A review of *Hesperia uncas* W. H. Edwards, 1863 in Mexico, with the description of a new subspecies (Lepidoptera: Hesperiidae: Hesperiinae)

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Abstract: Populations of *Hesperia uncas* W. H. Edwards, 1863 in Mexico and the adjacent United States are reviewed, and *Hesperia uncas nadineae* A. Warren, Gott & McGuire **ssp. nov.** is described from the northeastern Mexican states of Coahuila and Nuevo León.

Key words: Biogeography, butterfly, distribution, Sierra Madre Oriental, skipper.

Resumen: Se revisan poblaciones de *Hesperia uncas* W. H. Edwards, 1863 en México y la región adyacente de los Estados Unidos, y se describe *Hesperia uncas nadineae* A. Warren, Gott & McGuire **ssp. nov.** de los estados de Coahuila y Nuevo León, en el noreste de México.

Palabras clave: Biogeografía, distribución, hespérido, mariposa, Sierra Madre Oriental.

INTRODUCTION

Hesperia uncas W. H. Edwards, 1863, is a western North American skipper butterfly of open grassland landscapes, which displays a great deal of geographic variation across its wide distribution, from western Minnesota west to Oregon and California, and from southern Alberta, Manitoba and Saskatchewan in Canada, south into Mexico (MacNeill, 1964). Populations across this range have been divided into ten subspecies (Warren *et al*., 2017), although no comprehensive study of variation across the species' entire range has been conducted to date. In recent decades, several new subspecies of *H. uncas* have been described from California and Nevada (Austin & McGuire, 1998; McGuire, 1998), and the northwestern limits of its range in Oregon have become better known (Warren, 2005).

Considering its wide distribution in North America and the extent of geographic variation displayed, *H. uncas* remains very poorly understood in Mexico. The first report of *H. uncas* from Mexico was by MacNeill (1964), in his original description of *H. uncas gilberti* MacNeill, 1964. This taxon was described from a series of three males and two females from near Los Reyes, in the State of México, collected on 2 July 1952. Since then, there have been no additional published records of *H. uncas* from Mexico.

During field research by the third author (WWM) in 1977 in Coahuila, northeastern Mexico, a population of *H. uncas* was located southeast of the city of Saltillo. Study of this series, together with a few additional specimens collected nearby, in comparison with *H. u. uncas*, *H. u. lasus* (W. H. Edwards, 1864), and *H. u. gilberti*, showed that it represents a morphologically distinct taxon, which is described as a new subspecies below.

MATERIALS AND METHODS

In an effort to locate specimens relevant to this study of *Hesperia* Fabricius, 1793, the senior author reviewed collections of Lepidoptera containing Mexican Hesperiidae, as follows: C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins (CSU); Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (DZUP); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (IBUNAM); McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville (MGCL); Museo de Historia Natural de la Ciudad de México, Mexico City (MHNCM); Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City (MZFC); Private collection of James P. Brock, Tucson, Arizona (JPB); Private collection of the De la Maza Family, Mexico City (MAZA); Private collection of the Turrent Family, Mexico City (CFT); Research material of Andrew D. Warren (ADW); The Natural History Museum, London (NHMUK). Only MGCL, MHNCM and MZFC contained specimens of *H. uncas* from Mexico.

Male and female genitalia were prepared for examination by soaking abdomens in 10% potassium hydroxide solution for 12 hours before being dissected under a Leica MZ 16 stereomicroscope with a camera lucida attached. Subsequent to dissection, genitalia were soaked in a weak acetic acid solution for 10 minutes to neutralize any remaining potassium hydroxide. After study, genitalia were placed in small plastic vials containing glycerin for permanent storage. Photos of adults were taken with a Canon EOS 70D camera with a 100 mm macro lens. Images and plates were modified using Adobe Photoshop 2021 and Adobe Illustrator 2021. The distribution map was generated using QGIS 3.10 (Quantum Geographic Information System; QGIS Development Team, 2019). Terminology for forewing stigma and wing pattern elements follows MacNeill (1964), and terminology for genitalia follows Klots (1970) and Burns (1987).

RESULTS AND DISCUSSION

Despite our extensive search of museum collections and correspondence with lepidopterists who have conducted field work in northern Mexico, we still lack definitive records of *H. u. uncas* and *H. u. lasus* from Mexico. Nevertheless, we have included both of these taxa in our discussion below, since it is probable that both taxa occur within the northernmost reaches of the country.

Hesperia uncas uncas W. H. Edwards, 1863
(Figs. 1A-D, 8B, 9B, 10)

The nominotypical subspecies of *H. uncas* is characterized by its gray-green ventral hindwing coloration, comparatively pale orange dorsal coloration with a distinctly darker outer margin, whitish apical spots on the forewing, and females with whitish discal forewing macules. The mean forewing length of males is 14.9 mm (12.9-16.5 mm, n = 12 from Texas), and of females is 17.3 mm (15.4-18.7 mm, n = 12 from Texas). Note that the specimens in Figs. 1A-D are reared, so are somewhat smaller than most wild-caught individuals; they were not included in wing measurements.

We have examined specimens of typical *H. u. uncas* from the west Texas counties of Hudspeth (Sierra Diablo Mts., Figs. 1A-D), Culberson (Guadalupe Mts. National Park), Jeff Davis (Ft. Davis), and Brewster (Marathon area; all in MGCL), which suggests that *H. u. uncas* is likely to be present in adjacent parts of northern Coahuila and/or northeastern Chihuahua, Mexico. Records of *H. uncas* from west Texas are from April, May, June, July and August.

West Texas specimens examined (all in MGCL). Brewster Co.: 4.9 mi W of Marathon on US 90 [vic. 30°13'08"N, 103°19'12"W], 12-IV-1993, F. & J. Preston (1 male); 10 mi N Marathon [vic. 30°20'14"N, 103°15'57"W], 12-VIII-1962, H. V. Weems, Jr. (1 female); Culberson Co.: Guadalupe Mts. N.P., Dog Canyon [vic. 31°59'36"N, 104°50'02"W], 6-8-VII-1991, E. C. Knudson (1 male); same locality, 8-9-VIII-2000, C. Bordelon & E. C. Knudson (1 male, 1 female); Hudspeth Co.: Sierra Diablo Mts., 5 mi W Victoria Cyn. [vic. 31°18'12"N, 104°58'31"W], 5700', 23-VIII-1975, William W. & Nadine M. McGuire (1 male, 1 female); same locality and collectors, ex ovum, 29-XI-1975 (1 male); same locality and collectors, ex ovum, 3-XII-1975 (1 female); same locality and collectors, ex ovum, 5-XII-1975 (1 female); same locality and collectors, ex ovum, 29-XII-1975 (1 female); same locality and collectors, ex ovum, 31-XII-1975 (1 female); 15 mi N & 7 mi W Van Horn [vic. 31°15'08"N, 104°56'42"W], 18-V-1973, J. L. Harry (1 female); Jeff Davis Co.: Fort Davis [vic. 30°35'39"N, 103°53'36"W], 9-VI-1949, H. A. Freeman (2 females).

Hesperia uncas lasus (W. H. Edwards, 1864)
(Figs. 1E-H, 8A, 9A, 10)

This subspecies is characterized by its large size, beige ventral ground color, narrower ventral hindwing postmedian band which contrasts less with the ground color, extensive dull fulvous coloration above with an indistinct dark outer margin, fulvous forewing apical spots, and females with yellowish forewing macules (Austin & McGuire, 1998). The mean forewing length of males is 15.9 mm (13.8-16.9 mm, n = 12 from Santa Cruz County, Arizona), and of females is 18.1 mm (16.8-19.3 mm, n = 12 from Santa Cruz and Yavapai counties, Arizona).

