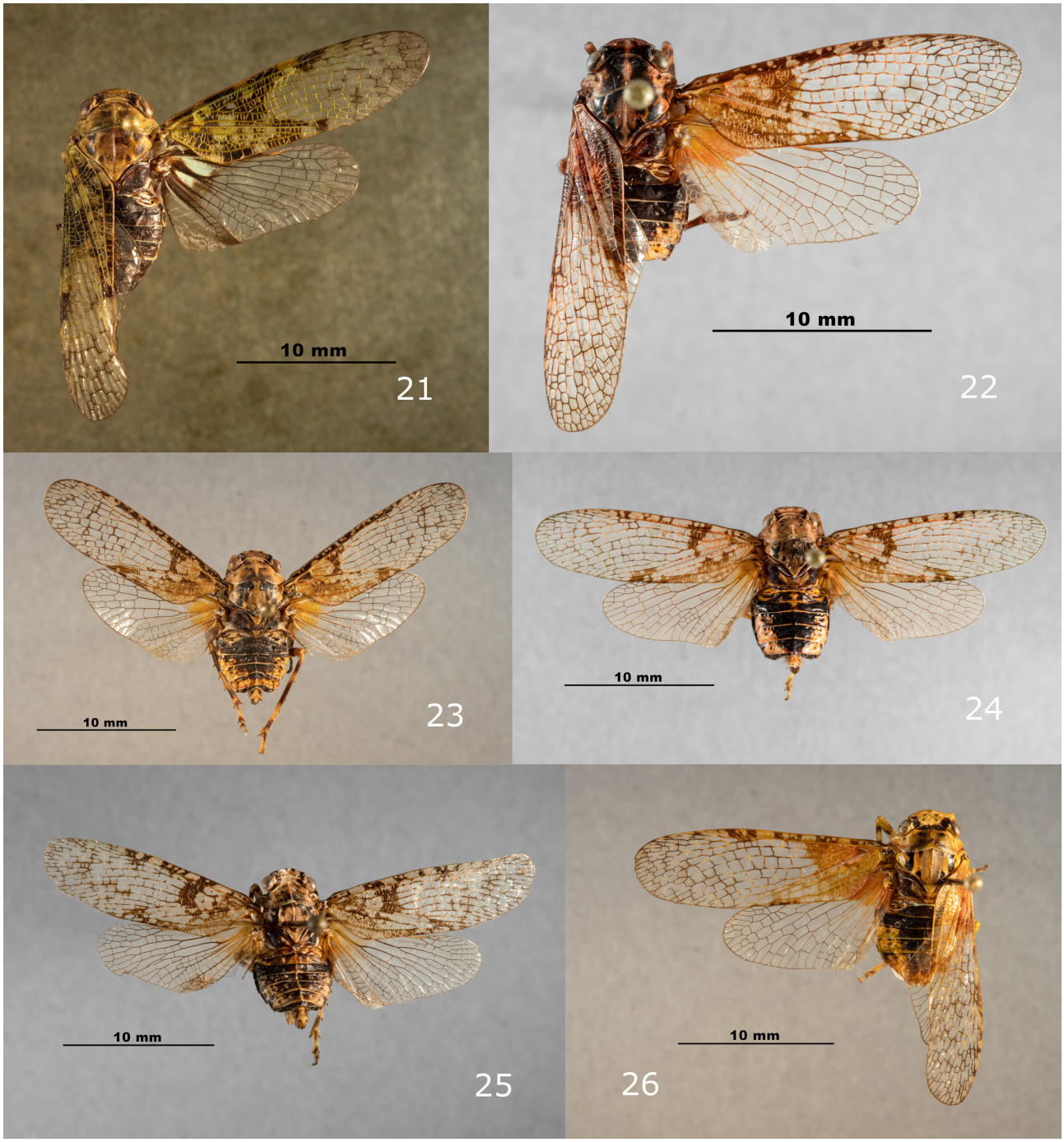
***Scaralina marmorata* (Spinola, 1839), comb. nov.**
(Figs 1, 16, 33, 48, 63, 76, 85)

= *Crepusia glauca* Metcalf, 1923 (synonymy by Ball, 1933, here restored); for other combinations, see Metcalf, 1947.

Note on synonymy. The three related taxa that co-occur in Arizona (*metcalfi*, *cristata*, and *aethrinsula*) are readily distinguished from one another and from *marmorata*, including forms at the extremes of variability in color and maculation, by even a quick glance at the thorax and forewings. Given the large number of specimens of all three taxa in collections (*metcalfi* is relatively rare, though the most similar to *marmorata*), it is fairly surprising that no one had recognized that the variants of “*Alphina glauca*” fell into three or four consistent and discrete morphotypes, including (and especially) in areas where they co-occurred, and where one putative “variant” lacked a female supra-anal plate; nonetheless, this problem has persisted for most of a century, with the additional complication that Metcalf’s 1947 catalogue reversed Ball’s synonymy of *Crepusia glauca* Metcalf with *Calyptoproctus marmoratus*



FIGURES 13–20. Habitus photos of *Scaralina* species. (13) *S. aethrinsula* (male); (14) *S. chapina* (male); (15) *S. cristata* (male); (16) *S. marmorata* (female); (17) *S. durango* (type female); (18) *S. gigantea* (type female); (19) *S. hawksi* (female, crushed somewhat); (20) *S. metcalfi* (male).



FIGURES 21–26. Habitus photos of *Scaralina* species. (21) *S. monzoni* (female); (22) *S. obfusca* (type male); (23) *S. obrienae* (male); (24) *S. orientalis* (male); (25) *S. rileyi* (male); (26) *S. sullivani* (female).

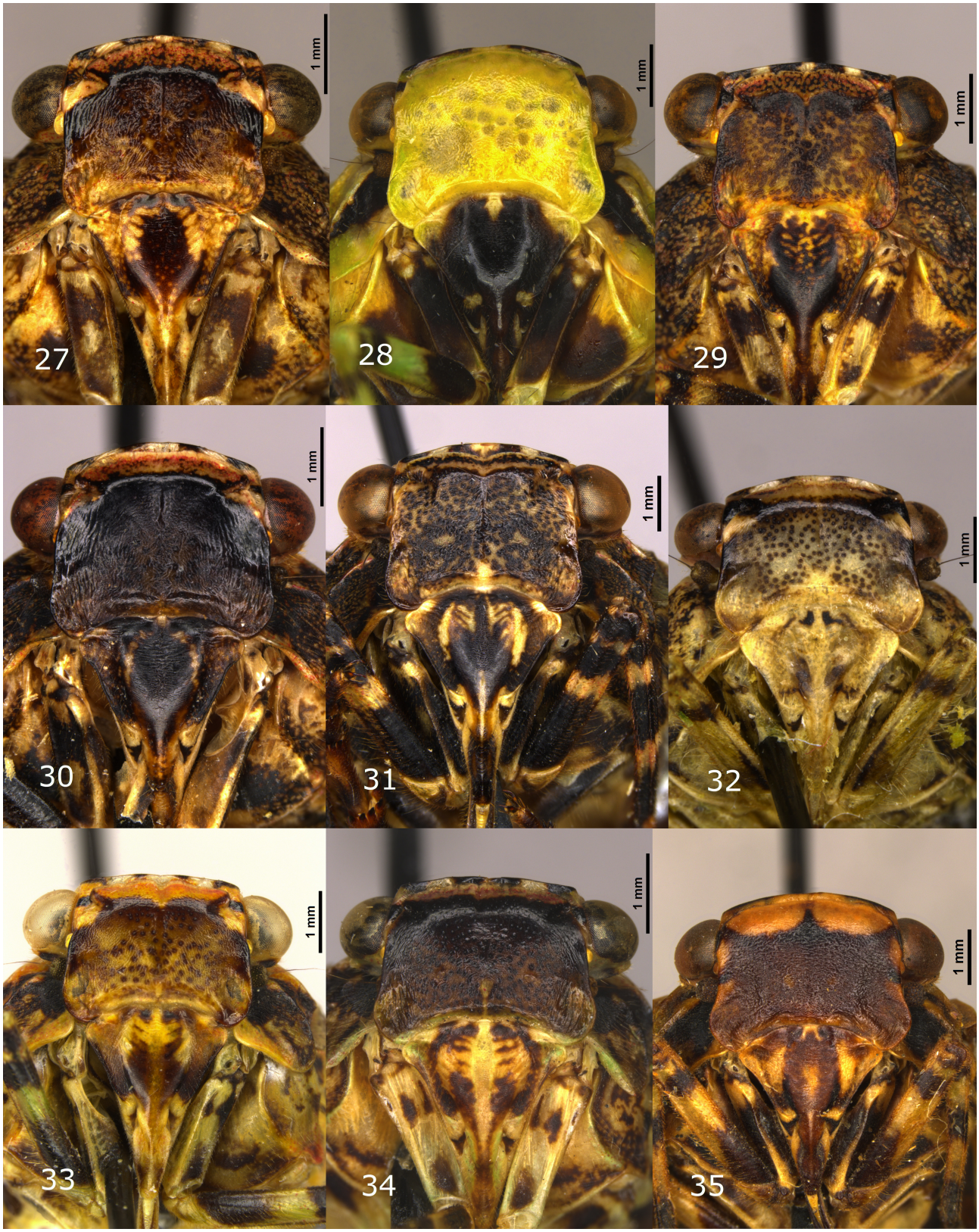
Spinola, which led to the almost complete abandonment of the latter name by taxonomists after 1947. Significantly, among specimens bearing Metcalf's personal ID labels, we were able to find a number of specimens labeled as "*Crepusia glauca*", all from Arizona (and all, thus far, of *S. cristata*), as well as several specimens of a true *Calyptoproctus*, from Mexico and Guyana, that he had labeled as *Ca. marmoratus*; that is, he mistakenly believed that Spinola's species was a true *Calyptoproctus*, because he had evidently never seen the type.

In the absence of Metcalf's holotype, and given that there are no specimens we have seen from any populations in habitat consistent with southern Texas that could be interpreted as belonging to a second, distinct species, and given that there is nothing in Metcalf's description which differs from *marmorata* as we understand it, we will follow Ball's synonymy (based, as it presumably was, on direct examination of Metcalf's now lost specimen) as

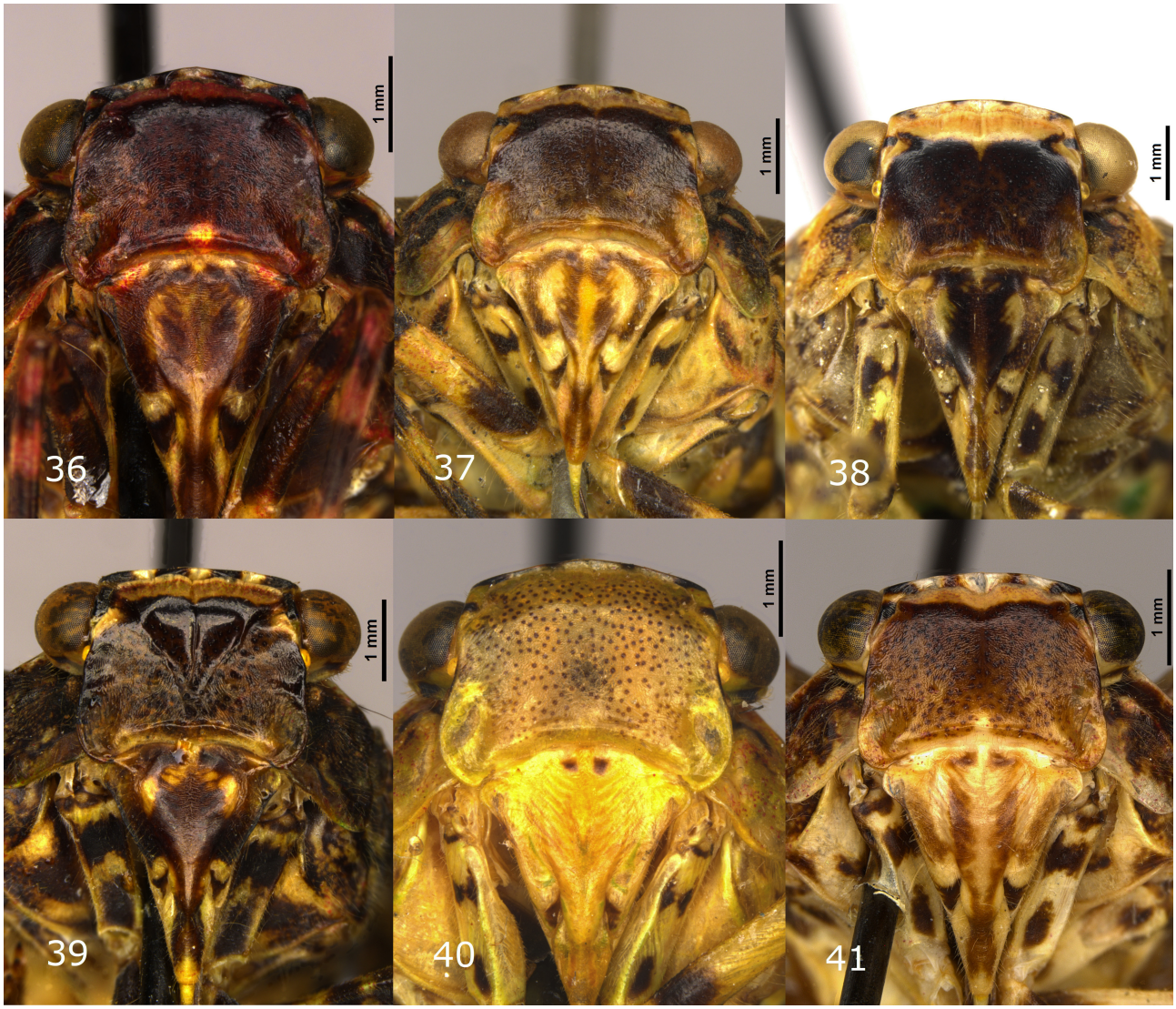
evidence that Metcalf's holotype was indeed a specimen of *Calyptoproctus marmoratus* Spinola. We further note that Spinola's type is a perfect match to the populations from southeastern Texas, even more so than populations of *orientalis* from Nuevo León and Tamaulipas, which are somewhat similar. We consider this the final compelling point for designating a Texan specimen as the neotype of *Crepusia glauca* Metcalf, in order to firmly establish its identity and synonymy, fulfilling all necessary requirements under the International Code of Zoological Nomenclature (Article 75.3; ICZN, 1999). Although Metcalf's type locality was Brownsville (Cameron Co., TX), we have not seen any U.S. specimens from within 300 kilometers of Brownsville, though we have seen Mexican material (of *orientalis*) that is marginally within this range (over 250 km). It does, in fact, seem improbable that specimens closer to the original type locality could be located: within Texas, this species seems restricted to the woodlands of east Texas, west to the wetter parts of the eastern Edwards Plateau, a habitat type which is not present near Brownsville. However, we consider it important to make Metcalf's taxon an objective synonym of Spinola's (by assigning it a neotype that clearly belongs to Spinola's taxon) rather than to assign it a neotype belonging to a different taxon from northeastern Mexico simply to preserve Metcalf's name, in large part because it would be very likely to cause people to assume that the former "*Alphina glauca*" and a reinstated "*Scaralina glauca*" are the same taxon, when the former name has been almost universally applied to multiple species from Arizona. We further feel that Spinola's type is so readily and unmistakably associated with the southeastern Texas populations (e.g., Bastrop, Brazoria, Brazos, Leon, Polk, and Travis counties; compare Fig. 1 to Fig. 16) that it is unnecessary to replace it with a specimen whose provenance is more explicitly known; that is, a neotype designation for *S. marmorata* is not justifiable under the ICZN.

Diagnosis. *S. marmorata* is the most widespread species in the genus, and it shows considerable, though highly localized, variation in color. Within any given population, individuals are fairly uniform in appearance, but over fairly short geographic distances the color patterns can change considerably between populations that are structurally indistinguishable. We consider the structural features to be taxonomically reliable, especially the very short notal pubescence, and male genitalia (though these too show slight population-level variation). Molecular analysis may ultimately reveal that this is a complex of species, each inhabiting relatively discrete "islands" of habitat and/or host plants; nonetheless, the structural similarities are too great to confidently exclude most of these populations from the circumscription of the species as a whole. The male gonostyli do not appear to vary significantly within the SE U.S. populations, nor does the short notal pubescence, and these are perhaps the most reliable diagnostic features for recognizing *marmorata*. The remaining taxa appear to be quite distinct from *marmorata*, and while there is ample tradition and precedent to designate subspecies for geographically isolated populations, as most of these taxa appear to be, we refrain from doing so here, and treat them all as full species. All of the other taxa described here have long notal pubescence, especially the other members of the *marmorata* species group (Fig. 3). The most similar taxa are the geographically proximate *orientalis* and *rileyi*, which share an impressed frons, and very similar male gonostyli; the primary difference is the long versus short notal setae, and this may be at best a subspecific feature, though the male genitalia also differ slightly. It is probably not a coincidence that *marmorata* is the only species routinely found at low elevations; all but three of the hundreds of confirmed records for species other than *marmorata* are over 1200m. We suspect that the reduction of notal pubescence is unique (within *Scaralina*) to *marmorata*, and associated with living at low elevations. The other species in the *marmorata* species group all possess long setae on the dorsal thorax, slightly longer than most members of the *cristata* species group.

Description. ***Head*** (Figs 33, 48). Rim of vertex dark anteriorly and laterally, with three prominent pale marks anteriorly; supra-ocular lobes pale apically; posterior rim mostly pale, except darkened adjacent to supra-ocular lobes; dark spots of vertex posterior in position; black markings very well-defined and restricted (generally only lateral bands and anterior spots), no tiny spots as in preceding species. Frons with a broad pale upper reflexed margin, very dark just below this (pale markings at corner of frontal crease near ocellus generally well-defined as in *aethrinsula*), and the ground color below a little less dark, except for darker spots surrounding setal bases; lower frons with surface very finely wrinkled, and with two low but distinct converging ridges forming a "V", surface somewhat impressed; sometimes a trace of a third, medial, ridge just below reflexed margin. Lateral margin of frons nearly straight, lower lobes of frons not distinctly expanded. Clypeus quite variable, typically palest in center and apically. Rostrum typical for genus, or slightly darker.



FIGURES 27–35. Faces of *Scaralina* species. (27) *S. aethrinsula*; (28) *S. chapina*; (29) *S. cristata*; (30) *S. durango*; (31) *S. gigantea*; (32) *S. hawksi*; (33) *S. marmorata*; (34) *S. metcalfi*; (35) *S. monzoni*.



FIGURES 36–41. Faces of *Scaralina* species. (36) *S. obfusca* (male); (37) *S. obrienae*; (38) *S. orientalis*; (39) *S. rileyi*; (40) *S. sullivani*; (41) *S. veracruzensis*.

