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in the United States of America and Canada

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Taxonomic notes on velvet ants of the genus *Timulla* Ashmead, 1899 (Hymenoptera: Mutillidae) in the United States of America and Canada

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Abstract. The exclusively New World velvet ant genus *Timulla* Ashmead, 1899 (Hymenoptera: Mutillidae: Mutillinae: Trogaspidiini) contains 180 species and ten subspecies. Most of these species are known from a single sex, and the validity of the subspecies has not been evaluated since their original description in 1937 and 1938. The *Timulla* fauna of the United States of America includes thirty species and eight subspecies, and the fauna of Canada includes three species. The faunas of these two countries were critically studied with the following results. Out of the eight total subspecies, seven were found to be structurally identical to and sympatric with the nominate subspecies. The subspecific differences were limited to cuticle and/or setal coloration in males and intergrades between them were found in several cases. With the senior synonym listed first, seven subspecies-level synonymies are proposed, which include: *Timulla barbiger* (Bradley, 1916) = *T. barbiger rohweri* Mickel, 1937, **new synonym**; *T. dubitata* (Smith, 1855) = *T. dubitata fugitiva* Mickel, 1937, **new synonym**; *T. hollensis* (Melander, 1903) = *T. hollensis melanderi* Mickel, 1937, **new synonym**; *T. ocellaria* Mickel, 1937 = *T. ocellaria rufidorsa* Mickel, 1937, **new synonym**; *T. suspensa* (Gerstaecker, 1874) = *T. suspensa jonesi* Mickel, 1937, **new synonym**, = *T. suspensa sonora* Mickel, 1937, **new synonym**; *T. vagans* (Fabricius, 1798) = *T. vagans rufinota* Mickel, 1937, **new synonym**. The final remaining subspecies, *Timulla navasota coahuila* Krombein, 1951, is raised to a full species, *Timulla coahuila* Krombein, 1951, **new status**, based on its unique female morphology. Also, four new sex associations are proposed, which include: *Timulla barbata* (Fox, 1899) = *T. wileyae* Mickel, 1937, **new synonym**; *T. euterpe* (Blake, 1879) = *T. compressicornis* Mickel, 1937, **new synonym**; *T. neobule* Mickel, 1937 = *T. nicholi* Mickel, 1937, **new synonym**; *T. subhyalina* Mickel, 1937 = *T. dubitatiformis* Mickel, 1937, **new synonym**. The former species, *T. dubitatiformis*, which was previously known only from females, is here recognized as being a morphologically-conservative complex of species; its synonymy with *T. subhyalina* effectively associates the remaining male-based members of the *Timulla ocellaria* species-group with it as well, which includes *Timulla hollensis* (Melander, 1903), *T. kansana* Mickel, 1937, *T. ocellaria* Mickel, 1937, *T. rufosignata* (Bradley, 1916), *T. sayi* (Blake, 1871), *T. subhyalina* Mickel, 1937, and *T. tolerata* Mickel, 1937. Further, two species-level synonymies are proposed, which include: *Timulla dubitata* (Smith, 1855) = *T. murcia* Mickel, 1938, **new synonym**; *T. vagans* (Fabricius, 1798) = *T. huntleyensis* Mickel, 1937, **new synonym**. Finally, *Timulla cyllene* (Cameron, 1894) is newly recorded in the United States of America from the state of Arizona.

Key words. Aculeata, Müllerian mimicry, Mutillinae, phoretic copulation, Trogaspidiini, wasps.

ZooBank registration. urn:lsid:zoobank.org:pub:891E0C92-B8BF-4487-84D4-42EB2254AF4A

Introduction

The velvet ant genus *Timulla* Ashmead, 1899 (Hymenoptera: Mutillidae: Mutillinae: Trogaspidiini) is endemic to the New World and is the only representative of the subfamily Mutillinae in the Americas (Mickel 1933; Waldren et al. 2023). The genus was comprehensively revised in two parts by the mutillidologist Clarence Mickel: the fauna of United States and Canada (Mickel 1937a) and the fauna of Mexico, Central America, South America, and the Caribbean Islands (Mickel 1938); an additional contribution covering the Mutillidae in the Massimiliano Spinola collection (including *Timulla*) was published by Mickel (1937b). The genus currently includes 180 species and ten subspecies (Pagliano et al. 2020), with most species being known from a single sex due to the extreme sexual dimorphism common to mutillids (Mickel 1937a, 1938). Nine of the ten subspecies that Mickel (1937a, 1938) proposed were based exclusively on differences in coloration of cuticle and/or setae in a single sex (Eight based on

male coloration and one based on female coloration). Only one of the subspecies was supported by morphology in the female sex only: *Timulla navasota nebulosa* Mickel, 1937, presently known as *T. navasota coahuila* Krombein, 1951 due to primary homonymy in the former name (Mickel 1937a, 1938; Krombein 1951).