Hesperia u. lasus was stated to occur in "northern Mexico" by MacNeill (1975), without additional details, but we have not seen specimens from Mexico. Likewise, *H. u. lasus* was not included in the recent list of butterflies of Sonora (Bailowitz *et al*., 2017). Through the 1980s and 1990s, *H. u. lasus* was present in the San Rafael Valley of Santa Cruz County, Arizona (Bailowitz & Brock, 1991), although it has not been seen there in recent decades (J. Brock, pers. comm., 2020). Most of the specimens of *H. u. lasus* we have examined from this area (*e.g*., Fig. 1E-F) were collected by James P. Brock, on a ridge at 1494 m elevation just west of Parker Canyon, exactly 2 kilometers north of the current USA-Mexico border fence (31°21'04"N, 110°33'34"W). Despite this, we still lack confirmed records of *H. u. lasus* from adjacent parts of Sonora, Mexico, although we feel it certainly does or once did occur in northern Sonora in habitats similar to the site in Parker Canyon. Records of *H. u. lasus* from southeastern Arizona are from May and August-September, indicating two annual broods (Bailowitz & Brock, 1991).

Southeast Arizona specimens examined (all in MGCL). Santa Cruz Co.: Bog Hole, San Rafael Valley [vic. 31°28'35"N, 110°37'08"W], 21-V-1993, J. P. Brock (3 males, 1 female); Nat. For. Rd. 61, 1/2 mi W Parker Cyn., San Rafael Valley [31°21'04"N, 110°33'34"W], 18-V-1981, J. P. Brock (1 male); same locality and collector, 24-V-1981 (3 males); same locality and collector, 31-V-1981 (6 males, 1 female); Rt. 82, 1 mi E of Sonoita [vic. 31°40'53"N 110°38'22"W], 17-VIII-1977, E. C. Olson (2 females).

Hesperia uncas gilberti MacNeill, 1964
(Figs. 1I-L, 2A-B, 7, 10)

This taxon was characterized by MacNeill (1964) as having rounded wings, a slender forewing stigma, and fulvous females, compared to *H. u. uncas*, as well as differences in the male genitalia. These differences were described as follows: "The uncus is slightly more tapered and prolonged apically, and the valvae lack the strong apical serration usually diagnostic of this species." However, he also noted that the female genitalia of *H. u. uncas* and *H. u. gilberti* share an "extremely close superficial resemblance", and based partly on this, named *gilberti* as a subspecies-level taxon. MacNeill (1964) concluded, regarding *H. u. gilberti*, "This population is, in any case, very closely related to *H. uncas* and the question of its possible specific

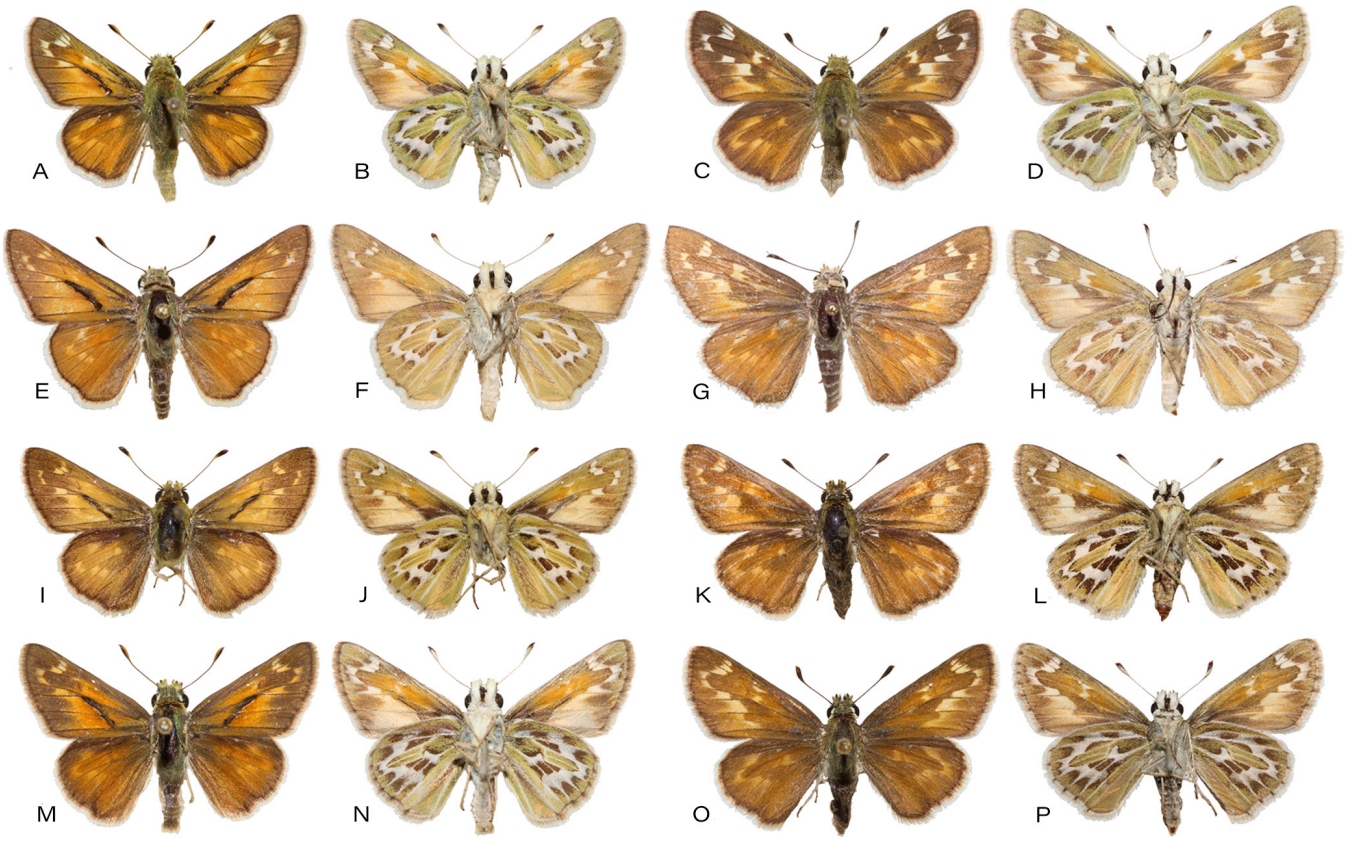

Figure 1. Adults of *Hesperia uncas* subspecies from Mexico and adjacent areas in Texas and Arizona, United States (all specimens in MGCL). A) Dorsal and B) ventral views of male *H. u. uncas* from 5 mi W Victoria Cyn., 5700', Sierra Diablo Mts., Hudspeth County, Texas, USA, ex ovum coll. 29-XI-1975, collected by William W. & Nadine M. McGuire; C) dorsal and D) ventral views of female *H. u. uncas*, same data as male; E) dorsal and F) ventral views of male *H. u. lasus* from Nat. For. Rd. 61, 1/2 mi W Parker Cyn., San Rafael Valley, Santa Cruz County, Arizona, USA, 31-V-1981, collected by James P. Brock; G) dorsal and H) ventral views of female *H. u. lasus* from Rt. 82, 1 mi E of Sonoita, Santa Cruz County, Arizona, USA, 17-VIII-1977, collected by E. C. Olson; I) dorsal and J) ventral views of paratype male *H. u. gilberti* from 2 mi SE Los Reyes, 7400', State of México, Mexico, 2-VII-1952, collected by C. D. MacNeill; K) dorsal and L) ventral views of paratype female *H. u. gilberti*, same data as male, collected by E. E. Gilbert & C. D. MacNeill; M) dorsal and N) ventral views of holotype male *H. u. nadineae* **ssp. nov.** from Hwy. 57, 18 mi SE Saltillo, 7000', Coahuila, Mexico, 19-IX-1977, collected by William W. McGuire; O) dorsal and P) ventral views of paratype female *H. u. nadineae*, same data as male, 22-IX-1977. Scale = 1.0 cm.

status is purely academic at the present state of our knowledge."