Thorax (Fig. 48). Pronotal spots well-defined, including an extra set of small spots behind the usual post-ocular spots (sometimes confluent); at least anterior portion of dorsal pronotal face pale, becoming darker towards posterior and center, medial carina entirely pale; may be more or less extensively dark over surface in different populations. Mesonotum center typically mostly pale (mesonotum also variably dark-marked); medial carina prominent; lateral carinae angled inward anteriorly and very weakly sinuate posteriorly; inner posterior carinae weak, granular dark spots large; posterior mesonotal lobe somewhat acutely rounded, and usually pale medially and dark laterally. Setae of dorsal pronotum shorter than interspaces between them, and slightly recumbent, but still visible in oblique view; Legs as in generic diagnosis, but pro- and metatarsi with light dorsal mark on third tarsomere sometimes nearly absent.

Wings (Figs 16, 63). Forewings with dark markings on basal half of 1st claval vein distinctly interrupted; other markings quite variable, but most commonly with a well-developed, continuous dark transverse patch from costa to clavus (with pale crossveins), at the level of the first branch of M, and translucent to opaque pale olivaceous, ochre, or orange basal markings (the most variable wing color feature among populations), often with extremely tiny red flecks along the venules; a few nearly opaque dark spots near the end of the claval vein; postcostal cell extensively black, with pale spots and at least 3 distinct, wide pale bands; remainder of wing mostly clear with variable, irregular dark but translucent spotting. Costal crossveins fairly numerous, mostly straight or slightly arcuate but oblique,

often obscure basally, or crossveins not reaching costa; M with 4–5 main branches, crossveins between them mostly straight, well-spaced, making square to rectangular cells; at first branch of M, M is closer to CuA than to Sc; CuA with 3–4 branches, rarely more than 1 of these coming directly off of CuA, and the first branch is typically near or slightly beyond the claval vein juncture; greatest distance between Pcu and A_1 veins slightly exceeds greatest distance between A_1 and wing margin; fused vein posterior to juncture relatively short. Hind wing hyaline except base, which is orange-infused.

Abdomen (Fig. 16) Posterolateral pale markings varying in size, grayish-yellowish, sometimes fairly small, commonly with pale markings medially on terga 2 and 3, and a narrow pale midline. Female supra-anal plate large, typically dark medially. Pleurites either entirely black or with pale posterior margin. Sternites typically pale tan except laterally and/or basally black.

Male terminalia (Figs 76, 85). Dorsal setose bulge weakly convex, setae generally reddish, short, and fairly dense. Dorsal margin curves inward at bulge, forming rounded right angle, and there is usually a low oblique ridge running from the setose bulge to the apex. Lateral hooks small, acute, tapering.

Type material.

Crepusia glauca Metcalf, 1923.

Neotype, male (here designated): "TEXAS: Brazos Co.", College Station, Lick Ck. Pk., VI-5-1996, E.G. Riley-353, UV" "NEOTYPE *Crepusia glauca* Metcalf, det. D. Yanega 2022" (TAMU).

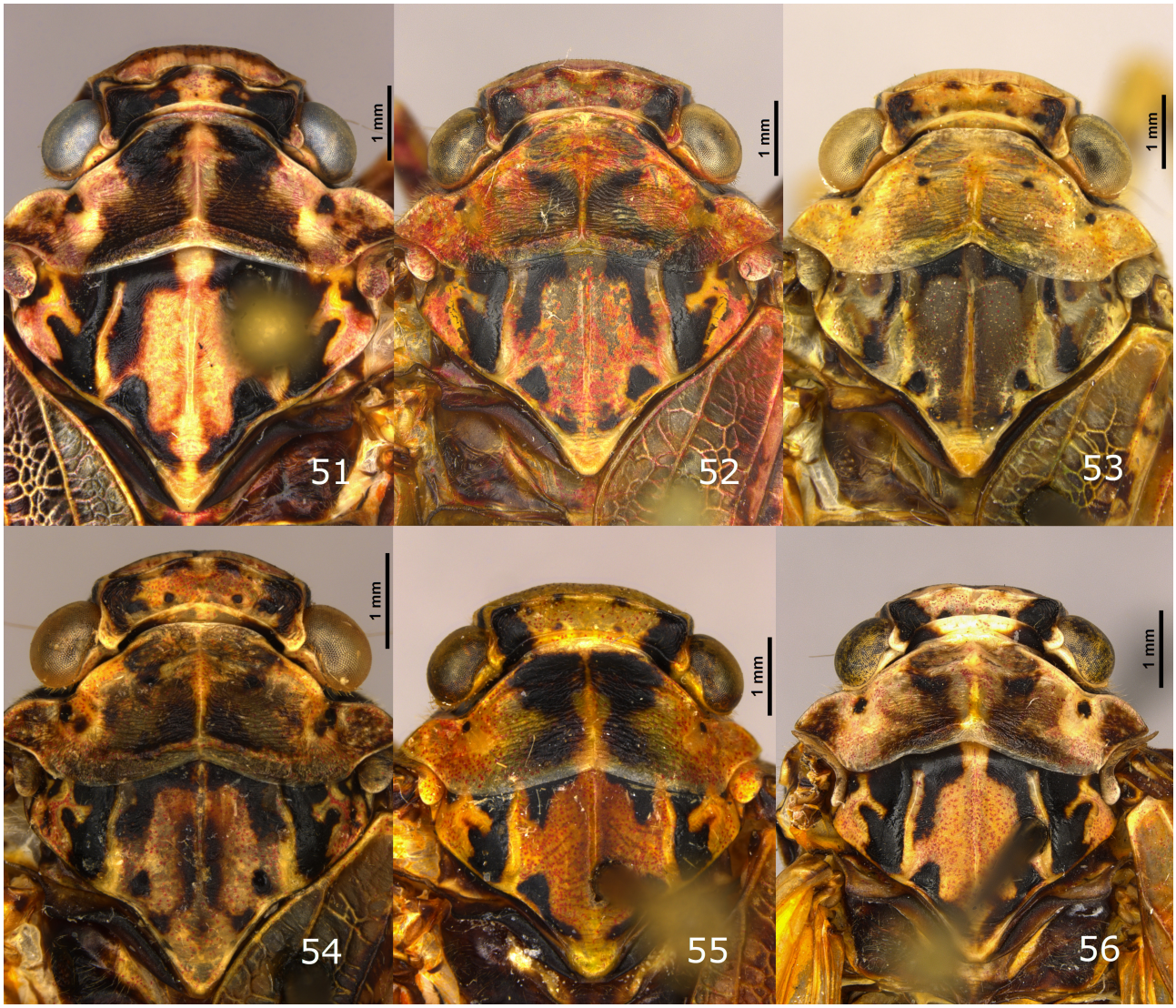
Calyptoproctus marmoratus Spinola, 1839

Holotype, male (photo only): "United States" (NMW) (Fig. 1).

Other material examined. **UNITED STATES**: **ARKANSAS**: **Bradley Co**.: Moro Bay State Park, 5.vi.1988, D.C. Hawks (UCRC ENT 54885); **FLORIDA**: **Clay Co**.: Mike Roess Gold Head State Park Campground, 27 mi NE Gainesville, 29°50'N, 81°57'W, 18.vii.1995, J.D. Oswald & L.A. Stange, "ex. Turkey oak scrub," 1M (TAMU); **Levy Co**.: Manatee Springs State Park, 21.vii.1973, 1F (AMNH); **GEORGIA**: **Charlton Co**.: Folkston, Trader Hills Rec. Area, N 30 46.74', W 82 01.61', 22.v.2004, N.H. Nazdrowicz, Hg vapor lamp, 1M; same but 15.vi.2004, 1M (UDCC); **Whitfield Co**.: Dalton, 31.viii.1990, J.K. Adams, 1F (UCRC ENT 104993); **LOUISIANA**: **Rapides Par**.: Kisatchie National Forest, 1.viii.1970, C.W. Griffin, UV light, 1F (TAMU); **St. Tammany Par**.: 4.2 mi NE Abita Springs, 30°30.986'N, 89°57.276'W, T6S R12E sec. 24, V.A. Brou, 1M (TAMU); **NORTH CAROLINA**: **Brunswick Co**.: Bald Head Island, 47 Fort Holmes Tr., 2.vi.2005, N.H. Nazdrowicz, Hg vapor lamp, 1M (UDCC); **SOUTH CAROLINA**: **Oconee Co**.: Oconee State Park, 10.vi.1991, E.G. Riley, 1M, 1F (TAMU); **TENNESSEE**: **Cooke Co**.: Cosby Ranger Station, Great Smoky Mountains National Park, 1800 ft, 35°46'21"N, 83°12'49"W, 5–8.vii.2004, E.G. Riley, UV, 2F (TAMU); **TEXAS**: **Angelina Co**.: 17.vi.1993, T, Bishop, 1F (UCRC ENT 156920); **Bastrop Co**.: "Stengl Ranch," 17.vi.1993, J. Gillaspy, 1M (UTIC); "Camp Swift. Nat. Gd.," 8.6 km N Bastrop, 25.v–28.vii.2009, J.C. Abbott, 1M (UTIC); **Bexar Co**.: Friedrich City Park, San Antonio, 11.v.1986, S. Hanselmann, 1M (TAMU); Judson Nature Trail, San Antonio, 23.vi.1987, J. & S. Hanselmann, "black lght," 1M (TAMU); **Brazoria Co**.: 4 mi S West Columbia, 11–15.vii.1976, 1F (UTIC); **Brazos Co**.: Bryan, 5.vi.1988, E.G. Riley, "mercury vapor & blacklight," 1F; same but 8.viii.1988, 1F (TAMU); College Station, Lick Creek Park, 24.viii.1997, E.G. Riley, UV, 2F; same but 13.vii.1997, 1M; same but 27.iv.1996, 1M (TAMU); 9 km SSE College Station, 15889 Woodlake Drive, 30°32"N, 96°17"W, 26–27.vii.1997, J. Oswald, UV, 1M; same but 3.viii.1997, 1F; same but 20.viii.1997, 1F; same but 24.viii.1997, 1F (TAMU); **Houston Co**.: Ratliff Lake Recreational Area, 11.vii.1996, W.F. Chamberlain, "at light," 1M, 1F (TAMU); **Kerr Co**.: Kerrville, 31.vii.1983, W.F. Chamberlain, "at light," 1F (TAMU); **Leon Co**,: 5 mi N Flynn, 24.v.1994, E. Riley, UV light, 1M (TAMU); **Nacogdoches Co**.: Nacogdoches, Park St., 8.viii.1990, W. Godwin, black light, 1F (TAMU); **Polk Co**.: Big Sandy Creek at FM 1276, 3 mi E Segno, 14.vii.1994, J.C. Abbott #204, J.W. Chirhart, M. Passanante, UV light, 1M (UTIC); **Travis Co**.: Austin, "Brackenridge Field Lab," 170m, 21.vi.1992, J.E. Gillaspy, 1M; same, but 30.vii.1992, 1M (UTIC); **Tyler Co**.: Kirby State Forest, 30°34'30"N, 94°25'03"W, 19.v–8.vi.2003, E. Riley, Lindgren funnel trap, 1M; same but 20.vii–24.vii.2003, 2F (TAMU) **Wharton Co**.: Mackay, 23.v.1984, Marlin Rice, black light, 1M (UDCC). There are also numerous images of this species online, such as iNaturalist, showing specimens from as far north as Kentucky and Virginia at the eastern end of the range, and Oklahoma at the western end.

Distribution: This species is found from southeast and central Texas (Bexar and Kerr counties) up to Arkansas and across to Fauquier county in Virginia, and all areas south and east of this, in areas where oaks are found.

FIGURES 42–50. Heads and nota of *Scaralina* species. (42) *S. aethrinsula*; (43) *S. chapina*; (44) *S. cristata*; (45) *S. durango*; (46) *S. gigantea*; (47) *S. hawksi*; (48) *S. marmorata*; (49) *S. metcalfi*; (50) *S. monzoni*.



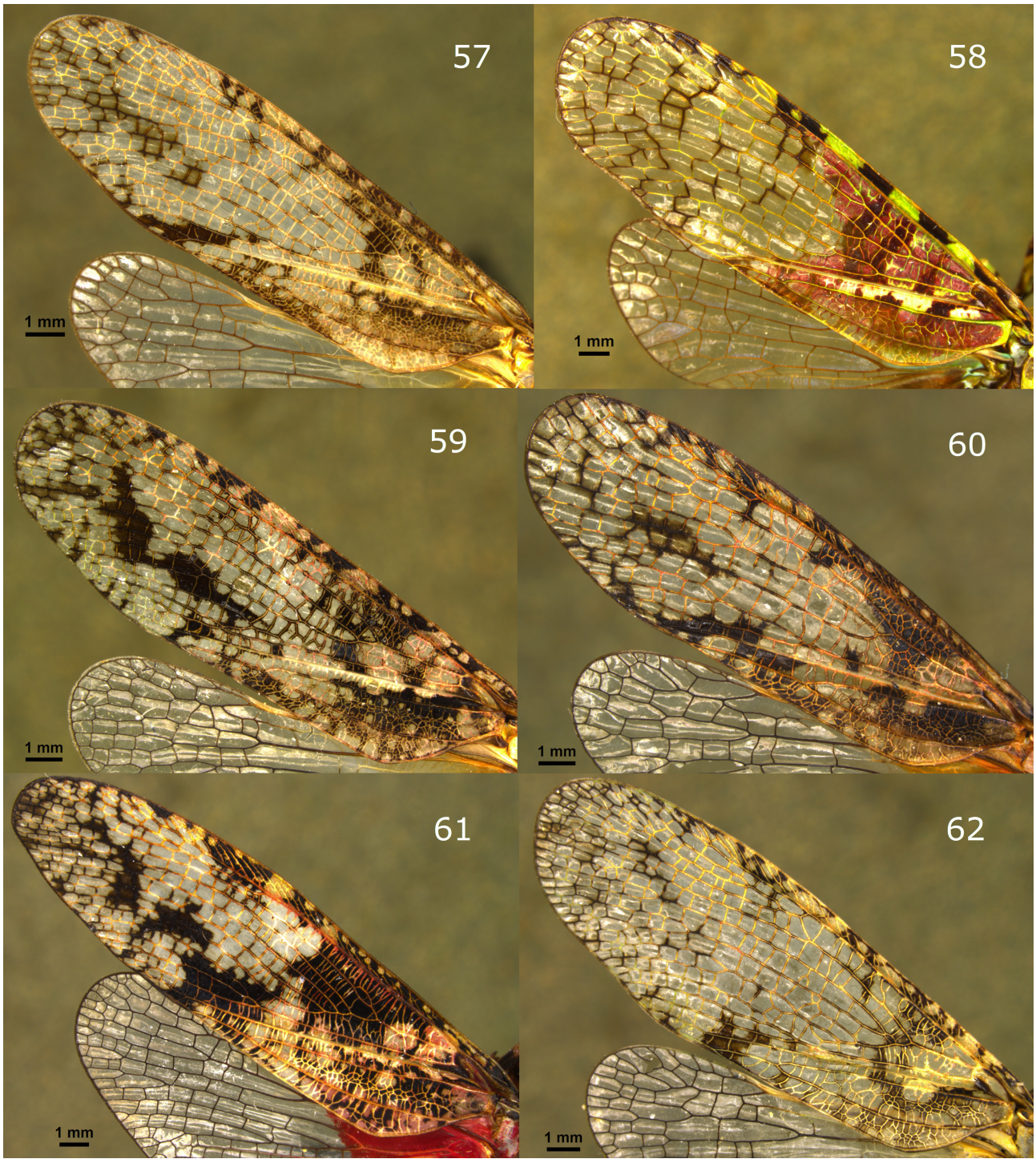
FIGURES 51–56. Heads and nota of *Scaralina* species. (51) *S. obfusca* (female); (52) *S. obrienae*; (53) *S. orientalis*; (54) *S. rileyi*; (55) *S. sullivani*; (56) *S. veracruzensis*.

***Scaralina metcalfi* Yanega & Van Dam, sp. nov.**
(Figs 20, 34, 49, 64, 77, 86)

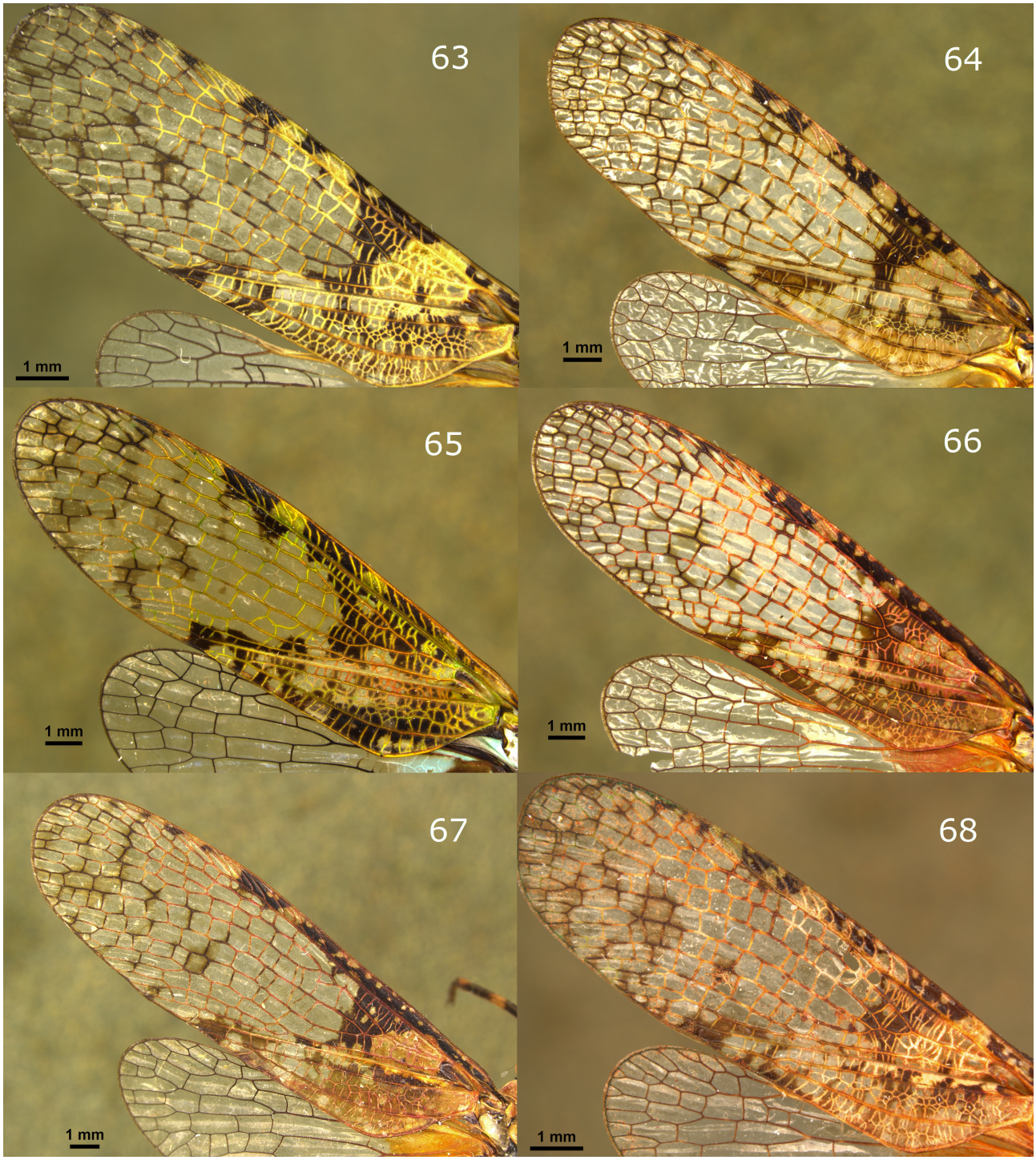
Etymology. This species is named to honor Z.P. Metcalf; although he might not have included specimens of this taxon in the paratype series of his *Crepusia glauca*, it is the only species of the three he might have seen that is in the same species group as *marmorata*.