A relatively significant amount of progress has been made on the Neotropical *Timulla* fauna since Mickel (1938), with the addition of two new species (Casal 1957, 1961) and twenty-seven sex associations (Giner Mari 1944; Mickel 1952, 1961; Casal 1957, 1961; Evans 1972; Cambra and Quintero 1993; Bartholomay et al. 2017; Cambra et al. 2018). The relatively large number of recent sex associations in *Timulla* is primarily due to their mating behavior in which males physically transport females by flight and/or foot during their mating event by carrying them with their mandibles; this behavior was termed mandibular phoretic copulation by Waldren et al. (2020). Mutillids which practice this type of mating behavior typically have a prolonged mating period which allows for them to be collected while *in copula* more frequently than other mutillids in which the mating period may last only seconds *in situ* (Waldren et al. 2020).

The Nearctic *Timulla* fauna, however, has received less attention than the Neotropical fauna despite having significantly fewer species and a greater amount of material available for study; only two taxonomic actions have been published regarding the Nearctic species since Mickel (1937a). First, *Timulla navasota nebulosa* Mickel, 1937 was given a new name, *Timulla navasota coahuila* Krombein, 1951, due to it being a primary objective homonym of *Timulla fortuita nebulosa* Mickel, 1935 (Mickel 1935b, 1937a; Krombein 1951). Second, Krombein (1953) associated and described the previously unknown female of *Timulla rufosignata* (Bradley, 1916). The *Timulla* fauna of the United States of America and Canada is currently represented by thirty species (thirteen known from both sexes, eleven known from the male only, and six known from the female only) and eight subspecies (Mickel 1937a, 1938; Krombein 1951, 1953, 1979; Pagliano et al. 2020). The objective of this contribution is to examine the validity of the eight subspecies occurring in the United States of America, to propose four new sex associations, to propose two species-level synonymies, and to document a new country record.

Materials and Methods

The phylogenetic species concept *sensu* Wheeler and Platnick (2000) was used for this study. These authors define a species as “... the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states.”

Tagma terminology follows Michener (1944): the mesosoma and metasoma refer to the apparent thorax and abdomen; the mesosoma includes the thorax plus the first true abdominal segment, referred to as the propodeum. The mesosternal area (= ‘mesosternum’ of Mutillidae researchers) refers to the ventral surfaces of the male mesopleura that are sometimes bilaterally armed with a tubercle, denticle, spine, carina(e), and/or process. The abbreviations MS1, MS2, etc., refer to the first, second, etc., metasomal segments (with MS1 being the second true abdominal segment). The abbreviations T1, T2, etc., refer to the first, second, etc., metasomal terga, and S1, S2, etc., refer to the first, second, etc., metasomal sterna. The abbreviations F1, F2, etc., refer to the first, second, etc., antennal flagellomeres. The scutellar area as defined by Bartholomay et al. (2018) is the region apparently composed of both mesoscutellar and metascutellar tissue that is found between the propodeal spiracles on the mesosomal dorsum in females. The scutellar scale is a transverse carina or lamella found anteromedially in this scutellar area in females.

The material examined in this study (4,012♂ and 3,526♀ *Timulla* specimens; 7,538 in total) or referenced herein is deposited in the following seventy-five entomological collections (abbreviations primarily based on Evenhuis (2023)):

- AMNH** American Museum of Natural History, New York, New York, USA.
- ANSP** Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA.
- ASUHIC** Hasbrouck Insect Collection, University of Arizona, Tempe, Arizona, USA.
- AUEM** Auburn University Entomology Museum, Auburn, Alabama, USA.
- BPBM** Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
- CASC** California Academy of Sciences, San Francisco, California, USA.
- CLEV** Cleveland Museum of Natural History, Cleveland, Ohio, USA.

CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
CNC	Canadian National Collection, Ottawa, Ontario, Canada.
CSCA	California State Collection of Arthropods, Sacramento, California, USA.
CSUC	Colorado State University, Fort Collins, Colorado, USA.
CUIC	Cornell University Insect Collection, Ithaca, New York, USA.
DEBU	University of Guelph Insect Collection, Guelph, Ontario, Canada.
DGMC	Donald G. Manley Collection, Florence, South Carolina, USA.
EBCC	Estación de Biología “Chamela,” Universidad Nacional Autónoma de México, San Patricio, Jalisco, Mexico.
EMEC	Essig Museum of Entomology, University of California, Berkeley, California, USA.
ENMU	Natural History Museum, Eastern New Mexico University, Portales, New Mexico, USA.
EMUS	Entomology Museum, Utah State University, Logan, Utah, USA.
ESUW	University of Wyoming, Laramie, Wyoming, USA.
FHSM	Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas, USA.
FMNH	Field Museum of Natural History, Chicago, Illinois, USA.
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA.
GCWC	George C. Waldren Collection, Houston, Texas, USA.
INHS	Illinois Natural History Survey, Champaign, Illinois, USA.
ISUI	Iowa State University, Ames, Iowa, USA.
KSUC	Kansas State University, Manhattan, Kansas, USA.
LSAM	Louisiana State Arthropod Museum, Louisiana State University, Baton Rouge, Louisiana, USA.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
MEM	Mississippi Entomology Museum, Mississippi State University, Starkville, Mississippi, USA.
MSBA	Museum of Southwestern Biology, Arthropod Division, University of New Mexico, Albuquerque, New Mexico, USA.
MSUC	Michigan State University, East Lansing, Michigan, USA.
MTEC	Montana State University, Bozeman, Montana, USA.
NCSM	North Carolina State University Insect Collection, Raleigh, North Carolina, USA.
NHMD	Statens Naturhistoriske Museum [= Natural History Museum of Denmark], Copenhagen, Denmark.
NHMUK	The Natural History Museum, London, UK.
NMNH	National Museum of Natural History, Washington, District of Columbia, USA.
NMSU	New Mexico State University, Las Cruces, New Mexico, USA.
OMNH	Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma, USA.
OSAC	Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA.
OSEC	K. C. Emerson Museum, Oklahoma State University, Stillwater, Oklahoma, USA.
OSUC	C. A. Triplehorn Insect Collection, Ohio State University, Columbus, Ohio, USA.
PCYU	Packer Collection, York University, Toronto, Ontario, Canada.
PERC	Department of Entomology, Purdue University, West Lafayette, Indiana, USA.
PMAE	Royal Alberta Museum, Edmonton, Alberta, Canada.
PMNH	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.
PSUC	Frost Entomological Museum, Pennsylvania State University, University Park, Pennsylvania, USA.
ROME	Royal Ontario Museum, Toronto, Ontario, Canada.
SDMC	San Diego Natural History Museum, San Diego, California, USA.
SDSU	Severin-McDaniel Collection, South Dakota State University, Brookings, South Dakota, USA.
SEMC	Snow Entomological Museum Collection, University of Kansas, Lawrence, Kansas, USA.
SFAC	Stephen F. Austin State University, Nacogdoches, Texas, USA.
SHSU	Sam Houston State University, Huntsville, Texas, USA.
TAMU	Texas A & M University, College Station, Texas, USA.
TTUZ	Natural Science Resource Laboratory, Museum of Texas Tech University, Lubbock, Texas, USA.
UAAM	The Arthropod Museum, Department of Entomology, University of Arkansas, Fayetteville, Arkansas, USA.
UAIC	University of Arizona Insect Collection, Tucson, Arizona, USA.
UCDC	R. M. Bohart Museum of Entomology, University of California, Davis, California, USA.
UCFC	University of Central Florida Collection of Arthropods, Orlando, Florida, USA.
UCMC	University of Colorado Museum, Boulder, Colorado, USA.
UCMS	University of Connecticut, Storrs, Connecticut, USA.
UCRC	Entomology Research Museum, Department of Entomology, University of California, Riverside, California, USA.
UGCA	University of Georgia Collection of Arthropods, Athens, Georgia, USA.

UKIC	University of Kentucky, Department of Entomology, Lexington, Kentucky, USA.
ULQC	Université Laval, Quebec City, Quebec, Canada.
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA.
UMRM	W. R. Enns Entomology Museum, University of Missouri, Columbia, Missouri, USA.
UMSP	University of Minnesota Insect Collection, St. Paul, Minnesota, USA.
UNAM	Universidad Nacional Autónoma de México, Mexico City, Mexico.
UNSM	University of Nebraska State Museum, Lincoln, Nebraska, USA.
UTIC	University of Texas Insect Collection, Austin, Texas, USA.
VTEC	Entomology Collection, Virginia Tech University, Blacksburg, Virginia, USA.
WFBM	W. F. Barr Entomological Collection, University of Idaho, Moscow, Idaho, USA.
WIRC	University of Wisconsin Insect Research Collection, Madison, Wisconsin, USA.
WSU	Maurice T. James Entomological Collection, Washington State University, Pullman, Washington state, USA.
ZMHB	Museum für Naturkunde [= Natural History Museum], Berlin, Germany.