MacNeill (1964) partly illustrated the male genitalia of *H. u. gilberti*, including a drawing of the uncus and tegumen in dorsal aspect, compared to *H. u. uncas* and *H. u. lasus* (his Fig. 13), a drawing of the inner surface of the left valva, compared to *H. u. uncas* and *H. u. macswaini* MacNeill, 1964 (his Fig. 19), and a drawing of the left valva from a caudal view, compared to *H. u. uncas* and *H. u. macswaini* (his Fig. 22). He also illustrated the slender forewing stigma of *H. u. gilberti*, compared to *H. u. macswaini* (his Fig. 12). MacNeill (1964) did not illustrate the female genitalia of *H. u. gilberti*, but did include a drawing of the female genitalia of *H. u. uncas* (his Fig. 25). The single male *H. u. gilberti* specimen that we have examined (Fig. 1I-J) is the same individual figured by MacNeill (1964: Plate 1, Fig. 2) in ventral aspect, which was already missing its abdomen at that time. It has a label affixed with "G-65" handwritten in pencil, suggesting that the genitalia were dissected, although the genitalia are no longer associated with the specimen, and MacNeill (1964) did not indicate which specimen(s) his genitalia drawings of *H. u. gilberti* were based on. As a result, we were unable to examine the male genitalia of *H. u. gilberti*. We dissected the genitalia of the single female *H. u. gilberti* currently available to us (Fig. 7), but did not detect any prominent differences between them and those of *H. u. uncas*, in accordance with MacNeill (1964), who considered the female genitalia of *H. u. gilberti* to be undifferentiated from those of *H. u. uncas*.

While MacNeill (1964) did not compare *H. u. gilberti* to *H. u. lasus*, the latter is a much larger insect, with paler fulvous coloration above, and a much paler ventral ground color. The forewing length of the two specimens of *H. u. gilberti* currently available to us are 14.3 mm (male, Fig. 1I-J), and 15.3 mm (female, Fig. 1K-L).

Specimens examined. MEXICO: D. F.: VIII (no additional data but likely over 100 years old), R. Müller Coll. 5525 (1 female, MHNCM); MEXICO: STATE OF MÉXICO: 2 mi SE Los Reyes, 7400', 2-VII-1952, C. D. MacNeill (1 male paratype, MGCL); same data, E. E. Gilbert & C. D. MacNeill (1 female paratype, MGCL); MEXICO: OAXACA: Mpio. Tepelmeme: road to Puente Colosal, [2030 m, 17°56'09"N, 97°17'50"W], 14-IX-2007, Ángel G. Vázquez (1 female, MZFC); Mpio Tepelmeme: 10 km N Tepelmeme, canyon W side of road, ca. 1 km N Comedor El Cardon, [2148m, 17°57'10"N, 97°21'20"W], July 2007, J. Kemner (1 female, MZFC). In addition to these specimens, we examined photographs of the holotype male and allotype female, with the same

Figure 2. Live male of *Hesperia uncas gilberti* from 6 kilometers NE of San Miguel Tequistepec, Mpio. San Miguel Tequistepec, Oaxaca, Mexico, 15 June 2018, photos by John Kemner. A) Dorsal view; B) partial ventral view.

data as the MGCL paratype female, deposited at the California Academy of Sciences (Warren *et al*., 2017).

Distribution and phenology. To date, *H. u. gilberti* has been recorded from the Valley of México in Distrito Federal (vic. 19°25'14"N, 99°11'10"W) and at the type locality southeast of Los Reyes in adjacent State of México (vic. 19°45'13"N, 98°58'17"W), yet we are unaware of recent (post-1952) records from this area, which is now mostly developed. Recently, *H. u. gilberti* was found in Oaxaca, in the Municipalities of Tepelmeme Villa de Morelos and San Miguel Tequistepec by John Kemner and Ángel G. Vázquez. As detailed above, two female specimens were collected in the Municipality of Tepelmeme Villa de Morelos in 2007; these are morphologically consistent with the few females we have examined of *H. c. gilberti* from the Valley of México. Subsequently, Kemner photographed males of *H. u. gilberti* in the Municipality of San Miguel Tequistepec, at 6 kilometers northeast of San Miguel Tequistepec, [2030 m, 17°49'34"N, 97°18'33"W], on 24 June 2014 and 15 June 2018 (Fig. 2). More recently, Amy McAndrews photographed a male of *H. u. gilberti* in the Municipality of Perote, Veracruz (vic. 19°36'16"N, 97°22'02"W), on 13 July 2020 (iNaturalist observation by "Sabrewing" https://www.inaturalist.org/observations/58161697). Records for *H. u. gilberti* are from mid- and late June, July, August, and mid-September.

Biogeography. The few known specimens of *H. u. gilberti* suggest it is endemic to the Valley of México and arid areas in Veracruz and northern Oaxaca, possibly with populations in Tehuacán-Cuicatlán Valley of the State of Puebla as well.

Discussion. The senior author searched several sites in the State of México, which appeared to be appropriate habitat for *H. u. gilberti*, between 2001 and 2008, without success. Even though much of the area around the Valley of México has been developed or highly modified, suitable habitats for *H. u. gilberti* in this region likely still exist.

As noted above, based on subtle differences in the male genitalia between *H. u. gilberti* and *H. u. uncas*, MacNeill (1964) thought that *H. u. gilberti* could possibly represent a species-level taxon. Subsequent authors have demonstrated subtle differences in the male genitalia between various subspecies of *H. uncas* (Austin & McGuire, 1998; McGuire, 1998), suggesting that minor differences in male genitalia between distant populations of *H. uncas* are to be expected, and are not necessarily an indication of species-level divergence. Furthermore, the discovery of the new subspecies described below provides additional evidence that *H. u. gilberti* is conspecific with *H. uncas*.

Hesperia uncas nadineae A. Warren, Gott & McGuire, **ssp. nov.**

(Figs. 1M-P, 3A-H, 4A-B, 5A-K, 6A-C, 8C, 9C, 10)

Description. MALE (Figs. 1M-N, 3A-B, 3E-F, 4A-B): mean forewing length = 13.1 mm (11.9-13.9 mm, n = 16, holotype = 13.8 mm); forewing apex pointed, termen slightly convex; hindwing termen convex, then slightly concave before weakly developed tornal lobe; forewing stigma in CuA_1-CuA_2, extending from along posterior vein of discal cell proximad from origin of CuA_1, curving slightly caudad to vein CuA_2 at about 1/6 distance to termen from its origin, and in CuA_2-2A from vein CuA_2 to about 1/6 distance from its origin to termen extending nearly straight almost to vein 2A at about 1/3 distance from its origin to termen; apical brush patch black, prominent; micro-androconial mass slender, dark gray; middle and lower brush patches black, well-developed; post-stigmal patch poorly developed; dorsum dark orange and gray-brown; orange on forewing most intense in discal cell, and proximad of stigma from CuA_1 to 2A; costa gray-brown with scattered dark orange scales towards apex; outer margin gray-grown, grading to dark orange proximad; quadrate pale orange-yellow apical spots in R_3-R_4, R_4-R_5, and R_5-M_1; semi-rectangular orange subterminal spots in M_1-M_2 and M_2-M_3, offset distad from postmedial and apical spots; orange postmedial spot in M_3-CuA_1 triangular, just distad of base of cell; extent of orange in CuA_1-CuA_2 and CuA_2-2A distad of stigma is highly variable; in most specimens orange gradually becomes diffused distad with gray-brown, and no distinct spots can be discerned; in other specimens, orange in these cells is reduced, leaving fairly well-defined semi-rectangular macules in CuA_1-CuA_2 and CuA_2-2A; fringe gray-grown proximad, pale gray distad. Hindwing coloration dark orange as on forewing; gray-brown coloration along costa and narrowly along distal margin, diffused with dark orange scales proximad; elements of ventral hindwing macular band variably visible, most prominent in Rs-M_1, M_1-M_3, and M_3-CuA_1, very weakly expressed in CuA_2-CuA_3 and at basal loop; fringe gray-brown proximad, pale gray distad.