Diagnosis. The diagnostic structural features of the pronotum and mesonotum are quite consistent, and generally unlike any of the populations of *marmorata* examined; the details of coloration also do not quite match any *marmorata* color variants known, though specimens of *rileyi* from western Texas are somewhat close, *metcalfi* differing most visibly in the dorsal abdomen being very broadly yellow-orange medially, and laterally grayish white. This particular feature distinguishes this taxon from all of the other taxa we consider to be closely affiliated with *marmorata*, most of which have the midline of the abdomen black or very narrowly yellow (though *marmorata* and *orientalis* typically have some pale sublateral markings on terga 2 and 3). The lateral mesonotal carinae, in their posterior development, are also unlike *marmorata* or its affiliated species, and the male genitalia differs significantly from these taxa, though it is more like other members of the *marmorata* species group than the *cristata* group. The slightly expanded lower frons is similar to *obfusca*, *obrienae*, and *sullivani*, and perhaps it is with these species that

its affinities lie. It is the only member of the *marmorata* group that is known to be sympatric with any members of the *cristata* species group (though it is possible that *S. obfusca* might also be), or occurs west of the Continental Divide in the United States. This taxon, like *S. aethrinsula* and *cristata*, appears to be limited to the "Sky Island" Madrean region in Arizona and adjacent northern Mexico, but is much rarer, and more geographically restricted, than the other species, though sympatric with them, suggesting it may feed on a rarer and more restricted host.

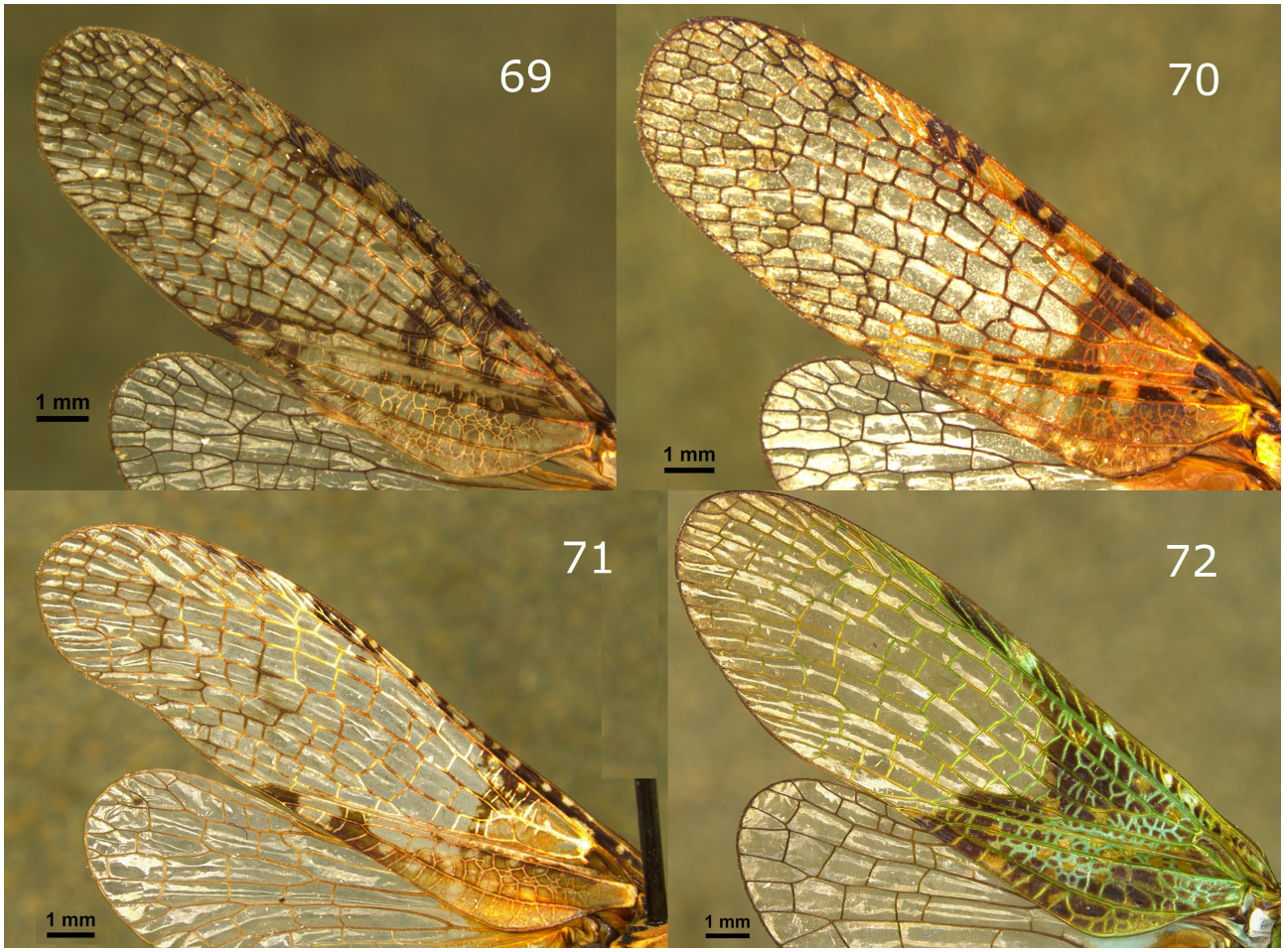


FIGURES 57–62. Forewings of *Scaralina* species. (57) *S. aethrinsula*; (58) *S. chapina*; (59) *S. cristata*; (60) *S. durango*; (61) *S. gigantea*; (62) *S. hawksi*.



FIGURES 63–68. Forewings of *Scaralina* species. (63) *S. marmorata*; (64) *S. metcalfi*; (65) *S. monzoni*; (66) *S. obfusca* (male); (67) *S. obrienae*; (68) *S. orientalis*.

Description. ***Head*** (Figs 34, 49). Median pale spot on anterior rim of vertex considerably smaller than lateral spots; supra-ocular lobes slightly narrower and more produced posteriorly than in *marmorata*. Frons coloration similar to *marmorata*, with the reflexed margin entirely pale, and the pale marks at the upper creased corners very small, but lacking converging frontal ridges sometimes seen in *marmorata*, *orientalis*, and very distinct in *rileyi*. Lateral margin of frons slightly concave, lower lobes of frons slightly expanded. Clypeus pale-marked at upper corners, along midline, and just laterad of midline, similar to *obrienae* (compare Figs 34 & 37).



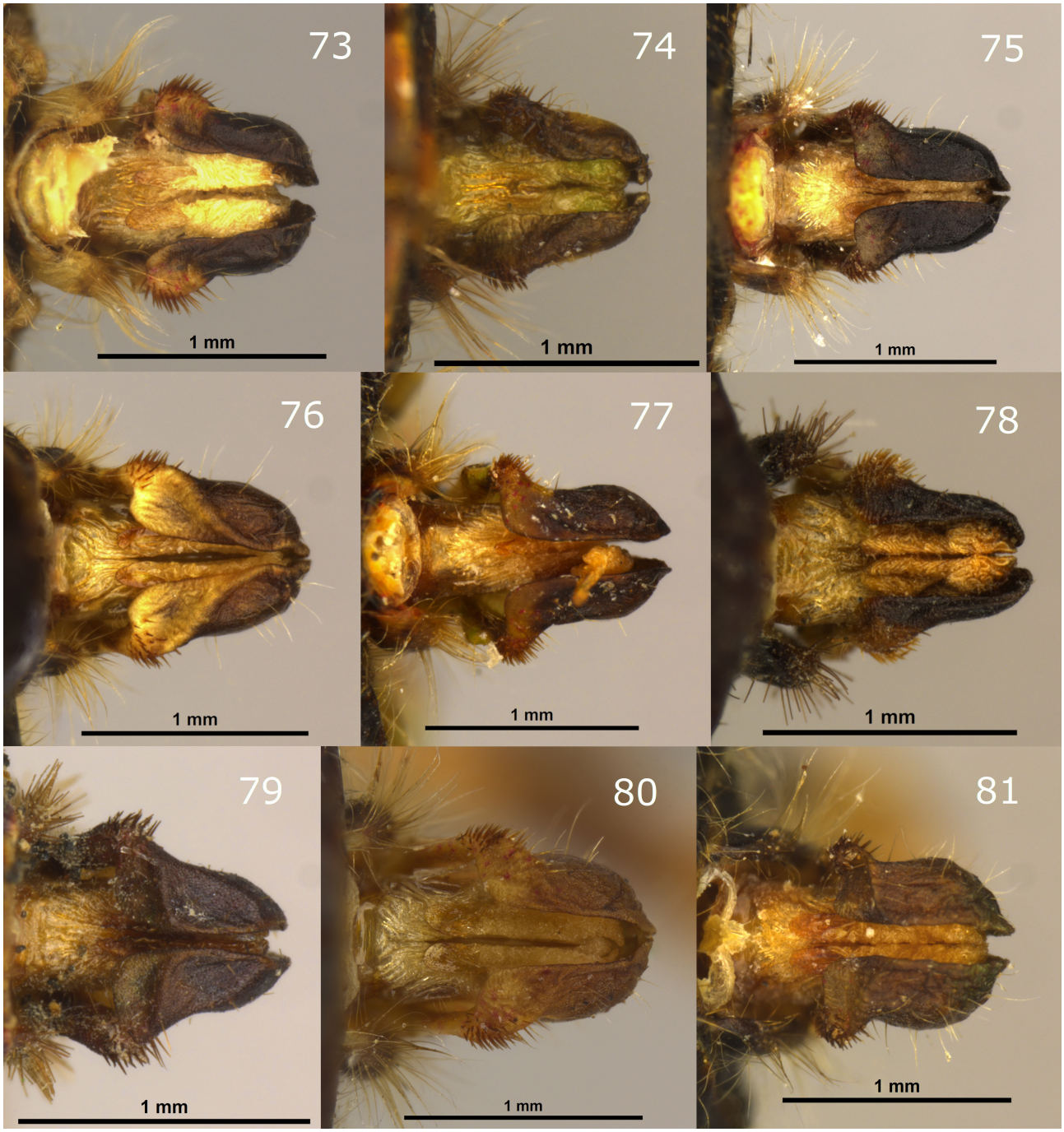
FIGURES 69–72. Forewings of *Scaralina* species. (69) *S. rileyi*; (70) *S. sullivani*; (71) *S. veracruzensis*; (72) *Scaralis* (*Alphinoides*) *inbio*.

Thorax (Fig. 49). Pronotal post-ocular spots confluent; dorsal pronotal face almost entirely gray, pale only along medial carina, rims, and adjacent to pronotal spots. Mesonotum mostly dark with typical lateral pale markings and pale carinae, also with submedian lighter gray patches; lateral carinae atypical for genus, in that they are slightly obscured posteriorly, and the semicircular inner posterior carina that runs around the posterior pronotal spots is strong and connects to the terminus of the lateral carina; in effect, then, the lateral carinae appear to be strongly recurved posteriorly and running inside the posterior spots, similar to the pattern seen in *gigantea* and *cristata*. Mesonotal lobe pale along the midline and lateral margins, otherwise black. Dorsal setae long. Forecoxae paler than in most other species, legs otherwise mostly corresponding to generic diagnosis.

Wings (Figs 20, 64). Forewings mostly similar to *marmorata*, but with prominent dark marks posteriorly along claval vein, touching juncture; never with basal pale areas opaque. Pale basal area of forewing with membrane translucent (not hyaline) and hardly pigmented, though the venules may be orange and/or have tiny red flecks. Costal crossveins simple and typically well-spaced past 1st branch of M, M with 4–5 branches, CuA rarely with more than one direct branch. Hind wing hyaline except base, which is slightly orange-infused.

Abdomen (Fig. 20) Dorsum with distinct medial yellow-orange band in addition to poorly-defined buff-grayish lateral bands, tending to become nearly confluent on psoterior terga. Female supra-anal plate large, extensively pale.

Male terminalia (Figs 77, 86). Gonostyle apically black. Setose bulge displaced more anteriorly to the incurved dorsal portion than usual, and at an almost vertical orientation rather than nearly horizontal as in other species. Dorsal surfaces of gonostyli nearly meeting at midline, without evident ridges. Lateral hooks relatively small, acute, with basal flap poorly developed.

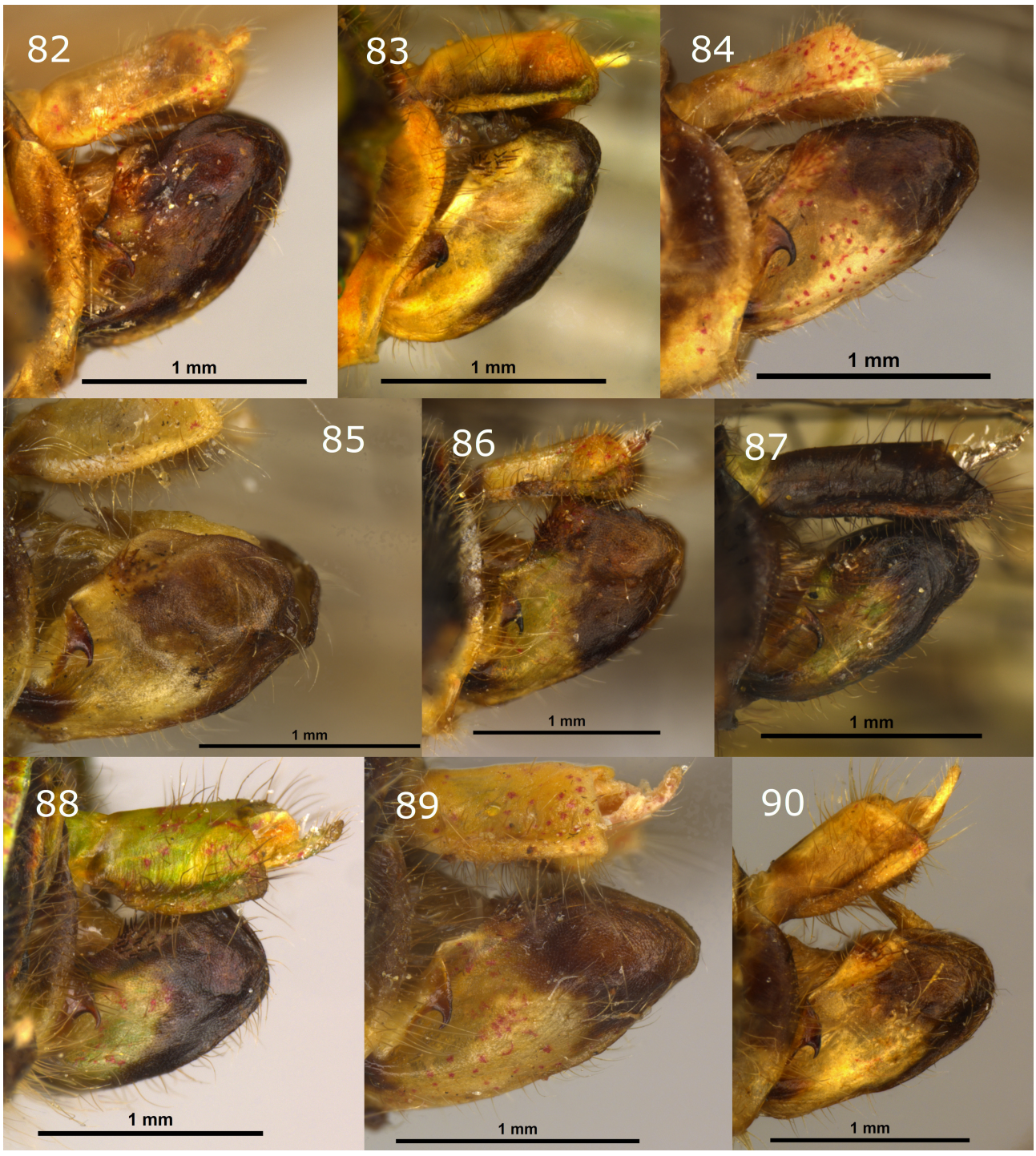


FIGURES 73–81. Male genitalia of *Scaralina* species, dorsal view, anal tube removed. (73) *S. aethrinsula*; (74) *S. chapina*; (75) *S. cristata*; (76) *S. marmorata*; (77) *S. metcalfi*; (78) *S. monzoni*; (79) *S. obrienae*; (80) *S. orientalis*; (81) *S. rileyi*. NOTE: *obfusca*, *sullivani* not included.

Type material. ***Holotype***, male: **ARIZONA**: **Cochise Co**.: Copper Canyon, Montezuma Canyon Road, 31°21’45”N, 110°18’01”W, 1850m, 29.vii.2002, D. Yanega (UCRC ENT 72827, at UCRC).