Results

Timulla barbata (Fox, 1899)

(Fig. 1)

Mutilla barbata Fox 1899: 272. Type ♂ (ANSP).

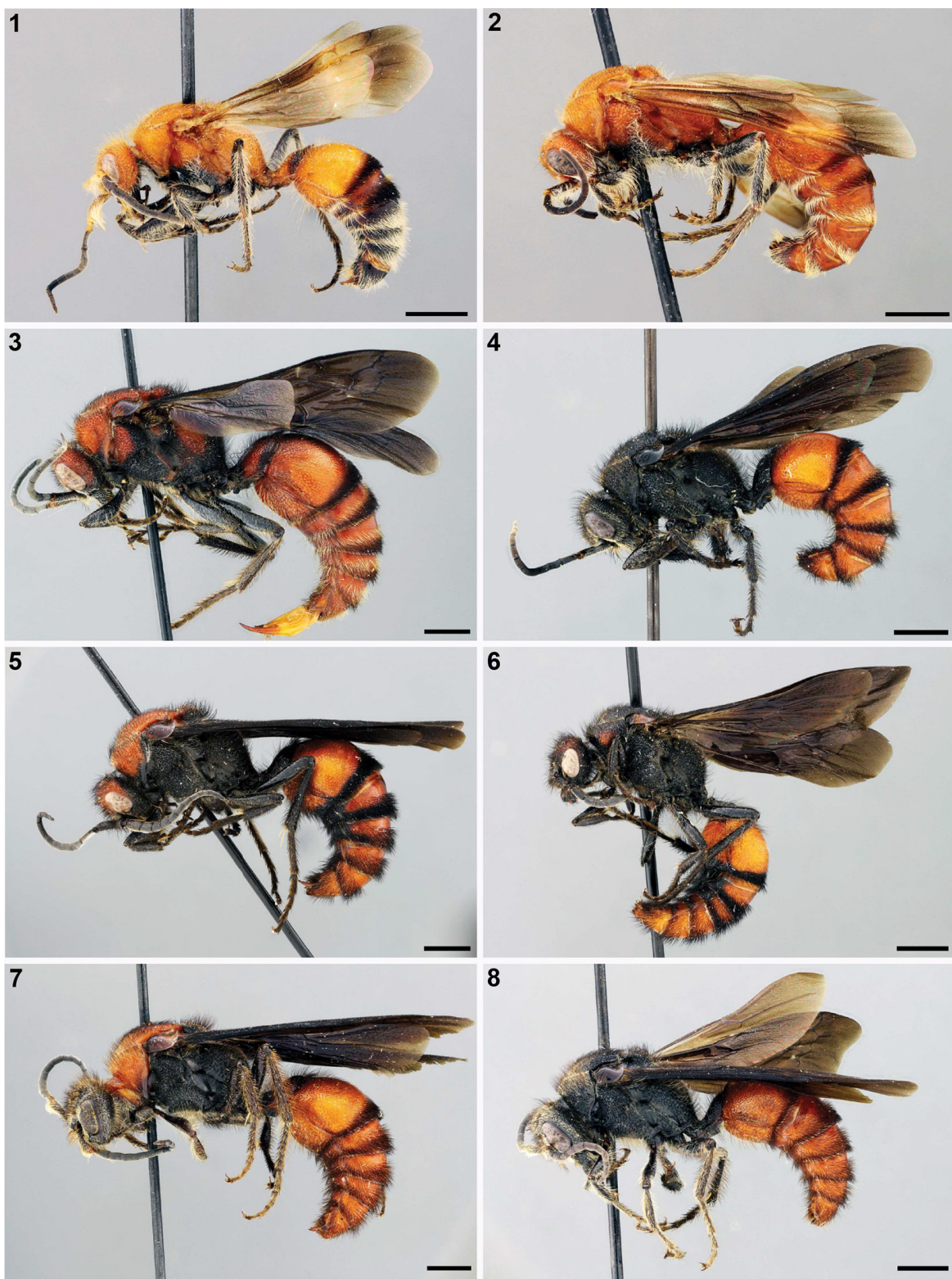
Timulla (*Timulla*) *wileyae* Mickel 1937a: 41. Holotype ♀ (UMSP). **New synonym.**