Ventral forewing dark orange in discal cell, grading to black proximad; dark orange extending into basal half of M_1-M_2 and M_2-M_3, basal 1/6 of M_3-CuA_1, and areas immediately adjacent to stigma pocket in CuA_1-CuA_2 and at base of cell; pale gray-green scales concentrated narrowly along costa, expanding at apex distad of apical and subterminal spots, and narrowly along

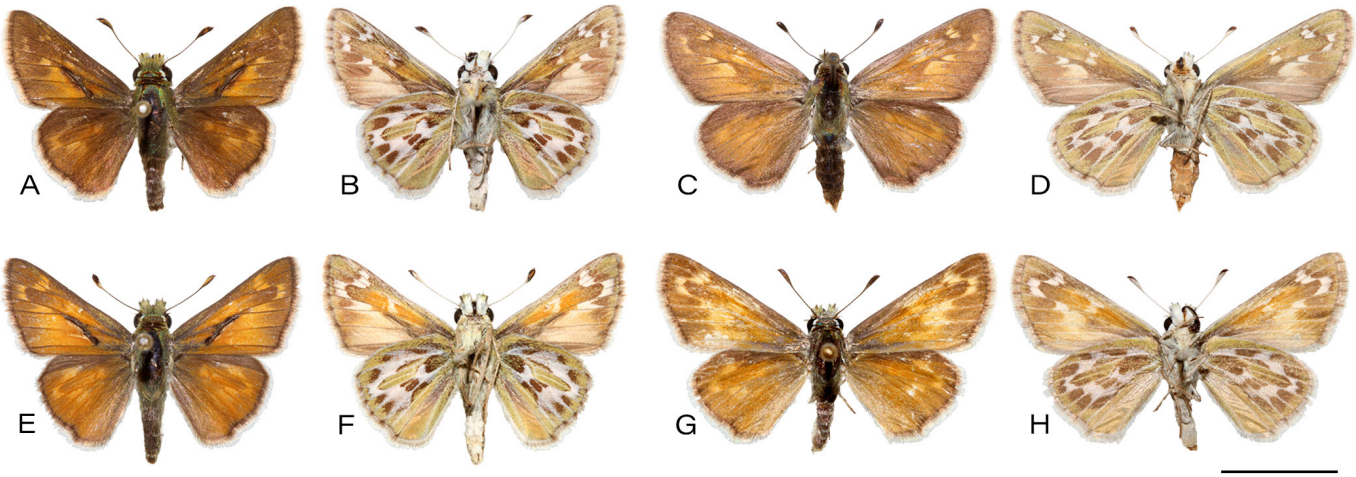

Figure 3. Paratypes of *Hesperia uncas nadineae* **ssp. nov.**, showing dark and pale extremes in coloration (all specimens in MGCL). A-B + E-F) Males; C-D + G-H) females. A-B) From Hwy. 57, 18 mi SE Saltillo, 7000', Coahuila, Mexico, 22-IX-1977, collected by William W. McGuire; C-D) from Los Pinos, 19 mi SE Saltillo, 6800', Coahuila, Mexico, 24-IX-1976, collected by J. A. Powell & J. A. Chemsak; E-F) from Hwy. 57, 18 mi SE Saltillo, 7000', Coahuila, Mexico, 19-IX-1977, collected by William W. McGuire; G-H) from Hwy. 57, vic. Los Pinos, 19.6 mi SE Saltillo, 7000', Coahuila, Mexico, 29-IV-1978, collected by William W. & Nadine M. McGuire. Scale = 1.0 cm.

outer margin to CuA_2; apical and subterminal spots repeated from dorsum, white; spot in M_3-CuA_1 white-ochreous; semi-rectangular patches of pale ochreous in central 1/3 of CuA_1-CuA_2, and central 1/2 of CuA_2-2A, extending distad along 2A almost to termen; inner margin pale ochreous distad, grading to black at base; fringe gray at base, grading to gray-white distad; conspicuously darker at vein ends. Ventral hindwing color pale gray-green with white macular band and basal loop; all wing veins highlighted with white, though diffused along Sc+R_1, grading to black at termen of each vein; additional white vein-like streaks in mid-M_1-M_3, and mid-CuA_2-2A; macular band of conjoined spots from Sc+R_1-Rs to 2A as follows: Sc+R_1-Rs, rectangular, centered just proximad of mid-cell, partly overlapping proximal portion of macule in Rs-M_1; Rs-M_1 semi-rectangular, centered just proximad of mid-cell, extending distad along M_1 to macule in M_1-M_3; M_1-M_3 irregular, centered in distal 4/5 of cell, extending proximad along M_3 to overlap distal portion of macule in M_3-CuA_1; M_3-CuA_1 semi-rectangular , centered near mid-cell, extending distad along CuA_1 and overlapping most of macule in CuA_1-CuA_2; CuA_1-CuA_2 semi-rectangular, centered near mid-cell, extending distad along CuA_2 and overlapping most of macule in CuA_2-2A; CuA_2-2A semi-rectangular in anterior 1/2 of cell and vaguely defined in posterior half of cell; basal loop consisting of two macules: small, triangular, in basal 1/4 of Sc+R_1-Rs; larger, semi-triangular, spanning across posterior half of distal end of discal cell into base of CuA_1-CuA_2 then into anterior half of CuA_2-2A; dark gray-brown patches bordering macular band as follows: Sc+R_1-Rs extensive, proximad and distad of macule; Rs-M_1 extensive, especially proximad of macule; M_1-M_3 reduced to only a trace of dark gray-brown scales both distad and proximad of macule, separated mid-cell by white vein-like streak; M_3-CuA_1 and CuA_1-CuA_2 extensive, proximad (extending to macule of basal loop) and distad of macule, CuA_2-2A present only in anterior half of cell cephalad of white vein-like streak, extensive proximad (extending to macule of basal loop), diffused distad with gray-green scales; small area proximad of larger macule of basal loop in caudal half of distal end of discal cell; fringe gray at base, grading to slightly paler distad; conspicuously darker at vein ends.

Dorsal hirsute vestiture predominantly greenish with scattered dark gray and cream; patch of short, white scales dorsad of eye; palpi mixture of beige and black scales on dorsum, white with slight beige tint on venter, third segment black; antenna gray on dorsum, venter white, club abruptly constricted to apiculus from basal nudum segments, club orange proximad, black distad on dorsum, venter white grading to black distad; nudum dark ochreous-brown, 10-11 segments; thorax dorsally with blue-green and grayish vestiture, whitish ventrally with scattered beige scales, legs gray proximad, very pale gray distad; abdomen gray dorsally with scattered beige scales, paler at segments, laterally and ventrally very pale gray with beige tint distad.

Male genitalia (Fig. 5A-K, 8C): Uncus short, broad, gradually narrowing to blunt, divided tip angled ventrad; gnathos divided, tips pointed dorsally, not extended caudally as far as uncus; tips of gnathos and uncus well separated; vinculum broad medially, gradually narrowing dorsally to tegumen, ventrally to saccus; saccus angled anteriad, forming rounded, narrow point, caudally expanded to form flat, triangular plate; valvae symmetric; harpe with single large point directed dorsally, smaller irregular points anteriad and posteriad of large point; costa with single large point directed dorsally; phallus with narrow, blunt coecum, gradually narrowing posteriorly to ductus ejaculatoris, then gradually widening until constriction at two-thirds length of phallus, gradually widening from constriction posteriorly to tip; rostellum with two points, directed to right of midline; vesica without cornuti; juxta heavily sclerotized, two narrow, blunt anterior projections forming "W" shape, abruptly widening to flat plate two to three times width of phallus at widest section; transtilla absent or not sclerotized.