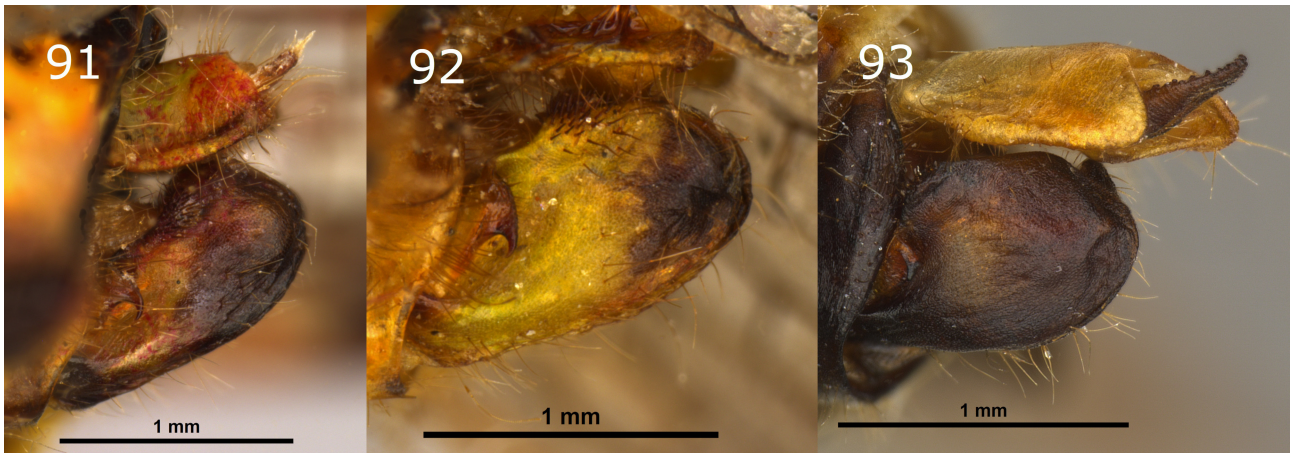
Paratypes (20 specimens): **ARIZONA**: **Cochise Co**.: Portal, 4700 ft, 29.iii.1983, L.D. Anderson, 1F (UCRC ENT 127490); SWRS, Chiricahua Mts, 3.viii.1969, L.D Anderson, 1F; same but 10.viii.1975, McNally, 1F (UCRC); East Turkey Creek, 31°54’49”N, 109°14’19”W, 1830m, 28.vii.2005 J. & E. Adams, 1F (UCRC ENT 128976); Miller Canyon Road, Huachuca Mts, 31°24’56”N, 110°16’32”W, 1760m, 21.viii.2004, D. Yanega, 4F, 1M (UCRC ENT 98265–69); Miller Canyon, 31°24.952’N, 110°16.539’W, 1750m, 3.viii.2007, J. Mottern, MV, 1M (UCRC ENT 323691); Ash Canyon, 18.viii.1982, A. Reifschneider, 1F (UNSM); **Pima Co**.: Madera Canyon, Santa Rita Mts,

13.viii.1952, M. Cazier, R. Schrammel, C. & P. Vaurie, 1M (AMNH); Bog Springs Campground, Madera Canyon, Santa Rita Mts, 13.ix.1964, L. & C.W. O'Brien, blacklight, 1M (TTU-Z 18693; TTCC); same but 25.vi.1985, on *Quercus*, W.F. Barr, 1F (UDCC); **Santa Cruz Co.**: Madera Canyon, 5400 ft, 3.viii.1988, at light, C.E. Seibert, 1F (MTEC); Upper Madera Canyon, 31°42'46"N, 110°52'25"W, 1660m, 3.ix.2011, D. Yanega, MV, 1M (UCRC ENT 309054); Upper White Rocks Campground, Peña Blanca Lake, 1200m, 29.vii.2003, A.L. Park, Hg vapor light, 1F (UDCC); Santa Rita Canyon, 31°42'06"N, 110°48'58"W, 1870m, 31.vii.2002, D. Yanega, 1M (UCRC ENT 72843); **MEXICO**: **Chihuahua**: Cuiteco, 19.viii.1969, T.A. Sears, R.C. Gardner, C.S. Glaser, 1M (CSCA); 3 km. S. of Temoris, 4700 ft, 21.viii.1969, T.A. Sears, R.C. Gardner, C.S. Glaser, 1F (CSCA).



FIGURES 82–90. Male genitalia of *Scaralina* species, lateral view. (82) *S. aethrinsula*; (83) *S. chapina*; (84) *S. cristata*; (85) *S. marmorata*; (86) *S. metcalfi*; (87) *S. monzoni*; (88) *S. obrienae*; (89) *S. orientalis*; (90) *S. rileyi*.

Distribution. While it might occur in other mountain ranges in the US besides the four it has been found in (the Atascosa, Chiricahua, Huachuca, and Santa Rita ranges), we would caution against such an assumption; the Santa Catalina and Patagonia ranges, for instance, have been well sampled, yielding numerous of specimens of *aethrinsula* and *cristata*, but not one recorded specimen of *metcalfi* thus far.



FIGURES 91–93. Male genitalia of *Scaralina* species, lateral view. (91) *S. obfusca*; (92) *S. sullivani*; (93) *Scaralis* (*Alphinoides*) *inbio*, sub-lateral view.

***Scaralina rileyi* Yanega, sp. nov.**
(Figs 3, 25, 39, 54, 69, 81, 90)

Etymology. This species is named to honor E.G. Riley, former curator at TAMU, whose assistance was invaluable for this study, and who collected the holotype specimen.

Diagnosis. The long pubescence of the pronotum and mesonotum are unlike any of the populations of *marmorata* examined; the details of coloration also do not quite match any *marmorata* color variants known. This taxon appears close to the geographically-proximate *orientalis*, but the stronger carinae on the frons, the oblique dorsal ridge on the gonostyli, and the lack of orange pigmentation on the forewing base appear to separate the two fairly readily. In *orientalis*, the forewing bases (and thorax) invariably display a strong peppering of microscopic reddish spots, as well as an orange tint to both the crossveins and to the wing membrane itself; in *rileyi* the crossveins are whitish, the basal wing membrane is entirely hyaline (i.e., other than the usual infuscated band), and the scattered reddish spots are faintly evident or nearly absent. The male gonostyli are perhaps most similar to *obrienae*, which is considerably more geographically disjunct. We suspect that *rileyi* will be found to feed on *Quercus grisea*, a very common oak in the Davis Mountains, and a very close relative of *Q. arizonica*, which is the host of some Arizonan *Scaralina*.

Type material. ***Holotype***, male: **TEXAS: Jeff Davis Co**.: Davis Mountains, Madera Canyon, 25.vi.1994, E.G. Riley, UV, 1M (TAMU).

Paratypes (9 specimens) as follows: **Jeff Davis Co**.: 5 mi NW Fort Davis, 16.vii.1988, R.W. Sites, Hg vapor, 1M (TTU-Z 18719; TTCC); Davis Mountains Resort, 21.viii.1987, B.C. Ratcliffe, 1M (UNL); same but 5800 ft, 28.vi.2002, D.G. Marqua, 1M (TAMU; dissected); same but 27.vi.1992, 1F (TAMU-ENTO X0631563); same but 30.vi.2002, 1M (TAMU); 22 mi NW Fort Davis, 27.vii.2005, J.K. Adams, 4M (UCRC ENT 129056–58, 562509).

Description. ***Head*** (Figs 39, 54) Most features as in *marmorata* but frontal ridges more well-defined, including a very distinct medial ridge that is often complete, the area between the ridges slightly smoother than in *marmorata*. Clypeus typically mostly dark, with light markings restricted to base of clypeus and widely-spaced lateral pale markings, but lower midline not pale, as also seen in *orientalis* (compare Figs 39 & 38 to 33 & 37).

Thorax (Figs 3, 54). Most features as in *marmorata* but dark markings more extensive on thorax and legs (including tarsi), except the posterior mesonotal lobe is paler; dorsal setae long; pale ground color more grayish than olivaceous, though there are populations of *marmorata* that are fairly similar outside of Texas.

Wings (Figs 25, 69) Most features as in *marmorata* but pale basal area of forewing hyaline and entirely unpigmented except veins. Costal crossveins simple and somewhat closely spaced past 1st branch of M. Hind wing hyaline except base, which is slightly orange-infused.

Abdomen (Fig. 25). Most features as in *marmorata* but tergum 2 pale medially, tergum 3 almost entirely dark, and terga 4 and beyond pale laterally, with a narrow pale midline and some very faint submedial marks. Female supra-anal plate large, and marked much like preceding tergum.

Male terminalia (Figs 81, 90). Somewhat similar to *marmorata* but gonostyli with a more projecting setose bulge, and a strong and almost transverse dorsal ridge (rather than oblique), and a very short basal impressed portion, the latter features therefore similar to *obrienae*.

Distribution. This taxon is presently unknown from outside of the Davis Mountains, but the Sierra Vieja in Presidio County (about 25 miles away) appears to be unexplored, and there are fairly similar habitats in the Chisos Mountains, yet no specimens have been reported from the area; given the disjunction of this habitat from the nearest similar habitats elsewhere, this may be an endemic taxon. If anything, the biogeography might connect it to the very northern limits of the Sierra Madre Oriental, and therefore to *orientalis*, but at present, the nearest records for the two taxa are separated by well over 400 miles. The nearest known populations of *marmorata* are slightly over 250 miles away, but in very different habitats, and there are populations of *cristata* less than 200 miles away, but that species is not in the *marmorata* species group.

MESOAMERICAN SPECIES (Map; Fig. 94):

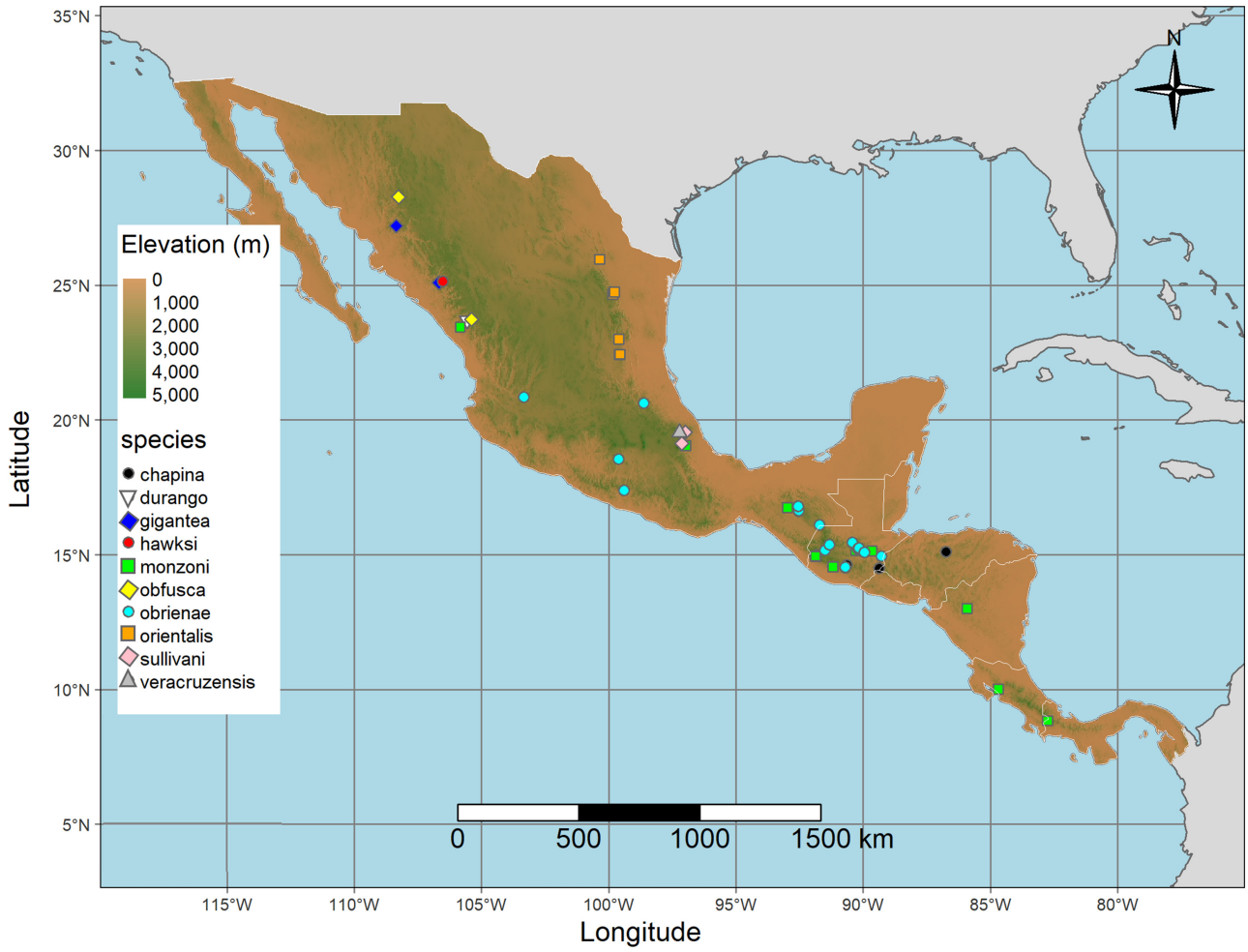


FIGURE 94. Map of Mesoamerican *Scaralina* species (type series only).

Scaralina chapina Goemans & Yanega, sp. nov.

(Figs 14, 28, 43, 58, 74, 83)

Etymology. The species epithet "chapina" is a colloquial name for a native of Guatemala, here treated as a noun in apposition.

Diagnosis. The brightly colored pale frons, lower prothorax, and forewings immediately distinguish this from all other species. It is perhaps most similar to *S. monzoni*, sharing a few unique features: the lack of spotting on

the lower frons, the lack of a distinct translucent area in the basal third of the forewing, and the blue-based hind wings of the females (the red hindwings of the males of *chapina* appear to be a unique form of sexual dimorphism in the genus; while the only known female is from Honduras, and all the males are from Guatemala, we consider it unlikely that there is a second related species in Honduras where both sexes have blue hindwings but are otherwise identical to *chapina*). The blue hindwings in these two species are somewhat similar to the putative sister genus, *Scaralis*, which virtually always has blue coloration on the hindwings. Males of *chapina* also have distinct subacute subocular lobes, and the gonostylar hooks are short and thickened, both features unlike any other *Scaralina* but very similar to *Scaralis s.s*. The dorsal incurved portion of the gonostyle is also very weak in this species. The large female tergal plate also further enhances the resemblance to species of *Scaralis*.

Description. ***Head*** (Figs 28, 43). Anterior rim of vertex mostly dark, except broadly pale medially; supra-ocular lobes pale apically; posterior rim mostly pale, except darkened adjacent to supra-ocular lobes; dark spots of vertex posterior in position, obscured by large ring-like black markings. Subocular lobes present and subacute in male but poorly-defined in female. Frons entirely bright, pale green, in strong contrast to the almost entirely black clypeus. Lateral margin of frons slightly concave, lower lobes of frons slightly expanded. Rostrum almost entirely black.

Thorax (Fig. 43). Pronotal ground color light greenish to olivaceous, dark markings black and mostly highly contrasting; anterior portion of dorsal face broadly dark, large black marks surrounding anteromedial spots, post-ocular spots small; lower portion of pronotum black above, bright green below. Central carina of mesonotum darker than ground color, flanked by large black marks; lateral carinae sinuate anteriorly, nearly straight posteriorly, often entirely pale; posterior spots very small; mesonotal lobe rounded, black at apex. Dorsal setae long. Legs mostly as in generic diagnosis, but procoxae with anterior face entirely dark, third tarsomeres of pro- and mesotarsi black, third metatarsomere pale-spotted dorsally, basal two metatarsomeres much darker than in other species.

Wings (Figs 14, 58). Forewings with dark markings on basal half of 1st claval vein distinctly interrupted by whitish opaque markings (only on dorsal surface of wing); dark transverse banding alternating with opaque rose/magenta nearly to the level of the claval vein juncture, no translucent basal area; veins and some crossveins contrasting, greenish; postcostal cell extensively black, with at least 3 distinct, wide, bright green bands; remainder of wing yellowish hyaline (lighter apically), with faint, irregular dark spotting. Costal crossveins very few, well-spaced, mostly straight or slightly arcuate but oblique, not contrasting, obscure or absent in basal half of cell; M with 4 main branches, crossveins between them mostly straight, well-spaced, making square to rectangular cells; at first branch of M, M is slightly closer to CuA than to Sc; CuA with 3–4 branches, rarely more than 1 of these coming directly off of CuA, and the first branch typically greatly precedes the claval vein juncture; greatest distance between Pcu and A_1 veins greatly exceeds greatest distance between A_1 and wing margin; fused vein posterior to juncture relatively short. Hind wing hyaline except base, which is pale blue in females, and red in males, with a small blackish infumated area posterior to the colored portion.

Abdomen (Fig. 14). Dorsum and venter both almost entirely black, with only a few poorly-defined irregular pale spotted areas laterally on the middle and apical tergites, and narrow orange margins on the tergites, ventral pleurites, and sternites. The female tergal plate in this species is nearly twice as long as any of the preceding terga, and almost completely covers the genitalia.

Male genitalia (Figs 74, 83). Incurved dorsal portion of gonostyle very weakly sclerotized mesad of setose bulge, basal hooks short, thickened, and blunt at tip.

Type material. ***Holotype***, male: **GUATEMALA**: **Sacatepequez**: "San Lucas, Cima de Cerro Alux, 10.v.2001, 2200m, Trampa de luz mercurio," G. Goemans & J. Monzón, 1M (UVGC 1152, at UVGC).

Paratypes (9 specimens) as follows; one male labeled exactly as holotype, but GGCB 0093 (UVGC 1150); **Chiquimula**: Plan Arada, 1600m, vii.1999, J. Monzón, 1M (GGCB 0088); **Sacatepequez**: "San Cristobal El Bajo Finca El Pilar, arriba 2010m," 14°32'28"N, 90°42'04"W, 10.v.2018, J. Monzón, M. Dickman, 1M (UVGC); "San Cristobal El Bajo Finca El Pilar, arriba 2175m," 14.vii.2011, J. Monzón, F.R. Camposeco, 1M (UVGC); "San Cristobal El Bajo Finca El Pilar, Cerro Cucurucho, 2600m," 14°31'06"N, 90°41'28"W, 22.iv.2017, Monzón, Naumann, 1M (UVGC); **San Marcos**: "Camino Fraternidad a Bojonal, 1600m," 14°56'45"N, 91°52'50"W, 3.v.2014, J. Monzón, F.R. Camposeco, 1M (UVGC); Reserva Municipal Plan de la Gloria, 2440m, 14°58'49"N, 91°50'18"W, 24.v.2017 F.R. Camposeco, 1M (UCRC ENT 516401); **Suchitepéquez**: Refugio del Quetzal, University del Valle, 1600m, 14°32'53"N, 91°11'36"W, 1.ix.2008, F.R. Camposeco, J. Monzón, 1M (UVGC); **HONDURAS**: **Olancho Dept**.: La Muralla National Park, 1480m, 15°05'49"N 86°44'17"W, 4–7.vii.2002, D. Yanega, 1F (UCRC ENT 71055).

Distribution. Guatemala to Honduras, at elevations above 1400 meters.

***Scaralina durango* Yanega, sp. nov.**
(Figs 17, 30, 45, 60)

Etymology. This species is named for its provenance, and treated as a noun in apposition.

Diagnosis. This species is most similar to *aethrinsula*, with which it shares the unmodified female tergum 6 that would have excluded it from consideration as a member of the "Calyptoproctina", but with some similarities also to *cristata*, as the pronotal carina is somewhat stronger than is typical, and the forewings are medially maculated. The face is very dark; the forewings are relatively heavily maculated, especially medially, with some orange tint to the translucent basal area; the hindwing bases are reddish-orange; the emargination of the female anal tube is more nearly semicircular than most species.

Description (female only; male unknown). ***Head*** (Figs 30, 45). Many features as in *aethrinsula*, but lower frons and clypeus much darker.

Thorax (Fig. 45). Many features as in *aethrinsula*, but pronotal medial ridge more prominent, mesonotum darker laterally; dorsal setae slightly longer.

Wings (Figs 17, 60). Forewings with membrane in several medial cells black and nearly opaque, though not quite as extensive as in *cristata*, and with somewhat more visible brownish-orange pigmentation to membrane near base; venation much like *cristata*, if not slightly coarser, generally not as finely anastomosing as in *aethrinsula*, especially not in the anal portion. Costal crossveins numerous, close, highly anastomosing, highly reticulate, more similar to *aethrinsula*. Veins and venules often outlined in black, though not quite as often as in *cristata*. Hindwing bases reddish-orange.

Abdomen (Fig. 17). Nearly identical to *aethrinsula*, though possibly with weaker medial pigmentation, tergum 6 unmodified.

Type material. ***Holotype***, female: **MEXICO**: **Durango**: "Coscomate Camps, 2450m
23°42'1"N 105°34'9"W, 25.vii.2019 D.C. Hawks MV" (UCRC ENT 533958, at UCRC).

Distribution. So far known only from the type locality in western Durango.