Remarks. The males of *Timulla barbata* (Fox, 1899) and *Timulla ornatipennis* (Bradley, 1916) are unique in *Timulla* in that they have banded wings, and their bodies are colored similarly to the females of the pompilid genus *Psorthaspis* Banks, 1911 that occur in the southeastern United States (Fig. 1 and 2; pers. obs.). These males also share the following combination of characters: the scape is ventrally covered with long whitish setae, F1 is more or less ventrally concave, the clypeus is relatively flattened and mostly impunctate, the mandible is ventrobasally armed with a tooth, the pygidial process is Y-shaped, S2 has an apical transverse carina/ridge present, and S6–S8 are armed with a lateral tubercle. Bradley (1916) described *Mutilla* (*Timulla*) *ornatipennis* from both sexes, with the holotype being a mating pair practicing mandibular phoretic copulation (Bradley 1916; Waldren et al. 2020). The female of *T. barbata*, however, remains unknown.

The female of *Timulla ornatipennis* (Bradley, 1916) is morphologically nearly identical with the female-based species *Timulla wileyae* Mickel, 1937. These females share the following combination of characters: the mesosoma is nearly parallel-sided and medially weakly emarginate in dorsal view, a scutellar scale is present, the pygidial plate is irregularly rugose in sculpture, and the clypeus has a prominent median tubercle present. The only two apparent morphological differences between these females are T2 being entirely orange with the anterior ovate setal patches absent in *T. ornatipennis* and T2 is entirely blackish with the anterior ovate setal patches present in *T. wileyae*.

Timulla barbata and *T. wileyae* are both known from the southeastern USA mostly west of the Mississippi River (Mickel 1937a). Both species have been collected in Latimer County, Oklahoma, at Camp Maxey, Texas, and in Nacogdoches, Texas. The record at Camp Maxey involves both sexes being collected in the same flight-intercept trap. The close relationship based on morphology between the males of *T. barbata* and *T. ornatipennis*, and the females of *T. wileyae* and *T. ornatipennis*, coupled with the overlap in distribution between the male-based species *T. barbata* and the female-based species *T. wileyae* with three cases of them being collected in the same county or city (and even the same trap), is considered strong evidence that the two are opposite sexes of the same species. As a result, *Timulla wileyae* Mickel, 1937 is here considered a **new synonym** of *Timulla barbata* (Fox, 1899).

Material examined (*Timulla barbata*) (10♂). **Non-type(s): USA: Oklahoma: Latimer Co.:** Oct.1988, K. Stephan (1♂–FSCA); Jun.1988, K. Stephan (1♂–FSCA); Aug.1988, K. Stephan (3♂–FSCA); Sep.1988, K. Stephan (3♂–FSCA). **Texas: Lamar Co.:** Camp Maxey, 16.Jun.–21.Jul.2003, W. Godwin, “Tallgrass, FIT #80” (1♂–SHSU–SHSUE016576). **Nacogdoches Co.:** Nacogdoches, 30.Sep.1959, R. Eubanks (1♂–EMUS).



Figures 1–8. Lateral habitus of *Timulla* males. 1) *Timulla barbata* (Fox, 1899). 2) *Timulla ornatipennis* (Bradley, 1916). 3) *Timulla dubitata dubitata* (Smith, 1855). 4) *Timulla dubitata fugitiva* Mickel, 1937. 5) *Timulla euterpe* (Blake, 1879). 6) *Timulla euterpe* (Blake, 1879). 7) *Timulla vagans rufinota* Mickel, 1937. 8) *Timulla vagans vagans* (Fabricius, 1798). Scale line = 2.0 mm.

Material examined (*Timulla wileyae*) (6♀). Non-type(s): USA: Oklahoma: *Latimer Co.*: Jan.1983, K. Stephan (1♀–DGMC); Apr.1983, K. Stephan (1♀–DGMC); May.1983, K. Stephan (1♀–DGMC); Mar.1988, K. Stephan (1♀–FSCA); Red Oak, 5 mi. W, 21.May.1977, K. Stephan (1♀–FSCA). **Texas:** *Lamar Co.*: Camp Maxey, 16.Jun.–21.Jul.2003, W. Godwin, “Tallgrass, FIT #80” (1♀–SHSU–SHSUE016551). *Nacogdoches Co.*: Nacogdoches, 10.Apr.1965, A. Reyer (1♀–EMUS).

In total, 28♂ and 96♀ of *Timulla barbata* (Fox, 1899) were examined (CNC, DEBU, DGMC, FSCA, GCWC, INHS, LSAM, MCZ, MSUC, NCSM, OMNH, OSEC, PERC, SEMC, SFAC, SHSU, TAMU, UMRM).