FEMALE (Figs. 1O-P, 3C-D, 3G-H): mean forewing length = 14.7 mm (13.0-15.4 mm, n = 6); forewing apex less pointed, termen slightly convex; hindwing termen convex, then slightly concave before weakly developed tornal lobe; dorsum dark orange and gray-brown; dark orange covering most of wing except macules and narrowly gray-brown with scattered dark orange scales along costa and outer margin, grading to dark orange proximad; quadrate pale yellow apical spots in R_3-R_4, R_4-R_5, and R_5-M_1; semi-rectangular pale yellow subterminal spots in M_1-M_2 and M_2-M_3, offset distad from postmedial and apical spots; pale yellow-orange postmedial spot in M_3-CuA_1 quadrate, centered near of mid-cell; CuA_1-CuA_2 quadrate, pale yellow-orange, centered near mid-cell; CuA_2-2A poorly defined semi-rectangular macule in anterior half of cell centered under macule in CuA_1-CuA_2, less well-defined, irregular macule in posterior half of cell, extended proximad along 2A; discal cell with two pale yellow spots near distal end, sometimes conjoined into a single spot, otherwise roughly hour-glass

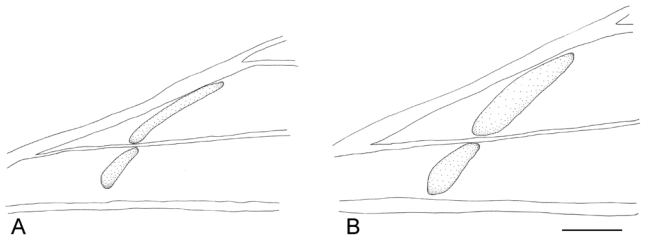

Figure 4. Variation in the development of the forewing stigma on males of *Hesperia uncas nadineae* **ssp. nov.** A) From Hwy. 57, 18 mi SE Saltillo, 7000', Coahuila, Mexico, 19-IX-1977, collected by William W. McGuire; B) from Hwy. 57, vic. Los Pinos, 19.6 mi SE Saltillo, 7000', Coahuila, Mexico, 19-IX-1977, collected by William W. McGuire. Most paratype males have narrower stigmas, similar to or slightly better-developed than A, while B represents the best-developed stigma in the type series. Scale = 1.0 mm.

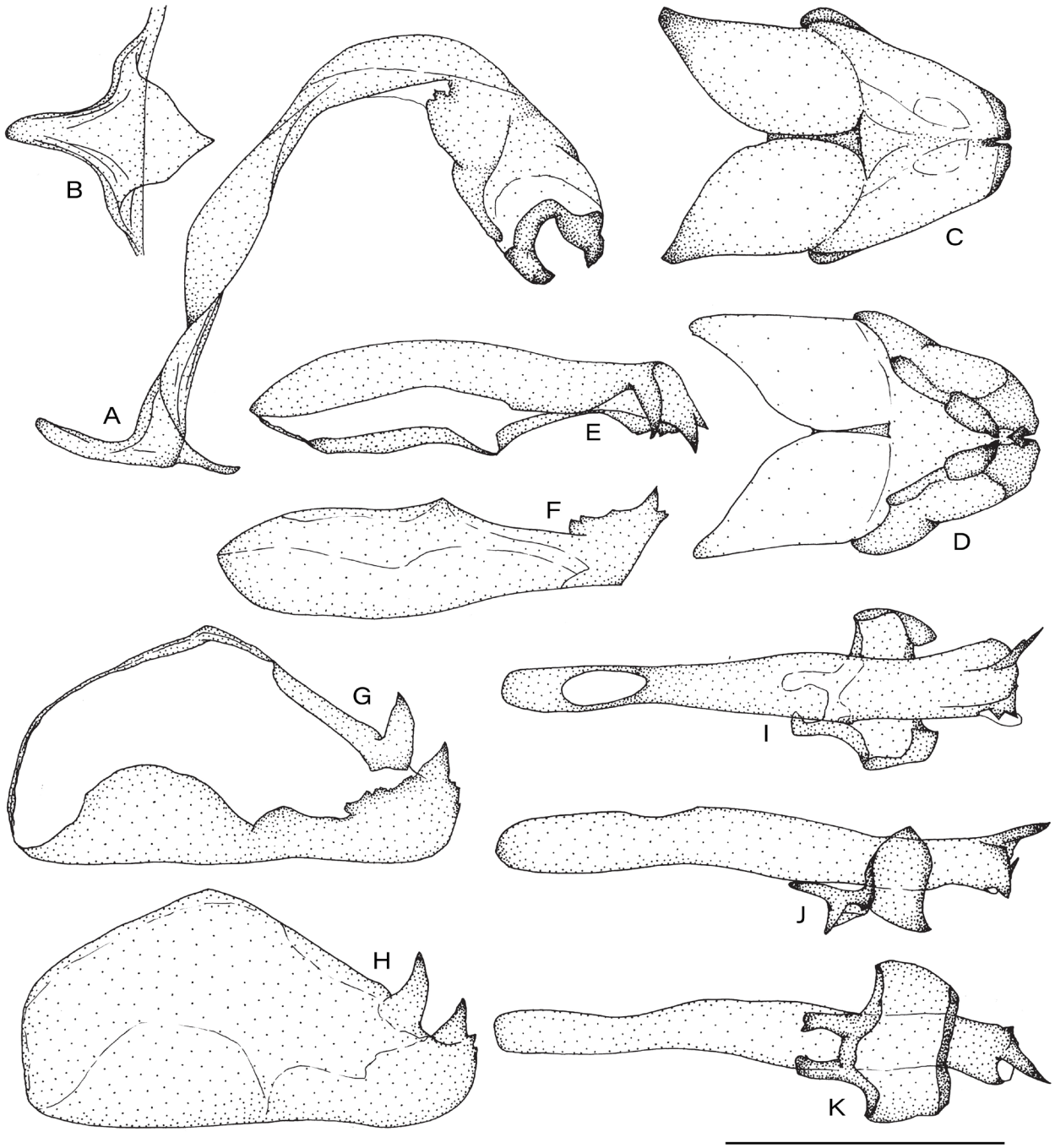

Figure 5. Male genitalia of *Hesperia uncas nadineae* **ssp. nov.** paratype, from Hwy. 57, 18 mi SE Saltillo, 7000', Coahuila, Mexico, 22-IX-1977, collected by William W. McGuire, Riley J. Gott dissection number RG0390. A) Left-lateral view of uncus, gnathos, tegumen, and saccus; B) ventral view of saccus; C) dorsal view of uncus and tegumen; D) ventral view of gnathos and tegumen; E) dorsal view of right valve; F) ventral view of right valve; G) interior lateral view of right valve; H) exterior view of right valve; I) dorsal, J) lateral, and K) ventral view of aedeagus, juxta, and transtilla. Scale = 1.0 mm.

in shape; fringe gray-grown proximad, pale gray distad, subtly darker at vein ends. Hindwing coloration dark orange as on forewing; gray-brown coloration along costa and narrowly along distal margin, diffused with dark orange scales proximad; elements of ventral hindwing macular band variably visible, most prominent in Rs-M_1, M_1-M_3, and M_3-CuA_1, very weakly expressed in CuA_2-CuA_3 and at basal loop; fringe gray-brown proximad, pale gray distad, subtly darker at vein ends.

Ventral forewing dark orange in discal cell, grading to grayish proximad, pale yellow macules in discal cell repeated from dorsum though somewhat larger; dark orange variably extending into basal half of M_1-M_2 and M_2-M_3, and basal 1/6 of M_3-CuA_1; pale gray-green scales concentrated narrowly along costa, expanding at apex distad of apical and subterminal spots, and narrowly along outer margin to CuA_2; apical and subterminal spots repeated from dorsum, white; spot in M_3-CuA_1 pale yellow; spots in CuA_1-CuA_2 and CuA_2-2A pale yellow-orange; CuA_2-2A divided mid-cell by white vein-like streak; inner margin pale yellow-gray distad, grading to dark grey at base; fringe gray at base, grading to gray-white distad; conspicuously darker at vein ends. Ventral hindwing color gray-green with white macular band and basal loop; all wing veins highlighted with white, though somewhat diffused along Sc+R_1, grading to black at termen of each vein; additional white vein-like streaks in mid-M_1-M_3, and mid-CuA_2-2A; macular band of conjoined spots from Sc+R_1-Rs to 2A as follows: Sc+R_1-Rs, rectangular, centered just proximad of mid-cell, partly overlapping proximal portion of macule in Rs-M1, extending proximad along Rs nearly to macule of basal loop; Rs-M_1 semi-rectangular, centered just