***Scaralina gigantea* Yanega, sp. nov.**
(Figs 18, 31, 46, 61)

Etymology. This species is named for its relatively large size, the largest specimens seen so far in the genus, including what appears to be the longest rostrum (extending well past the femoro-tibial joint, nearly to the abdominal tip). The epithet is adjectival.

Diagnosis. In addition to size, the bright red abdominal dorsum and hindwing bases, and the extensive dark forewing markings immediately distinguish this from all other species. The dark basal markings extend over 1/3rd the wing length, and the translucent basal area is greatly reduced compared to other species. It is most similar to *S. cristata*, sharing a few unusual features, as noted above. The small setae along the wing veins and in the wing membrane are relatively longer and greater in number than in any other species. It shows distinct structural affinities to *cristata*, with a strong, complete and posteriorly recurved mediolateral notal carina in addition to a strong medial pronotal carina; it also shares with *cristata* the strongly pigmented cells in the medial forewing, and the thoracic ground color of dark with pale fused spots.

Description (female only; male unknown). ***Head*** (Figs 31, 46). Frons similar to *cristata*, with ground color pale, but densely covered with dark spots, fused over much of surface; weak but distinct medial and transverse ridges. Rostrum relatively elongated, extending well past the femoro-tibial joint, nearly to the abdominal apex.

Thorax (Fig. 46). Many features similar to *cristata*, such as dark ground color with extensive pale spotting, very prominent medial pronotal ridge, and strongly sinuate lateral mesonotal carinae; overall slightly darker, with posterolateral mesonotal spots enclosed in raised pale circles. Dorsal setae long. Fore coxae almost entirely black except at base and apex.

Wings (Figs 18, 61) The forewing maculations are extensive and opaque, medially and distally, highly contrasting in the basal half of the wing with white veins and wing spots, and very small translucent spots at the base. Costal crossveins numerous, close, pale and strongly contrasting, often sinuous or slightly anastomosing, much as in *cristata*. The hindwings are scarlet red at the base, the coloration extending over a larger area than in most species. Veins and wing membrane with setae relatively longer and denser than in other species.

Abdomen (Fig. 18). Abdominal dorsum extensively scarlet red, with irregular dark markings; female supra-anal plate large, nearly 3 times the length of the preceding tergum, and concealing anal tube.

Type material. ***Holotype***, female: **MEXICO**: **Durango**: "W of Canelas, 1450m MV, 25°5'45"N 106°39'57"W, 28.vii.2019 D.C. Hawks" (UCRC ENT 533840, at UCRC).

Paratype, female: **MEXICO**: **Chihuahua**: 8 mi S Témoris, ~1435m, 1.ix.1969 (CSCA).

Distribution. So far known only from two localities, in western Durango and western Chihuahua, within 300 km of one another.

Scaralina hawksi Yanega, sp. nov.

(Figs 19, 32, 47, 62)

Etymology. This species is named for its collector, my colleague and friend Dave Hawks, who made a special effort to collect fulgorids we could use for this revision, and caught four undescribed taxa in one trip, of which this is one of two that was previously unknown.

Diagnosis. This species is very similar to *S. aethrinsula*, especially in the extensive yellow dorsal abdominal markings, but female tergum 6 is modified into an elongated supra-anal plate as in other members of the genus, and the frons is more extensively pale, with much smaller dark spots. The five very faint converging ridges on the frons, in addition to the lower transverse ridges, are atypical for *Scaralina*. The tip of the main rostral segment extends only slightly past the metacoxae, therefore among the shortest in the genus, and the clypeus is not quite as elongate as most other species.

Description (female only; male unknown). ***Head*** (Figs 32, 47). Frons and clypeus mostly pale with small dark spots, though upper frons with a strong transverse dark band; surface relatively smooth and flat but with five very faint converging ridges in addition to lower transverse ridge above clypeal base. Lateral margin of frons slightly concave, lower lobes of frons slightly expanded. Clypeus only slightly longer than broad. Dark granular spots on vertex very well-defined and contrasting with mostly pale surface. Rostrum with tip of the main rostral segment extending only slightly past the metacoxae.

Thorax (Fig. 47). Many features similar to *aethrinsula*, though the pale areas are rarely well-defined circular spots, especially not on the mesonotum, and the lateral mesonotal carinae are more weakly curved; dorsal setae slightly longer.

Wings (Figs 19, 62). Forewings similar to *aethrinsula*, but slightly less medial maculation, fewer fine anastomosing veins, and more contrast between pale basal veins against the dark background; basal translucent area very faintly pale orange with pale orange veins; medial venation often with more visible dark outline, somewhat similar to *cristata*. Costal crossveins numerous, close, often sinuous or slightly anastomosing, more similar to *cristata* than to *aethrinsula*. The dark transverse basal markings of the two specimens are broad but irregularly pigmented. Hindwings pale orange at base, much reduced compared to related species.

Abdomen (Fig. 19). Dorsal coloration mostly similar to *aethrinsula*, but medial and lateral markings less visibly separated; tergum 6 roughly twice as long as preceding tergum, forming a supra-anal plate, similar to others in the genus. [Note: both specimens crushed somewhat, but it is assumed that in better-preserved material the anal tube would be at least partially concealed.]

Type material. ***Holotype***, female: **MEXICO**: **Durango**: "Canelas, 1955m MV, 25°7'51"N 106°30'34"W, 29.vii.2019 D.C. Hawks" (UCRC ENT 533960, at UCRC).

Paratype, female: same data (UCRC ENT 533959).

Distribution. So far known only from the type locality in western Durango.

Scaralina monzoni Goemans & Yanega, sp. nov.

(Figs 21, 35, 50, 65, 78, 87)

Etymology. This species is named to honor José Monzón, an excellent biologist, collector, and guide to those visiting Guatemala, including the senior authors.

Diagnosis. The pattern of forewing coloration, extensively black basally with highly contrasting venation,

sharply demarcated, and with irregular distal infuscation, immediately distinguishes this species. This species has atypical features that, taken together, make it more like a *Scaralis* than any other *Scaralina* species; the large supra-anal plate; the sharp demarcation of the basal pigmented region in the forewings; the blue and black hindwing base, and the infumation of the hindwing anal region; the tip of the main rostral segment extending only slightly past the metacoxae, are all similar to *Scaralis* species. The 2nd antennal segment, however, is globose (albeit somewhat larger in diameter than in other species); the versteifung is large and weakly angulate; the fore- and midlegs are fully banded; the male gonostyli have an extremely well-developed basal hook, and a distinct incurved dorsal portion near the setose bulge. The degree to which the dark pigmentation of the forewings extends, and the degree of opacity, is somewhat variable over the range of the species; some specimens have dark basal pigmentation more greenish than black, or extending over a slightly smaller area. Even more variable is the dorsum of the mesoscutum, which ranges from broadly pale medially, to irregularly darkened, to having sharply-delimited medial longitudinal stripes. Despite this variation, the structural similarities are strong enough that we see no reason to divide the taxon into regional subspecies.

Description. ***Head*** (Figs 35, 50). Rim of vertex mostly pale; lateral black marks on anterior and posterior rims; dark spots of vertex posterior in position, almost joining large black lateral bands. Frons broadly pale olivaceous along upper margin, dark olivaceous below this (pale markings at corner of frontal crease near ocellus poorly-defined), lacking tiny dark spots; converging ridges varying from faint to absent, and surface finely rugose. Lateral margin of frons concave, lower lobes of frons expanded. Clypeus usually extensively pale, with strong dark markings surrounding yellowish center, these dark markings occasionally more extensive (more southern material); about 1.5 times as long as broad. Rostrum with tip of the main rostral segment extending only slightly past the metacoxae.

Thorax (Fig. 50). Pronotum (and mesonotum) ground color olivaceous, dark markings rarely black; post-ocular pronotal spots very small, as are anterior pronotal spots; midline of dorsal pronotal face pale but little contrasting, with small darkened anteromedian spots. Mesonotum center paler posteriorly, black markings unusually restricted in extent in most specimens, represented by only the posterior spots and two lateral patches, with only irregular darkening in the middle of the disc (in the two specimens from Nicaragua and Panama, however, there are two sharply-defined black vittae along the midline); medial carina well-developed; lateral carinae not contrasting, slightly sinuate anteriorly and posteriorly; posterior mesonotal lobe rounded. Dorsal setae moderately long, denser and darker than in other species. Legs not quite typical for genus; the procoxal faces are extensively dark, the third tarsomeres of the pro- and mesotarsi are black, but brownish on the metatarsi; basal two metatarsomeres somewhat darkened, including ventrally; the banding of the metafemur tends to be brownish and rather weakly contrasting, unlike any other species.

Wings (Figs 21, 65). Forewings with dark markings on basal half of 1st claval vein distinctly interrupted; dark transverse patch filling basal portion of wing, to the level of the claval vein juncture, pale basal markings limited to a few very small translucent spots rather than a defined translucent area as in most other species; veins and crossveins highly contrasting, mostly pale greenish, imparting a general greenish cast to the wing base; postcostal cell extensively black, with a few tiny pale spots and at least 3 distinct, wide pale greenish bands; remainder of wing mostly clear, with some weak but distinct, irregular, dark greenish spotting. Costal crossveins numerous, closely-spaced, highly contrasting, mostly straight or slightly arcuate but oblique, well-defined basally; M with 4 main branches, crossveins between them mostly straight, well-spaced, making square to rectangular cells; at first branch of M, M is equidistant from CuA and Sc; CuA with 3–4 branches, rarely more than 1 of these coming directly off of CuA, and the first branch typically precedes the claval vein juncture; greatest distance between Pcu and A_1 veins greatly exceeds greatest distance between A_1 and wing margin; fused vein posterior to juncture relatively short. Hindwings hyaline with black veins except base, which is very pale powdery blue with blackish infumation, and anal region very faintly infumated with fine gray veins.

Abdomen (Fig. 21) Dorsum almost solid black, tergites with very narrow greenish rim, and some red/orange spotting on posterior tergites near lateral depressions of terga 4–6. Ventral pleurites dark but grading into orange, especially posteriorly, and sternites dark basally but extensively orange otherwise. Female supra-anal plate relatively long, completely covering anal tube. Anal tube mostly black.

Male terminalia (Figs 78, 87). Dorsal incurved portion of gonostyle with apical portion narrowed, scarcely concealing apex of aedeagal apparatus. Basal hook of gonostyle relatively large, strongly curved and evenly tapered to very acute point, basal flap modified into a swollen protrusion bearing the hook; setose bulge with setae short and relatively sparse; apical half of gonostyle black, base pale.

Type material. ***Holotype***, male: **GUATEMALA**: **San Marcos**: km 1.2 Bojonal Road, 14°56'N, 91°52'W, 1600m, 13–14.vii.2001, D.C. Hawks, D. Yanega, 1M (UCRC ENT 66867, at UCRC).

Paratypes (13 specimens) as follows: **COSTA RICA**: **Puntarenas**: "Send. El Ripario a 3 Km NE. de progreso. 1300m," LS 319000, 597000, #47421, 2–4,vii.1997, E. Navarro, 1M (CRI002567715, INBIO); **GUATEMALA**: **Baja Verapaz**: Pantín Rd. 9 km N Salamá, 1600m, 5.vi.1993, A. Howden, 1M (ASULOB); **San Marcos**: Bojonal Rd. km 2.2, 1585m, 14°56'58"N, 91°52'47"W, 24.vii.2017, D.C. Hawks, 1M (UCRC ENT 524566); **Suchitepéquez**: Refugio del Quetzal, University del Valle, 1575m, 14°32'53"N 91°11'36"W, 20–21.v.2016, D. Yanega, 1F, 1M (UCRC ENT 479950 & 479951); same data except 15.viii.2018, J. Monzón, D. Hawks, 1F (UCRC ENT 516381); **Zacapa**: Sierra de las Minas, Cerro del Mono, "cloud forest 8 rd. km N of San Lorenzo marble mill," 2150m, 7.vi.1993, MV & UV light, W.B. Warner, 1M (ASULOB); **MEXICO**: **Chiapas**: "from swifts WCS-1985-32, HO-31," 3.vi–13.vii.1985, D.F. Whitacre, 1M (ASULOB); El Chorreadero, 22.vii.1978, "CRB," 1M (UNAM); **Sinaloa**: 2 mi SW Potrerillos (nr. El Brillante), "bl.", 12.viii.1986, 4200 ft, Brown & Powell, 1F (EMEC); **Veracruz**: Ixhuatlán del Café, 1355m, 19°3'3"N, 96°59'3"W, 6.viii.1985, Taylor & Sullivan, 1M (UCRC 54823); **NICARAGUA**: **Matagalpa**: Montaña Selva Negra, 7.5 km N Matagalpa, 1300m, 13°00'1"N, 85°54'32"W, 15–16.vi.2001, B. Ratcliffe, M.L. Jameson, R. Cave, 1M (UNSM); **PANAMA**: **Chiriquí**: Finca Hartmann, 18–20.v.1996, Wappes, Huether & Morris, 1M (ASULOB)

Distribution. From Guatemala to Panama, at elevations above 1250 meters.

Scaralina obfusca Yanega, sp. nov.

(Figs 22, 36, 51, 66, 91, 104)

Etymology. The epithet is a play on words, and may never have been used in Latin; there is a Late Latin verb "obfuscare" ("I make darker") from which the term "obfuscate" is ostensibly derived, referring simultaneously to the relative darkness of this taxon, and also to the complication of species circumscriptions this taxon represented late in the course of this revision, including the difficulty of associating the two sexes confidently. Since there is no evidence that it is a genuine Latin adjective, it is to be treated as a noun in apposition.

Diagnosis. This is another of the taxa that is very similar to *S. marmorata* in structural details, but geographically removed from other populations, and with coloration different enough to suggest it is probably not conspecific. The hindwing bases are more reddish than the orange typical of other taxa in the species group (other than *sullivani*), and the pattern of dorsal thoracic markings distinguishes this from all other taxa. Even in the female specimen at hand, the head, prothorax, and forelegs have more dark integument overall than any of the other *marmorata*-group taxa; while otherwise very similar to *obrienae*, including the structure of the male gonostyli, the evanescent costal crossveins, the expanded lower frons, and similar clypeal markings, it is decidedly outside of the range of variation seen in that taxon. The biogeography is such that the two known specimens of *obfusca* are from similar habitat some 400 miles apart, along the northwestern edge of the Sierra Madre Occidental. This does not appear to overlap the range of any other *marmorata*-group taxa, and only *metcalfi* occurs farther west. The paratype female differs from the holotype male in having the light portions of the body and wings much lighter and thus much more strongly contrasting, but we believe this is an artifact of differential preservation, with the male slightly darkened and discolored after pinning, and the female slightly bleached from being stored in ethanol for 12 years; the patterns of markings on the dorsal head and thorax are otherwise nearly identical (compare Figs 22 & 51), and the wing markings are also similar.

Description. ***Head*** (Figs 36, 51, 104) Frons and clypeus vary from extremely dark to largely pale, with scattered very fine dark or black spots (compare Figs 36 & 104), clypeus lighter along midline and just laterad of midline, upper inflexed portion of frons palest along upper edge. Lateral margin of frons slightly concave, lower lobes slightly expanded. Vertex almost entirely dark except along midline and supra-ocular lobes.

Thorax (Fig. 51). Prothorax with very large dark patches on either side of midline, laterally pale with irregular small dark markings. Mesonotum with highly contrasting black and pale areas, the latter most extensive along the midline, but also the lateral carinae, posterior mesonotal lobe, and areas behind the tegulae. Lateral carinae very weakly sinuate. Dorsal setae long.

FIGURES 95–98. *Scaralina* (*Alphinoides*) *inbio*. (95) habitus (holotype male); (96) head and thorax; (97) face; (98) male genitalia, dorsal view (anal tube removed).

Wings (Figs 22, 66). Forewings with many features similar to *obrienae*, though with basal crossveins more contrasting, and medial crossveins generally darker. Costal crossveins relatively few, obscure or absent in basal half or more of cell. Hindwings with basal markings distinctly more reddish-orange than in *marmorata*, *obrienae*, and other related species.

Abdomen (Fig. 22) Dorsal abdomen mostly black, pale laterally on terga 4–6.

Male terminalia (Fig. 91). Gonostyli very similar to *obrienae*, with a strong curving but mostly transverse ridge on the dorsal incurved surface separating the medial portion from the relatively short apical portion; however, the dorsal setose bulge has the setae somewhat denser, and lower edge of gonostyli nearly straight for much of their length rather than gently convex (compare Figs 88 & 91).

Type material. ***Holotype***, male: **MEXICO: Durango**: "3 mi S El Salto," 2440 m ("8000 ft"), 10.viii.1986, J. Brown (black light trap); (EMEC).

Paratype, female: **Chihuahua**: Hwy 16 nr. La Ladrillera, 28°16'48"N, 108°15'31"W, 2250m, 15.vii.2007 M. Van Dam (UCRC ENT 554759).

Distribution. So far known only from two localities, in western Durango and western Chihuahua, approximately 600 km apart.

Scaralina obrienae Yanega & Van Dam, sp. nov.

(Figs 5, 23, 37, 52, 67, 79, 88)

Etymology. This species is named to honor Lois O'Brien, a prominent researcher on Fulgoroidea, who was helpful throughout the present study, including supplying much of the material of this species.

Diagnosis. Many specimens of this taxon resemble the specimens of *S. orientalis* from northeastern Mexico, but in addition to the apparent allopatric distribution, some structural features, including the male gonostyli, rounded upper frons, and expanded lower frons, along with some coloration features such as the medially pale clypeus, suggest that it is more than just a geographic variant. As in *marmorata*, there is considerable variation in coloration between the various Mesoamerican populations (especially in the development of the orange coloration of the basal and claval regions of the forewing, and also the frons and clypeus), though they tend to be quite consistent at any given locality. For example, specimens from Guerrero have the frons pale with dark spots, while nearly all other populations have at least half the frons completely dark. Guatemalan specimens often have the frons almost entirely dark. One Guatemalan specimen entirely lacks the basal band on the forewing (both the dark and pale portions), but is otherwise identical to specimens collected at the same time and place. Specimens from Tejupilco and Calvillo have much more yellow on the abdomen, and some differences in the male gonostyli, so they are only tentatively associated with this species.

This is one of several taxa that show unmistakable affinities to *S. marmorata* in structural details, and while extremely similar, it is different enough to suggest they are not truly conspecific. In particular, the recognition of this taxon as distinct relies in large part upon the diagnostic utility of the male gonostyli, because if coloration alone were to be used as a guide, many localized color variants might be segregated and named if approached more typologically, or more apparent intergradation that might lead to consolidation if done conservatively. For example, while *obrienae* is fairly consistent in appearance from Guerrero and Chiapas through Guatemala, specimens from intermediate areas such as Jalisco and Aguascalientes show coloration more similar to *orientalis*, but the frons and male anatomy suggest they belong within *obrienae*. Any subdivisions will require much more extensive geographic sampling, or genetic analyses, or both. We suspect that this species will be found to feed on *Quercus laurina* or *Q. affinis*.