Timulla barbiger (Bradley, 1916)

Mutilla (Timulla) barbiger Bradley 1916: 206. Holotype ♂ (ANSP).

Timulla (Timulla) barbiger rohweri Mickel 1937a: 58. Holotype ♂ (NMNH). **New synonym.**

Timulla bargibera [sic] bargibera [sic]: Menard and Mitchell 2013: 74. Misspelling.

Timulla bargibera [sic] rohweri: Menard and Mitchell 2013: 74. Misspelling.

Remarks. *Mutilla (Timulla) barbiger* Bradley, 1916 was described from a single male specimen from Dallas, Texas (Bradley 1916). Mickel (1937a) described the unknown female of *T. barbiger*, as well as a new subspecies, *Timulla barbiger rohweri* Mickel, 1937, from only males. Mickel described this subspecies as follows: “Male.— Exactly like typical *barbiger* in the form of the scape and its pubescent brush, clypeus, tegulae, glabrous area and Y-shaped carina of last tergite, the tubercles of the sixth and seventh sternites, and the carinae of the hypopygium; differs in having the anterior fourth to third of the second abdominal tergite black, the second sternite almost entirely black, and the front, vertex, pronotum, mesonotum, scutellum, tegulae and the abdomen above and beneath (except the first tergite, first sternite and second sternite with sparse, erect, pale pubescence) all with erect and appressed, fulvous pubescence.” Mickel (1937a) treated all females as *T. barbiger barbiger*, suggesting there were no sufficient differences to enable associating a female with the male-based subspecies *T. barbiger rohweri* among the material he examined. One female Mickel (1937a) identified as *T. barbiger barbiger* was collected at the same date and location as a male *T. barbiger rohweri* (July 10, 1933 in Boise City, Oklahoma). Additionally, Mickel (1937a) recorded *T. barbiger rohweri* from western Kansas and extreme western Oklahoma, and *T. barbiger barbiger* also from western Kansas, extreme Western Oklahoma, eastern Texas, South Dakota, and the southeastern United States. There was no geographic distinction between the subspecies at the time of description in addition to being structurally identical.

Similar to Mickel, I have been unable to find any structural differences between both sexes of these subspecies either. Remarkably, two *T. barbiger rohweri* specimens were collected in Belle Glade, Florida in 1955 that have some or all of the metasomal terga apically fringed with orange-red setae. These specimens are well outside the known range of *T. barbiger rohweri* in the western Great Plains. One specimen is an intermediate between *T. barbiger barbiger* and *T. barbiger rohweri*, with T2 apically fringed with blackish setae, T3 apically fringed with black setae except medially with red-orange setae, and the remaining terga have red-orange setae. This situation is similar to that in *Timulla huntleyensis* Mickel, 1937 (see *Timulla vagans* (Fabricius, 1798) section below).

Based on the structural uniformity of both subspecies, the apparent uniformity of females, and the overlap in distribution, *Timulla barbiger rohweri* Mickel, 1937 is here considered a **new synonym** of *Timulla barbiger* (Bradley, 1916).

Material examined (*Timulla barbiger barbiger*) (1♂). Non-type(s): USA: Georgia: *Fulton Co.*: Atlanta, 24.Jun.1936, P.W. Fattig (1♂–EMUS).

Material examined (*Timulla barbiger rohweri*) (1♂). Holotype: USA: Kansas: *Unknown*: Unknown, Snow (1♂–NMNH–USNMENT 01545785).

Material examined (*Timulla barbiger barbiger/rohweri intermediates*) (2♂). Non-type(s): USA: Florida: *Palm Beach Co.*: Belle Glade, 15.Jul.1955, C.E. Seiler, “*Vigna sinensis*” (2♂–DGMC).

In total, 126♂ and 99♀ of *Timulla barbiger* (Bradley, 1916) were examined (AMNH, AUEM, CASC, CMNH, CSUC, CUIC, DEBU, DGMC, EMEC, ENMU, FHSM, FMNH, FSCA, GCWC, INHS, KSUC, LSAM, MCZ, MEM, MSUC, NCSM, NMNH, OMNH, OSAC, OSEC, PSUC, PERC, SEMC, SFAC, TAMU, TTUZ, UAAM, UAIC, UCDC, UCRC, UGCA, UMMZ, UMRM, UNSM, WIRC).

***Timulla coahuila* Krombein, 1951, new status**

Timulla (*Timulla*) *navasota nebulosa* Mickel 1937a: 29, pl. II, fig. 7 and 9. Holotype ♂ (UMSP). Junior primary homonym of *Timulla* (*Trogaspidia*) *fortuita nebulosa* Mickel 1935b: 263 according to Krombein (1951: 771).