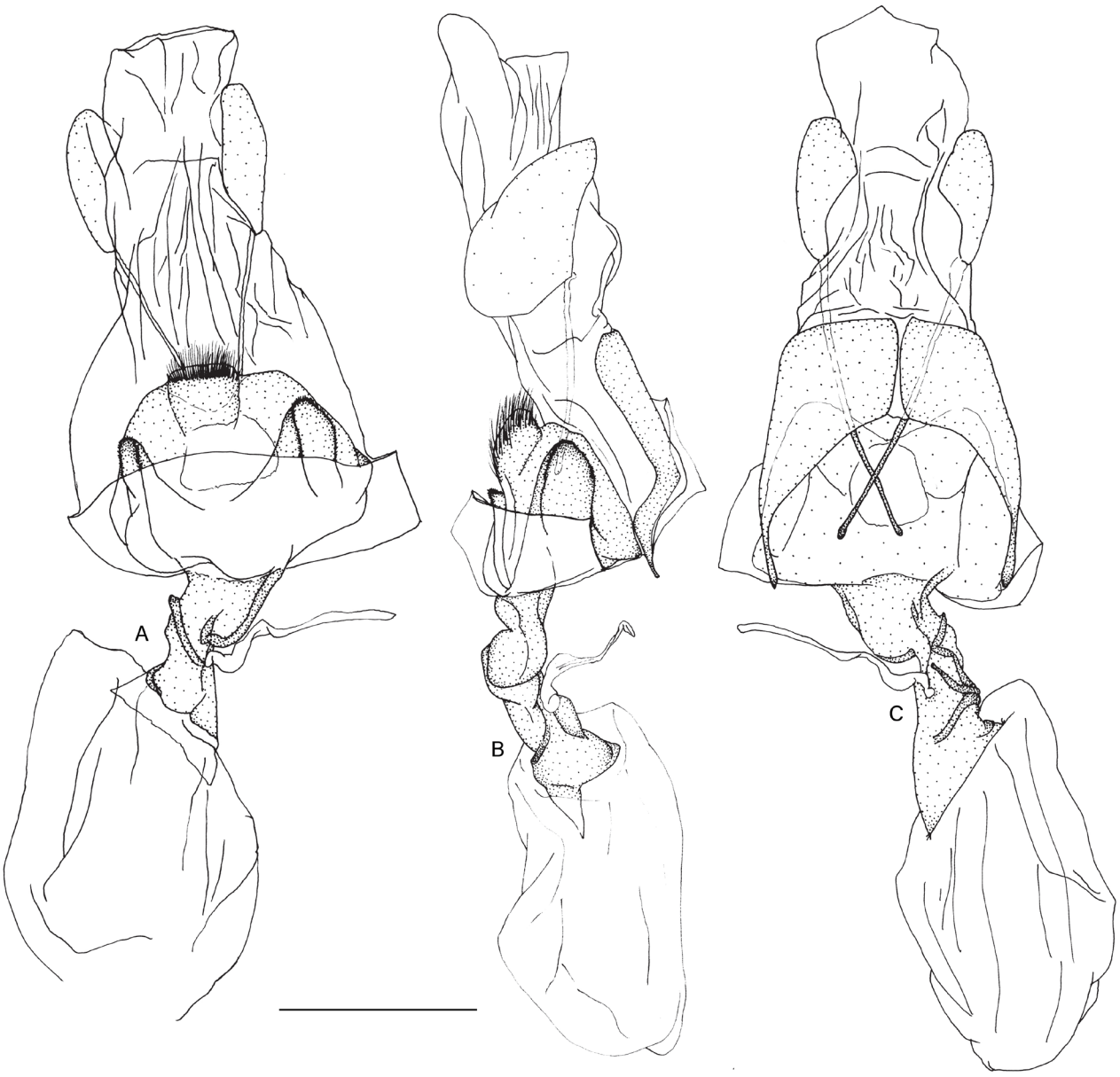

Figure 6. Female genitalia of *Hesperia uncas nadineae* **ssp. nov.** paratype, from Hwy. 57, 18 mi SE Saltillo, 7000', Coahuila, Mexico, 19-IX-1977, collected by William W. McGuire, Riley J. Gott dissection number RG0389. A) Ventral; B) right-lateral; C) dorsal views. Scale = 1.0 mm.

proximad of mid-cell, extending distad along M_1 to macule in M_1-M_3; M_1-M_3 irregular, centered in distal 4/5 of cell, extending proximad along M_3 to overlap distal portion of macule in M_3-CuA_1; M_3-CuA_1 semi-rectangular, centered near mid-cell, extending distad along CuA_1 and overlapping most of macule in CuA_1-CuA_2; CuA_1-CuA_2 semi-rectangular, centered near mid-cell, extending distad along CuA_2 and overlapping most of macule in CuA_2-2A; CuA_2-2A semi-rectangular in anterior 1/2 of cell and vaguely defined in posterior half of cell, with considerable gray-green overscaling; basal loop consisting of two macules: smaller, triangular, in basal 1/4 of Sc+R_1-Rs; larger, semi-triangular to triangular, spanning across posterior half of distal end of discal cell into base of CuA_1-CuA_2 then into anterior half of CuA_2-2A; dark gray-brown patches bordering macular band as follows: Sc+R_1-Rs extensive, proximad and distad of macule; Rs-M_1 extensive, especially proximad of macule; M_1-M_3 reduced to only a trace of dark gray-brown scales both distad and proximad, separated mid-cell by white vein-like streak; M_3-CuA_1 and CuA_1-CuA_2 extensive, proximad (extending to macule of basal loop) and distad of macule, CuA_2-2A present only in anterior half of cell cephalad of white vein-like streak, extensive proximad (extending to macule of basal loop), diffused distad with gray-green scales; very small area proximad of larger macule of basal loop in caudal half of distal end of discal cell; fringe gray at base, grading to slightly paler distad; conspicuously darker at vein ends.

Dorsal hirsute vestiture predominantly greenish with scattered dark gray and cream; patch of short, white scales dorsad of eye, then extensive white caudad of eye to venter; palpi mixture of beige, blue-green and black scales on dorsum, white with slight beige tint on venter, third segment black; antenna gray on dorsum, venter white, club abruptly constricted to apiculus from basal nudum segments, club orange proximad, black distad on dorsum, venter white grading to black distad; nudum dark ochreous-brown, 10-11 segments; thorax dorsally with blue-green and grayish vestiture, whitish to gray-white ventrally with scattered beige scales, legs gray proximad, very pale gray distad; abdomen gray dorsally with scattered beige scales, paler at segments, laterally and ventrally pale gray with beige tint distad.

Female genitalia (Fig. 6A-C, 9C): Apophyses posteriores reaching caudal edge of lateral carinae; apophyses anteriores connected to lamella postvaginalis with membranous integument; lamella postvaginalis sclerotized, broad; mesal furrow present; central carinae present; lateral carinae well developed, forming concave, bowl-like structures; ductus bursae sclerotized, caudal chamber expanded to right of midline in ventral view; ductus seminalis arising at midpoint between caudal edge of corpus bursae and anterior edge of lamella postvaginalis; corpus bursae spherical.