Description. ***Head*** (Figs 37, 52). Rim of vertex mostly pale; three very broad pale marks anteriorly, otherwise black; supra-ocular lobes pale apically; posterior rim mostly pale, except darkened adjacent to supra-ocular lobes; dark spots of vertex posterior in position; black markings very well-defined and restricted to lateral bands and posterior spots. Frons with a narrow pale upper margin, black just below this (pale markings at corner of frontal crease near ocellus evanescent), and the ground color near the lower margin variable, most typically a little less dark, except for darker spots surrounding setal bases, but sometimes almost entirely black, and occasionally significantly paler than upper frons. Lateral margin of frons slightly concave, lower lobes slightly expanded. Clypeus typically extensively pale (Fig. 37), though even the darkest specimens are pale-marked along midline and just laterad of midline. Rostrum typical for genus.

Thorax (Fig. 52): Pronotum ground color pale, orange-tinted tan, dark markings generally very highly contrasting; post-ocular pronotal spots well-defined, large; midline of dorsal pronotal face pale, with black submedian bands curving laterally towards posterior, and anterolateral corners also black. Mesonotum center mostly pale, black markings relatively extensive otherwise; medial carina low; lateral carinae pale, almost straight, very slightly sinuate anteriorly or posteriorly; posterior mesonotal lobe rounded. Dorsal setae long. Legs as in generic diagnosis, markings also highly contrasting.

Wings (Figs 5, 23, 67). Forewings with dark markings on basal half of 1st claval vein somewhat interrupted; a narrow, continuous dark transverse patch from costa to clavus, at the level of the first branch of M (which is

abbreviated relative to other species), and semi-translucent orange basal markings in the membrane; postcostal cell black with well-defined, small, pale orange spots throughout; remainder of wing quite clear, with very limited, faint spotting. Costal crossveins relatively few, mostly straight or slightly arcuate but oblique, very obscure or absent in basal half or more of cell; M with 2–3 main branches (generally 2), crossveins between them mostly straight, widely spaced, making exceptionally large, elongate-rectangular cells; at first branch of M, M is closer to CuA than to Sc; CuA with 3–4 branches, rarely more than 1 of these coming directly off of CuA, and the first branch typically precedes the claval vein juncture; greatest distance between Pcu and A_1 veins exceeds greatest distance between A_1 and wing margin; fused vein posterior to juncture very short. Hind wing hyaline except base, which is orange.

Abdomen (Fig. 23) Aside from posterolateral pale markings, the dorsum and venter both nearly solid black throughout most of the range, though occasional Mexican specimens may have some pale markings more medially on the terga. The female supra-anal plate is large and typically somewhat lighter apicomedially, merging with the pale lateral markings.

Male terminalia (Figs 79, 88). Gonostyli black apically, varying medially from largely pale to almost entirely black. Dorsal margin of gonostyle incurved strongly near the setose bulge, and at almost a right angle to the margin, and there is a strong curving but almost transverse ridge on the dorsal incurved surface separating the medial portion from the relatively short apical portion. Dorsal setose bulge very prominently convex and shelf-like, at a right angle to the side of the gonostyle, setae generally dark, short, and varying slightly in density, often appearing sparser than in other taxa. Lateral hook strong, apically curved, basal ridge feebly arcuate, often almost straight, and typically with a few very short setae.

Type material. ***Holotype***, male: **GUATEMALA**: **Baja Verapaz**: "km 156 on road to Coban," 19.ix.1990, P. Hubbell (ASULOB).

Paratypes (38 specimens) as follows: **GUATEMALA**: **Alta Verapaz**: "Reserva conservacion de orquideas, ORQUIGONIA, 1460m," 15°26'17"N, 90°24'44"W, 5.vii.2015, J. Monzón, 1M (UVGC); same data but 27.xi.2017, J. Monzón, Z. Falin, 1M (UVGC); **Baja Verapaz**: "km 156 on road to Coban," 19.ix.1990, P. Hubbell, 1F (ASULOB); same but 15.v.1991, P. Hubbell, 1M (GGCB 0171); same but "Hotel Posada Montaña del Quetzal," Purulhá, 1600m, 16.xi.2004, G. Goemans, 1M (GGCB 0264); same but 1646m, 15°11'45"N, 90°12'27"W, 15.ix.2009, J. Monzón, 1F (UVGC); 6 km E Purulhá, 26–31.v.1989, J.E. Wappes, 1F (ASULOB); **El Progreso**: "Cerro Pinalon, Bosque Pino, 2219m," 15°04'22"N, 89°56'53"W, 16–18.v.2010, J. Monzón, B. Sutton, G. Steck, P. Skelley, 6M (UVGC); **Guatemala**: [illegible] 15.v.1996, J. Schuster, 1M (GGCB 0175); **Huehuetenango**: Aldea Chiaque, 2040m, 15°10'10"N, 91°30'0"W, 16.viii.2018, D.C. Hawks, 1M (UCRC ENT 516400); same, but 18.vii.2012, J. Monzón 1F, 1M (UCRC ENT 516379 & 516380); Aguacatán, 2000m, at light, viii.2000, J. Monzón, 1M (GGCB 0269); **Sacatepequez**: "San Cristobal El Bajo Finca El Pilar, arriba 2175m," 14°32'03"N, 90°41'35"W, 12.vi.2009, J. Monzón, F.R. Camposeco, 1F, 3M (UVGC); **Zacapa**: "5 km SE La Union town, Finca Los Chorros, 1474m," 14°56'33"N, 89°16'33"W, 13.vii.2011, J. Monzón, F.R. Camposeco, 1F, 1M (UVGC); **MEXICO**: **Chiapas**: "9 mi N Teopisca on Pan Am Hwy," at light, 31.v.1987, W.B. Warner, 1M (ASULOB; dissected); "Hwy 199 11 km NE Sn Cristóbal," 8000 ft, at MV and UV, 28.v.1987, D.A. Rider, E.G. & T.J. Riley, 1M (ASULOB); 8 mi SE San Cristóbal, 17.v.1969, J.M. Campbell, 1F (CNC); 10 mi NE San Cristóbal, 5.v.1969, H.J. Teskey, 1F (CNC); 10 mi E San Cristóbal, 10–14.ix.1985, B. Ratcliffe, C. Messenger, 1F (UNSM); Lago de Montebello, 15.vi.1986, Reifschneider, 1M (UNSM); **Guerrero**: near Taxco, "from swifts WNS-1985-3, HO-31B," 27–30.vi.1985, D.F. Whitacre, 1M (ASULOB); 6 km NE Ximilcotitlán, 2065m, 17°22'13"N, 99°23'39"W, 5–7.viii.2018, J. Monzón, D.C. Hawks, 3F, 2M (UCRC ENT 516395–99); **Hidalgo**: "Hwy 105, 9 mi N Metzquititlan," 6700 ft, 16.vi.1983, C.W. & L. O'Brien, G.B. Marshall, 1F with strepsipteran (ASULOB); **Jalisco**: Paso de Guadalupe, 10 mi N Guadalajara, at light, 5.vii.1958, D.R. Giller, 1M (INHS 96444).

Additional material examined (not on map). **MEXICO**: **Aguascalientes**: Calvillo, 5.vii.1984, Carroll, Schaffner, Friedlander, Woolley, at light, 1M (ASULOB; dissected); **México**: Tejupilco, Temescaltepec, vii.1932, H. Hinton (CAS; dissected); same but 17.vi.1933, 1M (UDCC_NRI 9297); **Michoacán**: Morelia, 1917m, 15.viii.2022 (iNaturalist obs. # 131019897); one damaged male specimen labeled "COLUMBIA, Bogota, Dec 1931" (ASULOB), presumably mislabeled.

Distribution. Widely distributed in eastern and central Mexico, south to Guatemala; Guadalajara in Jalisco is as far north and west as any definitively confirmed specimens have been found, though this may be refined with better sampling.

***Scaralina orientalis* Yanega, sp. nov.**
(Figs 24, 38, 53, 68, 80, 89)

Etymology. This species is named for the Sierra Madre Oriental, the mountain range which appears to be the home of this taxon. It is treated as adjectival.

Diagnosis. The features of the pronotum and mesonotum, including the long notal pubescence, are unlike any of the populations of *marmorata* examined; the details of coloration also do not exactly match any *marmorata* color variants known, nor *rileyi*, though specimens of *rileyi* are very close. The coloration of *orientalis* is most similar to the southeastern Texas populations of *marmorata*. These three taxa (*marmorata*, *orientalis*, and *rileyi*) are certainly each others' closest relatives, and could perhaps justifiably have been designated as subspecies. We suspect that this species will be found to feed on *Quercus grisea*, or possibly *Q. affinis* or *Q. laurina*.

Description. ***Head*** (Figs 38, 53). Most features as in *marmorata* but frontal ridges weaker. Clypeus typically mostly dark, with light markings restricted to base of clypeus and widely-spaced lateral pale markings, but lower midline not pale, as also seen in *rileyi* (compare Figs 38 & 39).

Thorax (Fig. 53). Most features as in *marmorata* but in pinned material often appearing darker than typical for *marmorata*, not from pigmentation, but from a loss of the pale pigmentation in the medial portion (as is visible in Fig. 53); the posterior mesonotal lobe is entirely pale apically (no lateral dark pigmented spots); dorsal setae long and generally readily visible.

Wings (Figs 24, 68). Most features as in *marmorata* but pale basal area of forewing lightly orange-tinted rather than olivaceous. Costal crossveins simple and somewhat closely spaced past 1st branch of M. Hind wing hyaline except base, which is slightly orange-infused.

Abdomen (Fig. 24). Most features as in *marmorata* but tergum 2 pale medially, tergum 3 often with faint median pale marks, and terga 4 and beyond pale laterally, with a dark midline and some very faint submedial marks. Female supra-anal plate large, and marked like preceding tergum.

Male terminalia (Figs 80, 89). Most features as in *marmorata* but gonostyli with a less oblique dorsal ridge, smaller basal impressed portion, broader dorsal aperture, and more densely setose bulge.

Type material. ***Holotype***, male: **MEXICO**: **San Luis Potosí**: 4 km E Ciudad Maiz, 1425m, 25.vii.1981, B.C. Ratcliffe, C.L. Messenger (UNSM).

Paratypes (10 specimens) as follows: **MEXICO**: **Nuevo León**: "6 mi S Iturbide on Santa Rosa rd.," 1530m, 12.vii.1994, P. Lago, A.E. Zuccaro, 1M, 1F (ASULOB); 16.5 mi W Linares, Rio Viejo turnoff, 712m, 13.vii.1992, P.K. Lago, 1M (ASULOB); El Carmen, 30.iv.1980, H. Quiroz, 1F (UANL); **San Luis Potosí**: 4 km E Ciudad Maiz, 1425m, 25.vii.1981, B.C. Ratcliffe, C.L. Messenger, 1M (UNSM); 5 km E Ciudad Maiz, 1370m, 27.v.1984, B.C. Ratcliffe, 3M, 1F (UNSM); **Tamaulipas**: "15.5 km E Tula, 3.9 km N Hwy on dirt rd," ~1300m, 14.vii.1994, P.K. Lago, A.E. Zuccaro, 1F (ASULOB).

Additional material (not on map). **Nuevo León**: La Estanzuela Park, Monterrey, 25.548703, -100.270824. 17.iii.2023 (iNaturalist obs. #151875542); **Puebla**: 1 mi N Puebla, 27.vi.1964, C.D. Johnson, 1M (ASULOB).

Distribution. Northeastern Mexico, from Tamaulipas and Nuevo León south to Puebla; to date, no localities overlap the distribution of any other species, including *S. obrienae*.

***Scaralina sullivani* Yanega, sp. nov.**
(Figs 26, 40, 55, 70, 92)

Etymology. This species is named for Patrick Sullivan, one of the collectors of the holotype, who generously donated the specimen to UCR, and was an excellent and gracious host during field work in Arizona.

Description. The relative lack of dark markings on the face, legs, and pleura, make this species fairly readily distinguished from other similar taxa, as do the more reddish-orange hindwings (more persimmon than orange, similar only to *obfusca*). Both known specimens lack strong maculation in the forewing at the claval junction, but without more specimens it is unclear whether this is diagnostic. The head and thorax have coloration that is fairly similar to *S. veracruzensis*, but the lower frons is laterally expanded, and the male gonostyli are more similar to *marmorata* than to *obrienae*, with a weak setose bulge and poorly-developed dorsal ridge. The paratype female differs slightly from the holotype male in having the markings of the anterior pronotum divided rather than continuous.

Description. ***Head*** (Figs 40, 55). Frons and clypeus pale orange and, other than scattered fine dark spots on the frons, almost entirely without dark markings. Lateral margin of frons slightly concave, lower lobes slightly expanded. Vertex very similar to *veracruzensis*, with well-defined dark lateral markings.

Thorax (Fig. 55). Anterior pronotum very dark, more or less connected to more posterior dark markings on either side of the midline. Mesonotum mostly pale, with fairly well-defined black areas lateral to the carinae, posteriorly (including the posterior granular spots), and near the anterior arms of the lateral carinae, which are very weakly sinuate. Dorsal setae long. Legs with greatly reduced dark markings.

Wings (Figs 26, 70). Forewings fairly similar to *obrienae* or *obfusca*, but with the orange hues slightly more intense, and the dark markings of the basal and claval regions more brownish than black, somewhat larger orange markings in the postcostal cell, and no obvious dark maculation near the claval junction. Costal crossveins simple and typically well-spaced past 1st branch of M, not as evanescent as in *obrienae*.

Abdomen (Fig. 26). Dorsal abdomen mostly black, with fairly broad pale lateral markings on terga 4–6.

Male terminalia (Fig. 92). Gonostyli dark only in apical third, with a weakly projecting setose bulge and poorly-developed dorsal ridge.

Type material. ***Holotype*****,** male: **MEXICO**: **Veracruz**: "Escola; 1372 m," 1.viii.1975, T.W. Taylor & P.H. Sullivan (assumed to be Excola, 1972 m; UCRC ENT 536497, at UCRC).

Paratype, female: **Veracruz**: "6 air km SW of Banderilla, 1710m," 17.viii.1987, Brown & Powell (black light); (EMEC).

Distribution. So far known only from two localities in central Veracruz, within 60 km of one another.

Scaralina veracruzensis Yanega & Van Dam, sp. nov.

(Figs 41, 56, 71)

Etymology. This species is named for the Mexican state from which the only known specimen was collected.

Diagnosis. While this taxon somewhat resembles *S. sullivani*, which is also from Veracruz, it differs in many features. The pattern of coloration is different in many respects (e.g., *sullivani* has a paler face, many light abdominal markings, and lacks a strong black cell at the claval junction); the costal crossveins are completely evanescent basally, much as in *obfusca* and *obrienae*; the frons in *veracruzensis* has rather little expansion of the lower lateral lobes, so the lateral margins of the frons are nearly straight, rather than concave; the latero-basal carina of the clypeus is evanescent distally, but complete in *sullivani*. The strongly contrasting pattern on the mesonotum, and greatly reduced basal forewing markings, coupled with the disproportionately enlarged wing cells also apparently make this taxon distinctive; however, we do acknowledge that these are all features which can vary somewhat within a species (see note regarding *obrienae*), so it is possible that future collections of additional material will result in some change in the species diagnosis. The loss of the abdomen and accompanying dissection early during the study was very unfortunate, as we never had an opportunity to directly compare the male genital characters to other taxa such as *sullivani* or *obfusca*, but were instead limited to early notes that had been taken.

Description (male only; female unknown). ***Head*** (Figs 41, 56). Rim of vertex mostly pale; three very broad pale marks anteriorly, otherwise black; supra-ocular lobes pale apically; posterior rim mostly pale, except darkened adjacent to supra-ocular lobes; dark spots of vertex posterior in position; black markings very well-defined and restricted to lateral bands and posterior spots. Frons with a narrow pale upper margin, very dark just below this (pale markings at corner of frontal crease near ocellus evanescent), and the ground color below a little less dark, except for scattered fine black spots surrounding setal bases. Lateral margin of frons nearly straight, lower lobes not expanded. Clypeus extensively pale, with some dark markings, latero-basal carina evanescent distally. Rostrum typical for genus.

Thorax (Fig. 56). Pronotum ground color pale, orange-tinted tan, dark markings generally very highly contrasting; post-ocular pronotal spots well-defined, large; midline of dorsal pronotal face pale, with black submedian bands curving laterally towards posterior, and anterolateral corners also black. Mesonotum center mostly pale, black markings relatively extensive otherwise; medial carina low; lateral carinae pale, almost straight, very slightly sinuate anteriorly or posteriorly; posterior mesonotal lobe rounded. Dorsal setae long. Legs as in generic diagnosis, markings also highly contrasting.

Wings (Fig. 71). Forewings with dark markings on basal half of 1st claval vein somewhat interrupted; a narrow,

continuous dark transverse patch from costa to clavus, at the level of the first branch of M (which is abbreviated relative to other species), and semi-translucent orange basal markings; postcostal cell black with well-defined, small, pale orange spots throughout; remainder of wing quite clear, with very limited, faint spotting. Costal crossveins relatively few, mostly straight or slightly arcuate but oblique, very obscure or absent basally; M with 2–3 main branches, crossveins between them mostly straight, widely spaced, making exceptionally large, elongate-rectangular cells; CuA with 3–4 branches, rarely more than 1 of these coming directly off of CuA, and the first branch typically precedes the claval vein juncture; greatest distance between Pcu and A_1 veins exceeds greatest distance between A_1 and wing margin; fused vein posterior to juncture very short. Hind wing hyaline except base, which is orange.

Note. Genitalia and abdomen lost after dissection so only preliminary notes were taken] ***Abdomen*.** Dorsum and venter nearly solid black.

Male terminalia. Gonostyli black apically. Setose bulge has two rows of spinose setae extending posteriorly (?).

Type material. ***Holotype*,** male: **MEXICO: Veracruz**: "Serra Pescados nr. Perote" [no date] (ASULOB).

Distribution. So far known only from the type locality in central Veracruz, near the border with Puebla.

Scaralis (*Scaralis*) Stål, 1863

Type species. *Lystra picta* Germar, 1830, by subsequent designation of Distant, 1906.

Scaralis (*Alphinoides*) Yanega, subgen. nov.

Type species. *Poiocera quadricolor* Walker, 1858, by present designation.

Etymology. The name is coined as a reference to the general resemblance to members of *Alphina* in wing shape, head shape, and abdominal coloration. For purposes of gender agreement, the name, if subsequently elevated to generic rank, should be considered feminine (ICZN Art. 30.1.4.4).