Timulla (*Timulla*) *navasota coahuila* Krombein 1951: 771. New name for *Timulla* (*Timulla*) *navasota nebulosa* Mickel, 1937 due to being preoccupied by *Timulla* (*Trogaspidia*) *fortuita nebulosa* Mickel, 1935 as a junior primary homonym. *Timulla navasota cohahuila* [sic]: Pagliano et al. 2020: 267. Misspelling.

Remarks. In the remarks of his description of *Timulla navasota nebulosa* Mickel, 1937, Mickel (1937a) noted for the female: “*Nebulosa* differs from *navasota* in having the thorax more strongly narrowed posteriorly and in the much darker color of the abdomen, tibiae, and tarsi.” It is surprising that Mickel (1937a) considered the strongly posteriorly-narrowed “thorax” (*i.e.*, mesosoma) to be a subspecies-level character, as the relative widths of the female mesosoma in dorsal view were considered to be an important species-level character by Mickel (1937a, 1938) for other species of *Timulla*. I also consider this to be an important species-level character. Based on the unique mesosomal shape in dorsal view of females of *T. navasota coahuila* and *T. navasota navasota*, the former subspecies is given **new status** as a full species, *Timulla coahuila* Krombein, 1951.

Material examined (*Timulla navasota coahuila*) (1♀). Non-type(s): USA: Texas: Jeff Davis Co.: Fort Davis, 6–10 mi. W on TX-166, 5000 ft., 15–23.Jul.1948, H.E. Evans (1♀–MCZ–MCZ-ENT 00709355).

Material examined (*Timulla navasota navasota*) (2♀). Non-type(s): USA: Texas: Cameron Co.: Brownsville, 08.May.1935, J.N. Knull (1♀–OSUC–OSUC 0098496). Hidalgo Co.: 30.Mar.1960, D.J. & J.N. Knull (1♀–OSUC–OSUC 0098498).

In total, 253♂ and 45♀ of *Timulla coahuila* Krombein, 1951 were examined (AMNH, ASUHIC, AUEM, CASC, CNC, CSCA, CUIC, DGMC, EMUS, FMNH, GCWC, INHS, LSAM, MCZ, MSBA, NMNH, NMSU, OSAC, OSUC, PMNH, ROME, SEMC, TAMU, TTUZ, UAIC, UCDC, UCFC, UCRC, UMMZ, UTIC, WFBM, WIRC, WSU).

In total, 46♂ and 8♀ of *Timulla navasota* (Bradley, 1916) were examined (AMNH, CASC, CSUC, CUIC, DGMC, EMUS, GCWC, INHS, KSUC, MCZ, MEM, NMNH, OSAC, OSUC, SEMC, SFAC, SHSU, TAMU, UAIC, UGCA, UTIC).

***Timulla cyllene* (Cameron, 1894)**

Mutilla cyllene Cameron 1894: 266, pl. XIII, fig. 4–6. Lectotype ♂ and paralectotype ♀ (NHMUK). Lectotype designated by Mickel (1938: 643).

Remarks. A male and female practicing phoretic copulation were collected at Peña Blanca Canyon in Arizona, which represents a new record of this species in the United States. *Timulla cyllene* was previously only known from the Mexican states of Colima, Guerrero, Jalisco, and Veracruz (Mickel 1938).

Material examined (*Mutilla cyllene*) (1♂2♀). Paralectotype: MEXICO: Guerrero: Chilpancingo, Sep., H.H. Smith (1♀–NHMUK–NHMUK 010577202). Non-type(s): USA: Arizona: Santa Cruz Co.: Peña Blanca Canyon, 03.Sep.1968, W.J. Hanson, “Malaise trap” “Utah State University Intermountain Insect Survey” (1♂1♀–EMUS).

In total, 45♂ and 21♀ of *Timulla cyllene* (Cameron, 1894) were examined (AMNH, ANSP, ASUHIC, BPBM, CASC, CNC, CSCA, CUIC, DGMC, EBCC, EMUS, GCWC, MCZ, NHMD, NHMUK, NMNH, TAMU, UAIC, UCDC, UNAM).

***Timulla dubitata* (Smith, 1855)**

(Fig. 3 and 4)

Mutilla dubitata Smith 1855: 60. Type ♀ (NHMUK).

Mutilla dubiatta [sic]: Blake 1886: 201. Misspelling.