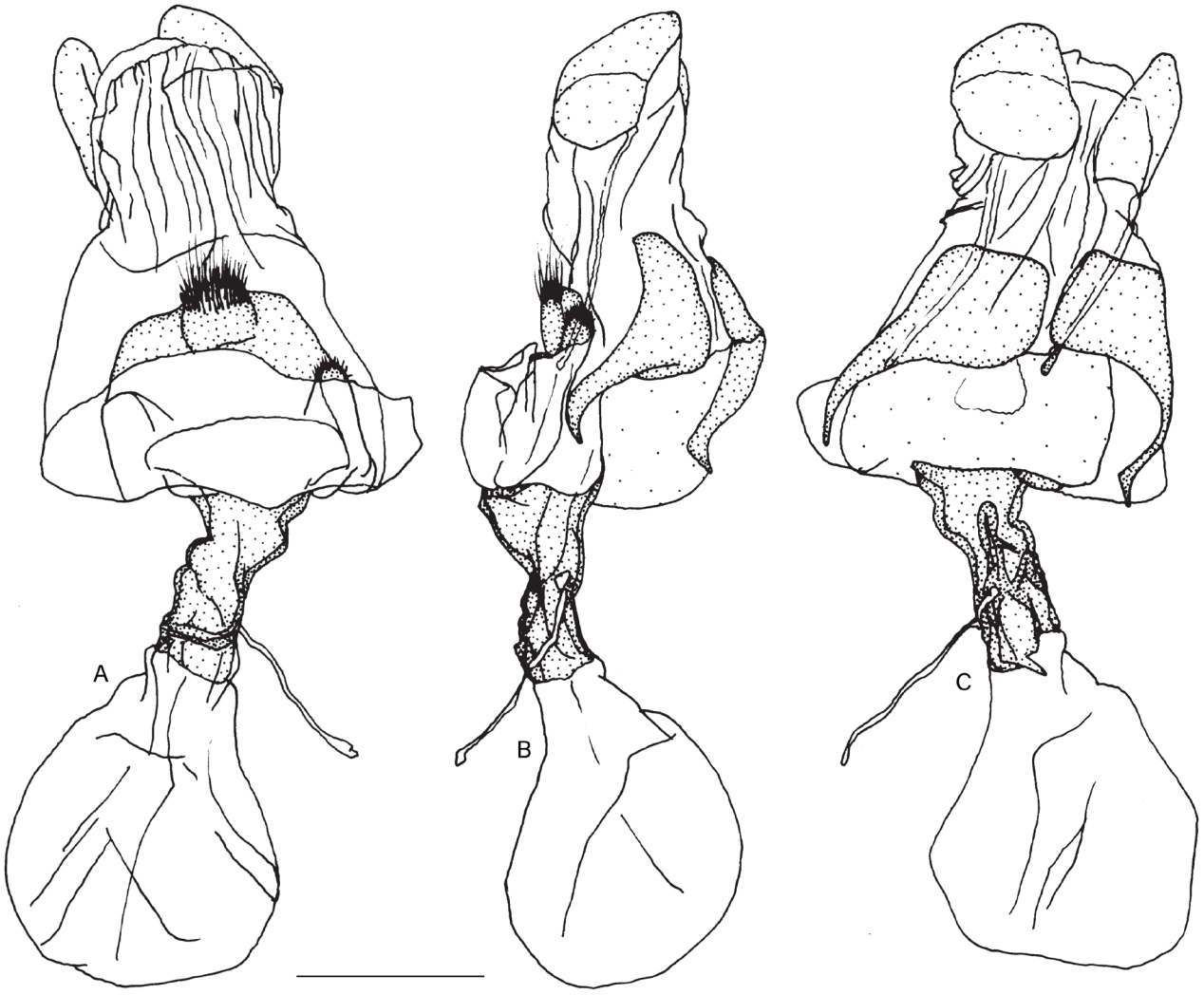

Figure 7. Female genitalia of *Hesperia uncas gilberti* paratype, from 2 mi SE Los Reyes, 7400', State of México, Mexico, 2-VII-1952, collected by E. E. Gilbert & C. D. MacNeill, Riley J. Gott dissection number LEP-78560. A) Ventral; B) right-lateral; C) dorsal views. Scale = 1.0 mm.

Specimens examined. Holotype male with the following labels: white, printed: / MEXICO / Coahuila: Hwy. 57, / 18 mi SE Saltillo / 7000' el., 19.ix.77 /; white, printed: / Wm. W. McGuire / collector /; white, printed: / Collection of / William W. McGuire /; white, printed: / FSCA / Florida State Collection / of Arthropods /; white, printed: / MGCL/FLMNH / Specimen no. / 35643 /; red, printed: / HOLOTYPE / *Hesperia uncas nadineae* / A. Warren, Gott & McGuire /. The Holotype is deposited at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville (MGCL). Eight male paratypes and three female paratypes, same data as holotype (MGCL). Additional paratypes from the same locality, 22-IX-1977, Wm. W. McGuire (7 males, 1 female, MGCL). Additional paratypes from: MEXICO: COAHUILA: Hwy. 57, vic. Los Pinos, 19.6 mi SE Saltillo, 7000', 19-IX-1977, Wm. W. McGuire (4 males, MGCL); same locality, 29-IV-1978, Wm. W. McGuire & Nadine M. McGuire (1 female, MGCL); Los Pinos, 19 mi SE Saltillo, 6800', 24-IX-1976, J. A. Powell & J. A. Chemsak (1 female, MGCL); MEXICO: NUEVO LEÓN: Hwy. 58, km. 79, W of Galeana Junction, 2030 m, vic. 24°41'00"N, 100°07'41"W, 13-IX-2007, Paul A. Opler (1 male, ADW).

Type locality. The site where most of the type series was collected, 18 miles southeast of Saltillo, along Hwy. 57, is situated in the vicinity of current junction of Hwy. 57D and Hwy. 112, at or near 25°20'57"N, 100°47'39"W. This is approximately 1.5 kilometers north of the "Los Pinos" area along Hwy. 57D, where *H. u. nadineae* **ssp. nov.** has also been found. The habitat at the time consisted of an open woodland dominated by *Juniperus* L., *Pinus* L. and *Quercus* L. Specimens were collected in open areas within a few hundred yards of the roadside.

Etymology. *Hesperia u. nadineae* **ssp. nov.** is named in honor of Nadine M. McGuire, an avid Lepidoptera collector involved in the initial discovery of this subspecies as well as numerous additional *Hesperia* and Megathyminae from throughout North America and Mexico, and the wife of William W. McGuire, M.D., whose collecting and research is focused on Hesperiidae.

Distribution and phenology. To date, *H. u. nadineae* **ssp. nov.** is known from arid habitats in the western part of the Sierra Madre Oriental of southeastern Coahuila and the far western part of central Nuevo León (Fig. 10). The southernmost known population in Nuevo León, southwest of Galeana Junction along Hwy. 58, is situated 100 kilometers southeast of the population centered around the type locality in southeastern Coahuila, suggesting that additional populations in this region are likely to exist. Likewise, the locality for *H. u. nadineae* **ssp. nov.** in

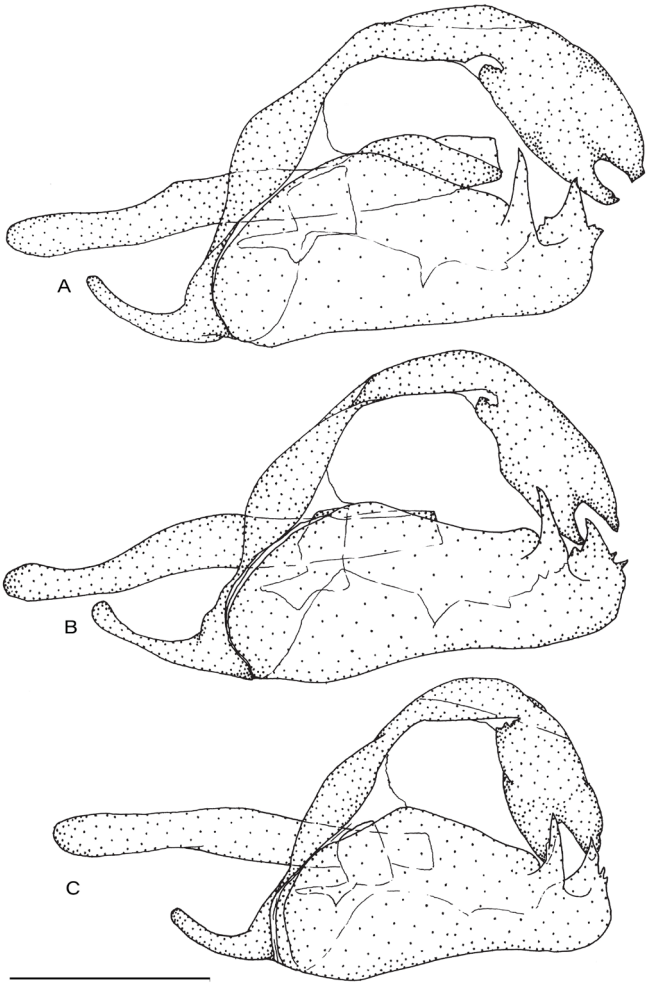

Figure 8. Male genitalia, in left-lateral view, of three subspecies of *Hesperia uncas*. A) *Hesperia u. lasus* from Nat. For. Rd. 61, 1/2 mi W Parker Cyn., San Rafael Valley, Santa Cruz County, Arizona, USA, 31-V-1981, collected by James P. Brock, Riley J. Gott dissection number RG0385; B) *H. u. uncas* from Dog Cyn., Guadalupe Mts. N.P., Culberson Co., Texas, USA, 8-9-VIII-2000, collected by Charles Bordelon & Ed Knudson, Riley J. Gott dissection number RG0387; C) *H. u. nadineae* **ssp. nov.** from Hwy. 57, 18 mi SE Saltillo, 7000', Coahuila, Mexico, 22-IX-1977, collected by William W. McGuire, Riley J. Gott dissection number RG0390. Scale = 1.0 mm.