Diagnosis. Examination of the holotypes of three species (*Scaralis nigronotata* Stål, 1863, *Poiocera quadricolor* Walker, 1858, and *Poiocera semilimpida* Walker, 1851), and "paratypes" of another (*Scaralis fluvialis* Lallemand, 1956; labeled by Lallemand as paratypes, but the original publication did not include them), reveals them to be very close to one another, and quite unlike species such as *neotropicalis*, *obscura*, *picta* (the type species of *Scaralis*), and *versicolor* Distant, 1906, and the former four species are here transferred to a new subgenus *Alphinoides*, in the hopes that future work will better reveal their relationships. We suspect that *Alphinoides* may prove to be a monophyletic lineage distinct from *Scaralis*, but this analysis is beyond the scope of the present work (as only one species extends into Mesoamerica, the proper circumscription of these taxa is not considered essential here). It may prove to be more closely related to *Scaralina* than *Scaralis s.s*. Fairly distinctive features of *Alphinoides* are the hindwings with an anal region that is broadly black in coloration (in all but one species examined; *semilimpida*); the vertex only 3–4 times as wide as long (5 or more times in *Scaralis s.s.*); the abdomen is dorsally entirely black, with a pale margin to the apical segment (in all but two species examined); the versteifung is low but somewhat more abbreviated and more nearly angulate than in *Scaralis s.s*. (Fig. 4); the pigmented portion of the forewings typically extends to the nodal arc, but not beyond as in *Scaralis s.s.* At least a few species (including some undescribed taxa known only from photos) have banded legs, typical of *Alphina* and *Scaralina*, but not shared with *Scaralis s.s*. The male gonostyli of the species for which males could be examined are broadly open dorsally but somewhat incurved apically, and the gonostylar hooks are small but sharply acute, both feature somewhat intermediate between *Scaralis s.s* and *Scaralina*. The anal tube is shorter, more tapering at the base, and apically shallowly emarginate, more similar to *Scaralina* than to *Scaralis s.s*. (compare Figs 10 & 11). The second antennomere is also intermediate, being slightly ovoid and asymmetric (Figs 7, 97), though not nearly so large as in *Scaralis s.s*. (Fig. 103). Several structural features show greater similarity to *Scaralina*, though the asymmetric antennae, weak pubescence, highly contrasting venation, and dorsally open aedeagal apparatus are similar to *Scaralis s.s*.

Composition. 6 species: *Scaralis fluvialis* Lallemand, 1956; *S. inbio* Yanega **sp. nov.**; *S. nigronotata* Stål, 1863; *S. quadricolor* (Walker, 1858); *S. semilimpida* (Walker, 1851); *S. spectabilis* (Walker, 1858).

Notes on included species. There has been some confusion between *Scaralis nigronotata* and *S. spectabilis* (Walker, 1858); many specimens in museum collections and identified online as *spectabilis* are indistinguishable

from the type of *nigronotata*, whose type we have examined, but Porion published a photograph of the type of *spectabilis* and it is not the same taxon as *nigronotata*. Regardless, it is closely related, and we here also place *spectabilis* in *Alphinoides*. The two "paratypes" of *S. fluvialis* may not be conspecific with each other or with the holotype, but they were seen by Lallemand and belong in this group of species, and Lallemand specifically indicated a relationship to *spectabilis*. Also, Porion's photograph of *nigronotata* from Guyana (miscaptioned as #52 in the plate, but corresponding to #55 in the text) is definitely not *nigronotata*, and likely to be an undescribed species. Finally, *Scaralis semilimpida* shows, in its head and wing shape, clear affinities to taxa such as *nigronotata*, though the red abdomen and hindwing bases are not consistent with any of the other described taxa in the subgenus. To this lineage, we add a species described here as new, *Scaralis inbio*, whose affinities lie clearly with *fluvialis*, *quadricolor*, and *spectabilis*, though it possesses a few of its own unique features.

Description. ***Head***. Vertex roughly 3 to 4 times as wide as long, defined by lamellate rim, produced into rounded supra-ocular lobes, which may be slightly elevated above dorsoposterior eye margin; posterior rim reflexed anteriorly. Rims may be pigmented, but otherwise vertex typically marked in the posterolateral corners, if marked at all. Sub-ocular lobes typically weak and rounded. Frons bulging and somewhat convex for most of its surface, smooth to slightly wrinkled and with or without dark markings; often with well-defined ridges, such as a medial ridge and/or converging lateral ridges, which may include ridges arising from the clypeal base (thus with 5 evident ridges all converging on a single point); laterally expanded below and sublobate at corners; reflexed along upper portion to form an appressed flap, the transition rounded rather than an obtuse angle (relative to the plane of the lower frons), delimited above by strong transverse crease, dorsal reflexed portion smooth. Clypeus triangular, only slightly longer than broad, fairly smoothly convex but often very shallowly concave near midline, with sides nearly straight to slightly concave; upper margin typically gently arcuate. Main segment of rostrum typically extending to metacoxae; in most species, mostly pale except apical segment, and anterior (ventral) ridges also somewhat darkened. Antennal base concealed in protruding socket; basal antennal segment often darkened dorsally, otherwise pale; second segment small (diameter slightly larger than antennal socket diameter), typically slightly ovoid (Figs 7, 97), with pale circular to ovoid sensillae; stylus apical, elongate, dark, with a small basal bulbosity, arising from slight indentation. Ocellus present in angle between frons and lower eye margin, translucent yellowish.

***Thorax*.** Dorsal and lateral surfaces with pubescence extremely short and fine, typically hardly evident. Pleura sometimes with fine pollinose wax layer. Pronotum with a well-developed medial carina; there is also a sub-lamellate lateral anterior rim that starts near the inner eye margin, and continues to near the middle of the tegula, below the eye; there is another oblique carina just ventral to this, continuing onto the ventral posterior lobe of the pronotum, which approximates the forecoxal bases and partly overlaps the anterior face of the mesepisternum; there is also commonly a low transverse ridge immediately preceding the dorsoposterior margin of the prontoum; typically with paired, dark granular spots, usually a somewhat pitlike anteromedial pair, a larger postero-medial pair, and a small lateral post-ocular pair (at the indentation immediately behind the outer posterior edge of the eye). Mesonotum with low longitudinal medial and lateral carinae, the latter sinuate to varying degrees, ending posteriorly at the outer edges of a pair of small and typically dark posterior granular spots (the inner edges of which may sometimes be bordered by a weak inner posterior carina that starts at the terminus of the lateral longitudinal carina), and the inner edges of much larger granular spots (dark at least in part) which are variously interrupted anteriorly; the lateral carinae at the extreme anterior edge are strongly angled inward and converge at the midline, but these anterior "arms" may be hidden underneath the posterior pronotal margin; the medial carina becomes obscure posteriorly, ending in an upward-angled semi-acute lobe that is typically creased or wrinkled transversely at its base. Mesopleuron delimited from mesosternum by a strongly and fairly evenly arcuate ridge running from the upper posterior corner of the procoxal membrane to the upper anterior corner of the mesocoxa. Mesocoxa with dorsoposterior spine absent or scarcely evident. Femora weakly convex on anterior face, more strongly so on posterior face, with only two well-defined longitudinal setose ridges, along the anterior dorsal and ventral edges, and sometimes faint traces of a posterior setose ridge. Legs generally uniform in color, sometimes with fore- and mid-tibiae strongly banded.

Wings. Forewings with nodal line absent or scarcely evident; versteifung low, somewhat trapezoidal, fairly short, and proximally not angulate (Fig. 4); pigmented portion (not counting the postcostal cell) typically extending over roughly half the length, sometimes reaching the weak nodal line; apical portion clear or stained hyaline, without maculations or patterning. Vein MP typically with 2–3 branches, CuA typically with 2, MP roughly equidistant between CuA and ScP+R. Venation of hyaline wing portions relatively coarse, though crossveins denser and much more irregular in pigmented portion, basal venation typically brightly colored, in contrast to nearly opaque black or dark brown pigmented membrane. Hindwings with membrane of anal region typically partially or entirely black,

sometimes extending to cover nearly half the wing; often with small pale blue markings near base, rarely red or orange.

***Abdomen*.** Most species with tergites and pleurites predominantly dark, and sternites predominantly pale (whitish to reddish); dorsal pale markings generally restricted to tergum 6, which may be white apically; a few species with orange-red coloration over 2 or more terga. Spiracles large, one dorsal at base of abdomen, others in the dorsal pleurites. Terga with sublateral pits concolorous with surrounding cuticle. Female tergum 6 produced into a supra-anal plate, but generally not entirely concealing anal tube; roughly twice the length of any of the preceding terga. Wax production evidently somewhat limited, typically a faint residue at the base of the genitalia, and traces in the spiracular apertures, rarely on abdomen or pleura.

Male terminalia. For the two species that have been possible to assess: The gonostylar hooks are small and short, but evenly tapered and acute, unlike *Scaralis s.s*. (Fig. 93); dorsal margin of gonostyli swollen at setose bulge but otherwise poorly developed, margin very thin, and incurved, apically, only enclosing the extreme tip of the aedeagal apparatus (if the anal tube is removed, the aedeagal apparatus is almost fully exposed) (Fig. 98). Anal tube short with broad, shallowly semicircular apical concavity (Fig. 11).

Scaralis (*Alphinoides*) *fluvialis* Lallemand, 1956, stat. nov.

Specimens examined. **PERU**: 2 specimens in the Gembloux collection (FSAG), labeled as paratypes; also **Madre de Dios:** nr Puerto Maldonado, Posadas Amazonas, 12°48.115’S, 69°18.019’W, 609 ft., 30.ix–3.x.2004, C.R. Bartlett, 1M (UDCC).

Notes. The two specimens we have examined that Lallemand deposited as “paratypes” were not mentioned at all in the original description (Lallemand, 1956), and therefore cannot be genuine paratypes. They are very similar to one another, though not identical. The forewing cells are larger in one, and the margin of the basal forewing markings is well-defined and strongly arcuate in this same specimen, and irregular and less arcuate in the other, though we assume that at least one of them is truly *fluvialis*, and both are *Alphinoides*. The other specimen from Peru that we have seen corresponds to the latter of these two “paratypes”, and some details do not match the description of *fluvialis*. Despite this confusion, this species, and *Scaralis (A.) inbio*, are closely related to each other, *S. quadricolor*, and *S. spectabilis*, and there may certainly be additional undescribed species. As in most other species, the vertex has at most very small dark markings in the posterolateral corners adjacent to the supraocular lobes, and the crossveins of the basal forewing are numerous and highly contrasting.

Scaralis (*Alphinoides*) *inbio* Yanega, sp. nov.

(Figs 11, 72, 93, 95–98)

Etymology. This species is named for the Costa Rican Instituto Nacional de Biodiversidad (INBio), responsible for the major cataloguing and collection effort to document that nation’s biodiversity. The epithet is here treated as a noun in apposition.

Diagnosis. Despite considerable variability in the darkness and connectedness of the mesonotal markings, and variation in the forewing membrane from almost clear (especially common in specimens from Guanacaste) to brownish translucent, the available material is all clearly a single species. The thin, continuous black line along the rims of the vertex is unique among all Mesoamerican poiocerine species examined, though some *Alphinoides* species from South America (e.g., *fluvialis*) share this feature, and the anterior rim is more dorsally produced than any other species we have seen. The smoky infuscation of the anal area of the hindwing is slightly less pronounced in this species than any other *Alphinoides* examined (other than *semilimpida*), which typically have much more extensively pigmented anal and basal regions, and the pale blue markings are slightly more extensive than in *fluvialis*, *quadricolor*, or *spectabilis*. It has bands on the fore- and midtibiae, similar to *Scaralina*, though not on the femora, and has noticeable setae on the thoracic dorsum, though still much shorter than in any Mesoamerican *Scaralina*. It shares with its relatives a feebly carinate frons, and slightly ovoid second antennal segment. The male gonostyli are somewhat incurved at the extreme apex, but otherwise outcurved and open dorsally, with the setose bulge along the swollen lateral margin, and the gonostylar hooks are very small but acutely pointed (these features therefore not quite matching the condition in either *Scaralis s.s.* or *Scaralina*). The anal tube is more broadly open

at the apex than in *Scaralis s.s.*, therefore similar to *Scaralina*. The pigmented portion of the forewing is distinctly smaller than in other *Alphinoides*, and more similar to *Scaralina*. The head is similar to other *Alphinoides* species, however, with the eyes relatively larger and vertex relatively narrower (longer relative to its width, and also relative to the pronotum). The forewing shape is intermediate between *Scaralina* and other *Alphinoides*; if one draws a line from the point where the claval vein reaches the wing margin to the point where the subcostal reaches the wing margin, in most *Alphinoides* the angle between this line and the claval vein is only barely more than a right angle (less than 100 degrees), where in *Scaralina* this angle is closer to 110 degrees. In this species, the angle is close to 100 degrees, and therefore not quite matching any genus (the angle is even wider in *Scaralis s.s.*). This species therefore highlights the difficulty in finding clear synapomorphies for the different related lineages, a problem we feel will be considerably more complicated when the South American fauna is more exhaustively assessed.

Description. ***Head*** (Figs 96–97). Most features conforming to subgeneric diagnosis. Supraocular lobe of vertex not appressed, slightly upturned at apex. Anterior and lateral rims of vertex dark, anterior rim greatly elevated relative to dorsal surface of vertex, which is unmarked. Frons evenly convex, pale and unmarked, with lateral margins concave and lower corners expanded and lobate. Clypeus concolorous with frons basally, but dark apically.

Thorax (Figs 95–96). Most features conforming to subgeneric diagnosis. Dark markings on dorsal thorax variable in development, prothorax generally mostly dark except margins and midline; mesothorax varying from mostly pale with numerous separated dark marks to mostly dark with only the raised carinae pale (compare Figs 95 & 96). Legs with strong contrasting bands on the fore- and midtibiae, femora basally dark, becoming lighter apically, though not well-defined bands. Faint traces of wax pollinosity on pleura.

Wings (Figs 72, 95). Basal pigmented area of forewings well-developed, with very strongly arcuate outer edge, markedly prolonged along the subcosta. Costal crossveins numerous, closely-spaced, highly contrasting, mostly straight or slightly arcuate but oblique, well-defined basally. Apical membrane varying from almost clear hyaline to uniformly brownish stained, cells unpigmented and mostly short-rectangular. Hindwings mostly hyaline, with basal markings blue and black, anal area smoky translucent. Versteifung black, very low and short, and trapezoidal in posterior view.

Abdomen (Fig. 95). Tergites mostly black, with broad reddish margins posteriorly on terga 4–6, and some small pollinose wax deposits laterobasally on terga 3–4. Female with supra-anal plate mostly concealing anal tube.

Male terminalia (Figs 11, 93, 98). Gonostyli black, barely reaching apex of anal tube, outcurved near setose bulge, so the inner gonostylar face is explanate and visible in dorsal view, if the anal tube is removed. Basal gonostylar hooks small, short, acute. Dorsal margin swollen at setose bulge but very thin, and incurved, apically, only enclosing the extreme tip of the aedeagal apparatus. Anal tube pale but epiproct black and slightly crenulate at margins.

Type material. ***Holotype***, male: **COSTA RICA**: **Guanacaste**: Estación Pitilla, 700m, 9 km S. Santa Cecilia, P.N. Guanacaste, 6–19.ix.1993, P. Rios, LN 330200_380200 #2345 (CRI001614251 at MNCR-A).

Paratypes (46 specimens; all 44 Costa Rican specimens are from MNCR-A) as follows: **COSTA RICA**: **Guanacaste**: same data as holotype but 19–23.vi.1993, C. Moraga, #2897, 1F (CRI001869876); same but vi.1994, #3002, 1M (CRI002048273), 2F (CRI002048274–75); same but 6–19.ix.1993, P. Rios, #2345, 1M (CRI001614251); same but vi.1994, #2996, 1M (CRI001883435), 2F (CRI001883436–37); same but vii.1994, #3140, 1M (CRI002049191); same but xi.1992, (no #), 1M (CRI000959431); same but ix.1989, C. Moraga & P. Rios, 1M (CRI000078094); same but xi.1989, 1F (CRI000112433); same but xii.1989, 1F (CRI000166379); same but xi.1988, "GNP Biodiversity Survey", 1M (CRI000109980); same but v.1990, "II curso Parataxon.", 1M (CRI000254114); same but LN 329950, 380450, xii.1994 P. Rios, #4372, 1M (CRI002137090); same but ii.1995, #4356, 1M (CRI002134969); same but ix.1996, C. Moraga, #8398, 1M (CRI002473361); **Herédia**: "Estación Magsasay", 200m, P.N. Braulio Carrillo, LN 264600, 531000, v.1991, A. Fernández, 1M (CRI001204106); same but M.A. Zumbado, 1F (CRI001311274); **Puntarenas**: Estación Quebrada Bonita, 50m, Res. Biol. Carara, LN 194500, 469850, iv.1993, J.C. Saborio, #1997, 1M (CRI001805694); same but xi.1993, #2470, 1F (CRI001969828); same but iii.1994, #2690, 1M (CRI001681049); same but x.1994, #3288, 2M (CRI002045455–56), 1F (CRI002045457); same but v.1992, no #, 1M (CRI000804585); same but viii.1989, R. Zuniga, 1M (CRI000037027); same but x.1989, 1M (CRI000017404); same but iii.1991, 1M (CRI000066547); same but vi.1991, 1F (CRI000349140), 2M (CRI000349166, CRI000349167); same but 1–29.vii.1992, R. Guzmán, 1M (CRI000878221); same but 4–26.i.1993, 1M (CRI001329574); same but 17.iii–30.iv, P. Campos, 1F (CRI000507258); Finca Cafrosa, Estación Las Mellizas, 1300m, P.N. Amistad, LS 316100, 596100, v.1990, M. Ramirez & G. Mora, 2M (CRI000653183–84);

Finca Cafrosa, 1300m, Avenida El Pizote, 1.4 km NE la Tigra, LS 318500, 597100, 28–29.xi.1997, A. Picado, #48774, 1F (CRI002524839); same but 25.ii.1998, #49666, 1F (CRI002411863); Estación Sirena, 0–100m, P.N. Corcovado, LS 270500, 508300, vii.1992, J.C. Saborio, 1M (CRI000777873); Estación Biol. Las Alturas, 1500m, Coto Brus, LS 322500, 591300, viii.1991, M. Ramirez, 1F (CRI000631825); Rancho Quemado, 200m, Peninsula de Osa, LS 292500, 511000, 8–28.xi.1993, A. Marin, #2469, 1M (CRI001622777); Bosque Esquinas, 200m, Peninsula de Osa, LN 302450, 545100, v.1994, M. Segura, #2937, 1F (CRI001964951); **GUATEMALA**: **Izabal**: "Finca Firmeza, 1000m" 15°22'44"N, 88°41'41"W, 27–30.viii.2007, J. Monzón, F.R. Camposeco, 1F (UVGC); "Finca Firmeza del Banco, Sierra de Caral, 350m" 15°24'57"N, 88°42'53"W, 18.iv.2009, J. Monzón, F.R. Camposeco, 1M (UVGC).

Distribution. From Guatemala to the northern half of Costa Rica.

Scaralis (*Alphinoides*) *nigronotata* Stål, 1863, stat. nov.

Type material. ***Holotype***, (NMW): **FRENCH GUIANA**: Cayenne.

Notes. The holotype of this species shows a greater extent to the black pigmented basal hindwings, somewhat fewer crossveins in the basal forewings, and more extensive dark markings on the vertex, than in any of the other species listed here.

Scaralis (*Alphinoides*) *quadricolor* (Walker, 1858), stat. nov.

Type material. ***Holotype***, male (BMNH): **BRAZIL**: Amazonas.

Notes. The holotype of this species is rather similar in many respects to *fluvialis*, though it does not have dark rims on the vertex.

Scaralis (*Alphinoides*) *semilimpida* (Walker, 1851), stat. nov.

(Figs 4, 7)

Type material. ***Holotype***, (BMNH): **BRAZIL**: Amazonas.