Nuevo León is situated approximately 550 kilometers north-northwest of the northernmost known record of *H. u. gilberti* at its type locality in the State of México. All but one of the known specimens of *H. u. nadineae* **ssp. nov.** were collected in September, although the female from late April indicates that there are likely two annual broods, with flights in the spring and late summer-fall.

Biogeography. *Hesperia u. nadineae* **ssp. nov.** appears to be endemic to arid habitats on the west slope of the Sierra Madre Oriental in northeastern Mexico. This area is well known for a high degree of endemism in plants and animals (*e.g.*, Luna *et al*., 2004; Salinas-Rodríguez *et al*., 2017).

Diagnosis and discussion. *Hesperia u. nadineae* **ssp. nov.** differs from *H. u. gilberti*, the most similar *H. uncas* subspecies, in its more pointed forewing shape, especially pronounced in males, its somewhat thicker forewing stigma, its tawnier dorsal coloration, and in details of the ventral color and pattern; the white highlighting along wing veins is better defined on *H. u. nadineae* **ssp. nov.** than on *H. u. gilberti*, the dark areas on the ventral hindwing are larger and paler, but not as well-defined on *H. u. nadineae* **ssp. nov.** as they are on *H. u. gilberti*, and the ventral ground color of *H. u. nadineae* **ssp. nov.** is grayer and greener than that of *H. u. gilberti*.

As detailed above, adults of both *H. u. uncas* and *H. u. lasus* are on average considerably larger than those of *H. u. nadineae* **ssp. nov.**, and are paler fulvous above. The ventral hindwing of *H. u. nadineae* **ssp. nov.** is most similar to *H. u. uncas*, with a gray-green ventral coloration (though grayer than in *H. u. uncas*) and a broad postmedian band that contrasts strongly with the ground color.

The male and female genitalia examined of *H. u. lasus*, *H. u. uncas*, and *H. u. nadineae* did not differ structurally in geographically correlated patterns associated with the distribution of each taxon, but instead most variation observed is attributed to individuals. Two consistent differences noted in male genitalia among the three subspecies (Fig. 8) include the decrease in size from *H. u. lasus* (Fig. 8A) to *H. u. uncas* (Fig. 8B) to *H. u. nadineae* **ssp. nov.** (Fig. 8C), and the angle between the gnathos and saccus becoming more acute as size decreases from subspecies to subspecies, with *H. u. lasus* (Fig. 8A) having the widest angle and *H. u. nadineae* **ssp. nov.** (Fig. 8C) having the narrowest among the taxa examined. In females, the caudal chamber (Fig. 9) varies in size among individuals as noted previously by MacNeill (1964) and Burns (1987), and is not considered to be consistent within the subspecies examined. Although the male genitalia of *H. u. gilberti* were not directly examined, illustrations from MacNeill (1964) show similar genitalic morphology to *H. u. nadineae* **ssp. nov.**; we did not detect any prominent differences between the female genitalia of *H. u. gilberti* (Fig. 7) and *H. u. nadineae* **ssp. nov.** (Fig. 6). Limited genitalic differences observed among specimens examined and the gradual decrease in male genitalic size from northern to southern localities, which corresponds with overall adult size, supports the placement of *H. u. nadineae* **ssp. nov.** as a subspecies-level taxon.

Hesperia u. nadineae **ssp. nov.** and *H. u. gilberti* are clearly closely related, and future research could find that they are part of a long, gradual cline, should additional populations of *H. uncas* be found in the roughly 550 kilometers of terrain separating currently known populations of the two taxa. Nevertheless, the more pointed forewings, broader forewing stigma, and elements of the ventral color and pattern of *H. u. nadineae* **ssp. nov.** suggest some influence from *H. u. uncas*, where these traits are even better expressed. In this sense, the discovery of *H. u. nadineae* **ssp. nov.** further supports the subspecific status afforded to *H. u. gilberti*, as originally assigned by MacNeill (1964), despite his reservations.

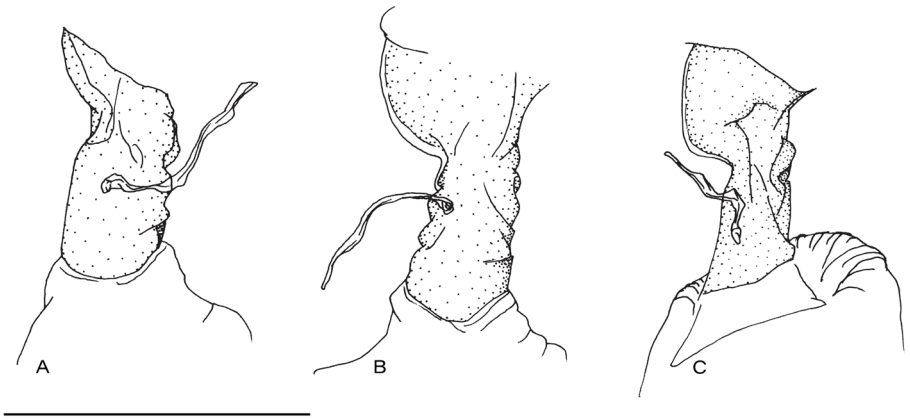

Figure 9. Female genitalia of three subspecies of *Hesperia uncas* depicting right-lateral view of ductus bursae, showing variation of the caudal chamber. A) *Hesperia u. lasus* from Rt. 82, 1 mi E of Sonoita, Santa Cruz County, Arizona, USA, collected by E. C. Olson, Riley J. Gott dissection number RG0383; B) *H. u. uncas* from 15 mi N and 7 mi W Van Horn, Hudspeth County, Texas, USA, collected by Jack L. Harry, Riley J. Gott dissection number RG0386; C) *H. u. nadineae* **ssp. nov.** from Hwy. 57, 18 mi SE Saltillo, 7000', Coahuila, Mexico, 19-IX-1977, collected by William W. McGuire, Riley J. Gott dissection number RG0389. Scale = 1.0 mm.

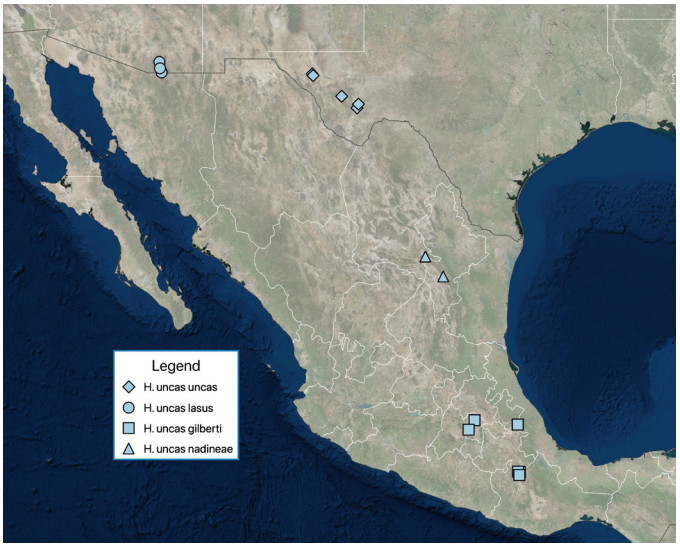

Figure 10. Distribution of *Hesperia uncas* subspecies in Mexico and adjacent parts of the United States.

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