Additional material. **BRAZIL**: Amazonas; additional specimen figured by Porion (1994), Plate 4, Fig. 58; **FRENCH GUIANA**: no data, 1F (UCRC).

Notes. This species has the abdomen, and the base of the hindwings, red, unlike the other *Alphinoides* species, or any other species of *Scaralis* we have examined. There is also a slightly paler band in the middle of the pigmented region of the forewing, rather than having the entire basal area dark with contrasting veins, as in the other *Alphinoides* examined. In the molecular analysis by Urban & Cryan, 2009, *semilimpida* was placed as sister taxon to *Matacosa miscella*, and more distantly related to *Scaralina* (as "*Alphina glauca*"). The specimen from French Guiana (Fig. 7) has the dark thoracic markings much reduced compared to the holotype, but we assume this indicates intraspecific variation rather than a different taxon.

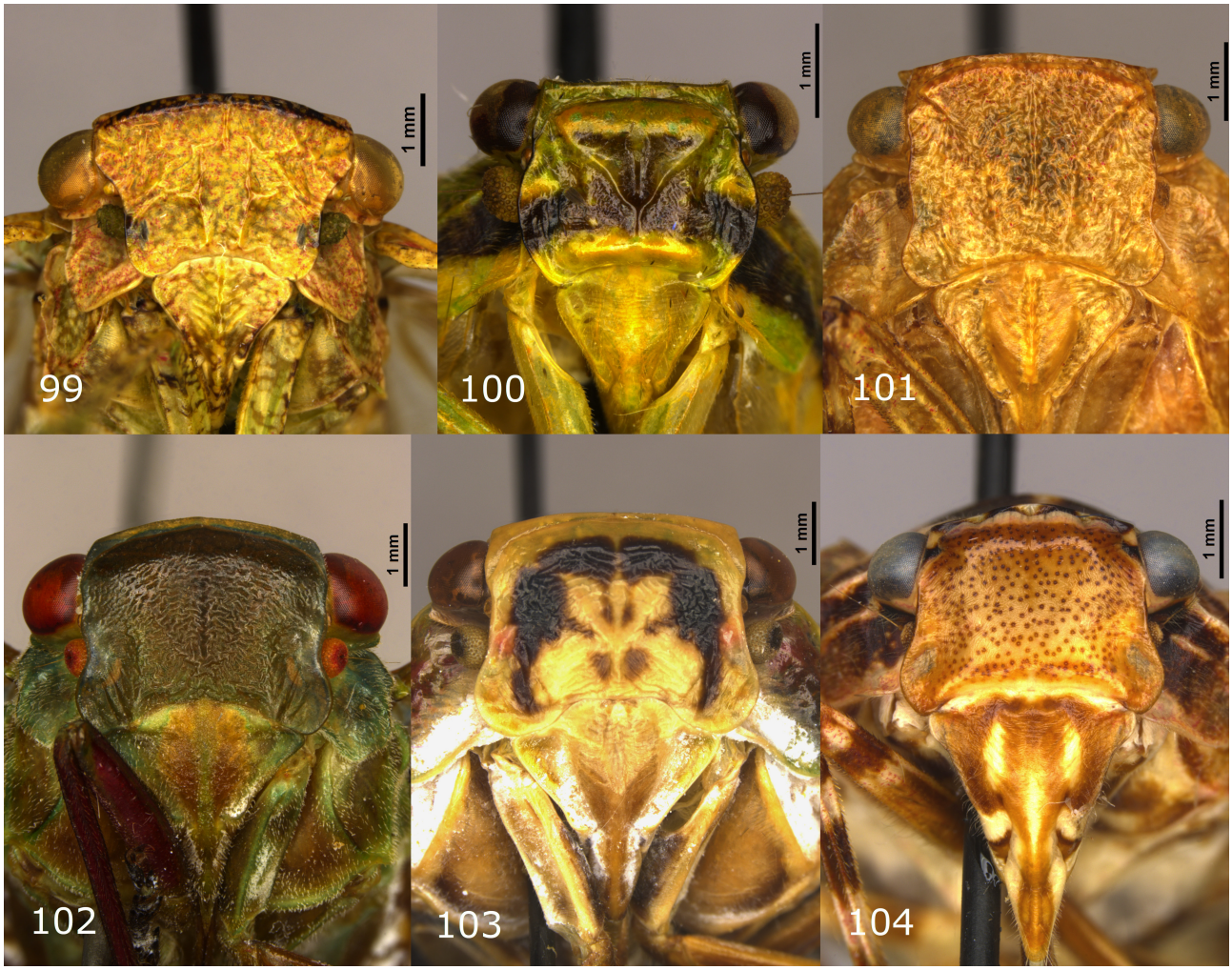
Scaralis (*Alphinoides*) *spectabilis* (Walker, 1858), stat. nov.

Type material. ***Holotype***, female (BMNH): **BRAZIL**: Pará; figured by Porion (1994), Plate 4, Fig. 60.

Notes. While this was the only *Alphinoides* species previously reported to occur in Mesoamerica (Panama; Distant, 1887), it seems certain that this record refers instead to *Scaralis (A.) inbio*, as the type locality of *spectabilis* is Pará, Brazil. The markings on the thorax of *fluvialis*, *spectabilis*, and *inbio* are very similar, though some features of the wings and abdomens are quite different. Metcalf (1938) placed *spectabilis* into *Poblicia*, not having examined the type, and not realizing it was a "calyptoproctine".

SUPPLEMENTAL KEY TO THE GENERA OF "CALYPTOPROCTINA" OCCURRING NORTH OF PANAMA

Poiocerini genera where females may have supra-anal plates; here including *Hypaepa*, (number in parentheses indicates the number of species in Mesoamerica only).



FIGURES 99–104. Faces of different genera of Poiocerini. (99) *Calyptoproctus* sp.; (100) *Hypaepa* nr. *zapotensis*; (101) *Jamaicastes basistella*; (102) *Matacosa miscella*; (103) *Scaralis* sp.; (104) *Scaralina obfusca* (female).

1. Frons much shorter than broad and distinctly broadest above (Fig. 99) **2**
-. Frons broadest below, or medially, or parallel-sided **3**
2. Fore femora strongly flattened, apically foliose, with lamellate forecoxae; forewings narrowed, costal margin nearly straight; vertex flat . . . . . ***Cyrpoptus* Stål** (Panama to U.S.; 11 spp.)
-. Fore femora not flattened, forecoxae not lamellate; forewings normal, costal margin evenly convex; vertex with median pit . . . . . ***Calyptoproctus* Spinola** (Brazil to Mexico; 3 spp.)
3. Vertex almost flat, bordered anteriorly by a low carina, with posterior corners slightly enlarged and angled upwards above eyes (Fig. 101); frons unmarked and coarsely vermiculate-rugose; upper posterior edge of mesocoxa with large, prominent tubercle, almost as large as that on metacoxa; fore- and hindwings with apical half pigmented; forefemoral apices with well-defined setose ridges (2 complete dorsal ridges, 2 complete ventral ridges, the latter defining a shallow groove against which the tibia rests) . . . . . ***Jamaicastes* Kirkaldy** (Antilles, possibly Ecuador & Bolivia; 2 spp.)
-. Vertex concave, bordered by carina that is distinctly elevated anteriorly, with posterior corners appressed to inner posterior margin of eyes; frons variable; upper posterior edge of mesocoxa with at most a small, acute tubercle; forewing with apical half mostly or entirely clear or stained hyaline other than occasional irregular maculations, hindwing apically clear hyaline; femoral apices with at most two or three well-defined ridges (typically 1 anterodorsal, 1 anteroventral, no definite ventral groove) . . **4**
4. Eyes protruding laterally and dorsally; frons widest medially or just below middle; terminal antennomere nearly half as large as eyes (Fig. 100) . . . . . ***Hypaepa* Stål** (Brazil to Guatemala; 4 spp.)
-. Eyes fairly closely appressed to anterior prothorax; frons nearly parallel-sided, widest below at clypeal juncture; terminal

antennomere much smaller than eyes **5**

5. Terminal antennomere small, almost spherical or pyriform, diameter subequal to antennal socket; thoracic dorsum typically with numerous fine erect setae; femora with contrasting bands; hindwings with basal membrane often orange to red (if blue, then with very little black); clypeus typically at least 1.5 times as long as broad and almost straight on sides (Fig. 104); male gonostyli distinctly incurved apico-dorsally for nearly half their length . . . . . ***Scaralina* gen. nov.** (Panama to U.S.; 15 spp.)

-. Terminal antennomere weakly to strongly asymmetrically ovoid, diameter clearly exceeding antennal socket; dorsum with or without obvious short setae; femora without contrasting bands; hindwings with basal membrane with considerable black, and usually also blue; clypeus distinctly less than 1.5 times as long as broad, and somewhat constricted laterally; male gonostyli open dorsally and converging at apex **6**

6. Head and thorax uniformly greenish in coloration; dorsum and pleura with numerous short setae (Fig. 102); forewings with apical cellules very small and crowded, also greatly elongated and narrow, often well over 5x longer than broad . . . . . ***Matacosa* Distant** (Colombia to Costa Rica; 1 sp.)

-. Head and thorax heavily patterned with contrasting markings (Figs 95–96, 103); dorsum bare or with few, short, scattered setae; forewings with apical cellules square to rectangular, 4x longer than broad or less **7**

7. Forewing broad with apices rather oblique; nodal line strongly arcuate and impressed; vertex much broader than wide, especially relative to eyes; male gonostylar hooks somewhat distorted, blunt at tip (Fig. 9) and anal tube widest near middle with narrow aperture (Fig. 10); large species (forewings >18 mm) . . . . . ***Scaralis* (*Scaralis*) Stål** (Brazil to Mexico; 2 spp.)

-. Forewing narrow with apices more rounded (Figs 72, 95); little or no impressed nodal line; vertex narrower than preceding, especially relative to eyes (Figs 95–96); male gonostylar hooks sharply acute at tip (Fig. 93) and anal tube widest near apex with broad aperture (Fig. 11); small species (forewings <16 mm) . . . . . ***Scaralis* (*Alphinoides*) subgen. nov.** (Brazil to Guatemala; 1 sp.)

Discussion

The confusion of four or five different taxa with one another was a long-lasting problem that should be resolved by the present work. The new genus, *Scaralina*, erected for these and related species, still poses some significant questions: (1) What, exactly, are the host plants of these species, and what are their life histories in the natural systems they inhabit? For insects that are so large and relatively abundant, the lack of biological data is rather surprising. To date, we have only been able to keep adults of two species (*S. aethrinsula* and *cristata*) alive, and ovipositing, on oaks (*Quercus*; Gómez-Marco *et al*., 2023), and we have seen only a single museum specimen with a host record (simply "oak"). Live immatures have never been reported in nature, even after pyrethrin fogging of oaks in Arizona, though we have been able to obtain some 1st instars from field-harvested egg masses in the same area and keep them alive on oak saplings (Gómez-Marco *et al*., 2023). If *Quercus* species are confirmed as host plants for other *Scaralina* species, is it possible that the various species are specialist feeders on different host oaks? (2) What are the actual distributions of the taxa involved, and how many more species, cryptic or otherwise, are included in this group? Given the overall fragmentation of the "Sky Island" ecoregion into so many isolated high-altitude populations, and parallel patterns of speciation and diversity in other insects in the same habitats, such as the scarab genus *Chrysina* Kirby, 1828 (Robacker *et al*., 2022), it is likely that the species diversity of *Scaralina* in Mesomaerica is greater than currently recognized. The Mesoamerican material available to us for the present study was very limited, and several species are known only from one or two specimens or localities. More significant, perhaps, is the question of whether the variation in the southeastern U.S. populations of *S. marmorata* indicates that some of the variants may inhabit isolated habitat patches, or different hosts, and represent functional species-level taxa. Much of this should be possible to resolve with genetic analyses based on broad and exhaustive geographic sampling.

We assume that it is not a coincidence that the two species groups (*cristata* and *marmorata*) have almost no geographical overlap; the comparatively narrow distributional pattern of the *cristata* group suggests that is the more recently-evolved lineage, as the *marmorata* group extends much farther south, and links in turn to South American genera, with South America being the apparent center of diversity from which the *Scaralina* lineage diverged as it migrated north. Within the *marmorata* group, various shared structural features along with biogeography suggest that *metcalfi*, *obfusca*, *obrienae*, and *sullivani* may form a natural subgroup, while *marmorata*, *orientalis*, and *rileyi* may comprise another, and possibly more derived. The placement of *veracruzensis* is uncertain, as it shares features with members of both subgroups. It bears mention that the biogeographical history of oaks, the presumed hosts, appears to be almost the exact opposite of the pattern we suspect is shown by these planthoppers; that is, oaks migrated into Mesoamerica from North America, and diversified as they spread southwards (Hipp *et al*., 2018), while the phylogeny of the New World fulgorids suggests that the few North American representatives are terminal taxa derived from very diverse South American lineages (Urban & Cryan, 2009).

Examination of numerous genera within the Poiocerinae, while not exhaustive, suggests that there are different combinations of ground plan (presumably plesiomorphic) character states present in *Scaralina* and *Scaralis*, and other features may be homoplasies. For example, both genera have reduced femoral ridges and mesocoxal spines, but character states based on reduction clearly have a much higher likelihood of arising through homoplasy, and thus may be misleading, and these traits are also shared with *Alphina* and *Matacosa*. Another feature, the stunted and distorted gonostylar hooks in *Scaralis*, could be assumed to be a derived condition, compared to the many poiocerine lineages where these hooks are well-defined and acute (the character polarity of ancestral versus derived would seem clear-cut in this case), but this could also be a homoplasy. Similarly, the sublobate lateral expansion of the lower frons in genera such as *Jamaicastes*, *Matacosa*, *Scaralina*, and *Scaralis* (Figs 101–104) is probably plesiomorphic, with the somewhat reduced lobes in the *Scaralina cristata* species group being a derived condition. However, without an exhaustive morphological and/or genetic sampling of the South American poiocerine genera, a definitive resolution of the phylogeny (and proper character polarization) is not possible. Nonetheless, the delimitation of *Scaralina* as presented here yields the best practical classification, and this lineage is likely to remain monophyletic upon further analysis, even though its sister taxon is difficult to determine at present. In contrast, we suspect that the present circumscription of *Scaralis* may not correspond to a monophyletic group, and the subgenus *Alphinoides* may eventually prove to be monophyletic and distinct.

Examination of specimens or photos of both known *Alphina* species show that some of their features are similar to both *Scaralina* and *Alphinoides*, such as a nearly globose second antennomere. However, the fore- and hindwings of *Alphina* differ from other genera, with the wings being slightly shorter relative to the body; the forewings relatively narrow with the apices distinctly spatulate, and rounded rather than oblique; the hindwings with a relatively expanded anal region; the vertex is also not nearly as wide relative to its length as in *Scaralis s.s*. or *Scaralina*, the eyes relatively wide (similar to *Alphinoides*); the anterior lobe of the pronotum is much more narrowly rounded, forming a truncate projection medially; the dorsal thorax and wing veins appear to be essentially bare, as in *Scaralis*. No other named species we have seen would seem to be properly placed alongside the two known *Alphina* species, though of all described taxa we've seen, the species placed here in *Alphinoides* are most similar.

Of the remaining "calyptoproctine" genera we have been able to examine, the only ones that appear to potentially be part of the same lineage are *Jamaicastes*, the type species of which shares a parallel-sided frons (Fig. 101), and the monotypic genus *Matacosa* Distant, 1906 (Fig. 102), which appears very similar to *Scaralis*, though it has a distinctly setose dorsal thorax and exceptionally fine venation (in the molecular analysis by Urban & Cryan, 2009, *M. miscella* was placed sister to *Scaralis* (*Alphinoides*) *semilimpida*, but the analysis may not have included any members of *Scaralis s.s.* and did not include *Jamaicastes*). The type species and at least a few members of the genus *Hypaepa* (previously not considered a calyptoproctine despite some species having a large supra-anal plate) may also be related, though some species in this group (e.g., *H. laetabilis* (Walker, 1858) and *H. rubricata* Distant, 1887) appear unrelated. Therefore, *Scaralis*, *Jamaicastes*, and *Hypaepa* may not be monophyletic and may require DNA sequencing to achieve resolution. It is difficult to find any morphological features that might even potentially be diagnostic for monophyletic lineages. However, among the New World Poiocerinae, very few genera have the apical regions of both the fore- and hindwings largely hyaline, and with fairly coarse forewing venation, and nearly all of these are "calyptoproctines". Only *Crepusia* and *Florichisme* Kirkaldy 1904 appear to be exceptions, and we have not had the opportunity to examine specimens of these to determine if they might belong to this lineage. Among the "calyptoproctines", *Calyptoproctus* and *Cyrpoptus* do not share this character set, but molecular analyses very clearly indicate they are only distantly related to each other, or the remaining genera (Urban & Cryan, 2009). Some species of *Hypaepa* share this character set, while *Jamaicastes* do not, but sequence data are not available for either taxon. *Matacosa* has very fine forewing venation but is otherwise similar to *Scaralis*, and Urban & Cryan's analysis places it as a close relative.

Many of the taxa we examined for the present work (*Scaralis*, *Hypaepa*, *Jamaicastes*) appear to not be monophyletic in their present circumscriptions, and it is unclear what to do about species that are misplaced. A larger issue remains with the numerous small, poorly-known "calyptoproctine" taxa, all from South America, that were unexplored in the present revision (at a minimum, *Coptopola* Stål 1869, *Curetia* Stål 1862, *Learcha* Stål 1863, *Oeagra* Stål 1863, and *Tabocasa* Distant 1906, plus two additional species of putative *Jamaicastes*; other authors have at various times included genera such as *Brasiliana* Lallemand 1959, *Kutariana* Nast 1950, *Talloisia* Lallemand 1959, and *Zepasa* Distant 1906, all monotypic). The original descriptions of most of these are inadequate

to determine what their true affinities may be, and comprehensive morphological studies are unlikely to be helpful given the high degree of character homoplasy. At least one of the unexamined monotypic taxa, *Curetia*, might be related to *Alphina*, *Scaralis*, and *Scaralina*. As noted above, some species in the genus *Hypaepa*, hitherto classified as a Poiocerina, may also be affiliated with these "calyptoproctine" genera.

The tribe Poiocerini is full of undescribed New World taxa; we have material at hand from Peru that includes at least one species intermediate in several features between *Scaralis* and *Scaralina*, one *Alphinoides*, and one species of *Scaralis*, none of which correspond to any of the known *Scaralis* species (though we cannot fully exclude the possibility that one or more of these may have already been described under a different generic name). Even a cursory examination of material from well-known Poiocerini reveals inconsistencies between type species versus other species placed into the same genera, such as *Poblicia* and *Alaruasa*, or very poorly-differentiated genera whose constituency appears to overlap, such as *Zeunasa* and *Acraephia*. Online images (e.g., iNaturalist), especially from Venezuela, Brazil, French Guiana, Mexico, and Guatemala, reveal many undescribed poiocerine taxa that are frequently unplaceable to genus. We have avoided describing these taxa, and excluded South America from the present study, other than the placement of a few taxa into *Alphinoides*, to achieve a reasonable circumscription of *Scaralina*. The present study will hopefully serve as a starting point to stimulate further investigations into this diverse and poorly studied group of insects.

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