Timulla (*Timulla*) *dubitata fugitiva* Mickel 1937a: 39, pl. I, fig. 6. Holotype ♂ (UMSP). **New synonym.**

Timulla (*Timulla*) *murcia* Mickel 1938: 653, pl. 4, fig. 61. Holotype ♀ (CUIC). **New synonym.**

Remarks. Mickel (1937a) described *Timulla dubitata fugitiva* Mickel, 1937 as follows: “Male.—Exactly like the subsp. *dubitata* except the head and thorax entirely black; emargination of mandibles, form of clypeus, elongate, glabrous area and Y-shaped carina of last tergite, tubercles of fifth and sixth sternites, and carinae of seventh

sternite and hypopygium, all the same as in subsp. *dubitata*. Length, 17 mm.” Regarding the females of *T. dubitata fugitiva*, in his remarks for *T. dubitata dubitata*, Mickel (1937a) noted: “I have attempted to find some morphological character in the females which would separate them into groups having the same geographical distribution as the two subspecies of male, but have been unsuccessful. The females appear to me to be uniform throughout the entire geographic range.” The two subspecies of *T. dubitata* are represented in Fig. 3 and Fig. 4.

Additionally, there was no geographic distinction between the subspecies in Mickel (1937a), as he reported specimens of both subspecies from Georgia, Maryland, New Jersey, Oklahoma, Texas, and Virginia (Mickel 1937a). After Mickel’s revision, both subspecies and intergrade specimens were collected in Kill Devil Hills, North Carolina during the same collecting event in 1959 by D. G. Shappirio; one intergrade specimen of *T. dubitata fugitiva* has the pronotum laterally with red cuticle (pronotum elsewhere entirely black), another specimen with the vertex transversely with red cuticle (head elsewhere entirely black) and the mesoscutum with both black and red cuticle, and another specimen with the vertex transversely with red cuticle (head elsewhere entirely black) and the scutellum entirely with black cuticle. Further, both subspecies were also collected in Latimer County, Oklahoma in apparently the same flight-intercept trap in 2002. Based on the subspecies being structurally identical in both sexes, the existence of intergrade specimens, and having an overlap in distribution, *Timulla dubitata fugitiva* Mickel, 1937 is here considered a **new synonym** of *Timulla dubitata* (Smith, 1855).

Another taxon described by Mickel (1938), *Timulla murcia* Mickel, 1938, was based on a single female specimen collected in Santa Rosa, Mexico by the dipterist C. H. T. Townsend. Only the city and country were provided on the collection label, and there are numerous cities in Mexico named Santa Rosa. Townsend arrived in south Texas in November of 1894 and spent a month of fieldwork in northern Mexico to gather information on the boll weevil; the holotype of *T. murcia* was collected on December 7, 1894 (Townsend 1895; Evenhuis et al. 2015). Townsend did some of his fieldwork in the city of San Juan Allende in Coahuila (Townsend 1895), and there is a city 100 km southwest of it named Santa Rosa [de Múzquiz] in which Townsend possibly collected the holotype (Neal Evenhuis pers. comm.). Mickel (1938) considered *T. murcia* to be related to *Timulla dubitata* and he differentiated the two species in *T. murcia* having “the abdominal tergites for the most part black and black pubescent, the anterior margin of the posterior marginal band on the second tergite sinuate instead of angulately dilated at the middle, and the head and dorsum of thorax less strongly punctate.” I consider these diagnostic characters of *T. murcia* to fall within the range of variation of *T. dubitata* which is widely distributed throughout the eastern United States, although no records of *T. dubitata* have been found from Mexico.

Specimens of *T. dubitata* from south Texas were unknown to Mickel (1937a), which may have factored into his decision to treat *T. murcia* as a distinct species. I have found several *T. dubitata* among collections from Atascosa, Bexar, Kenedy, and Willacy Counties in south Texas; the type locality of Santa Rosa [de Múzquiz], Coahuila is consequently within reason for *T. dubitata* although perhaps at the edge of its distribution. The Nearctic species *Timulla leona* was also collected by C.H.T. Townsend at the same date and locality of Santa Rosa as the holotype of *T. murcia*; *Timulla leona* shares much of its distribution in the United States with *T. dubitata* (Mickel 1937a) (Mickel identified this lone *T. leona* specimen, housed at OSEC, as *Timulla tyro* Mickel, 1937 in Mickel (1938)). Based on shared morphology and close geographic distribution, *Timulla murcia* Mickel, 1938 is here considered a **new synonym** of *Timulla dubitata* (Smith, 1855).

Material examined (*Timulla dubitata dubitata*) (5♂ and 8♀). Non-type(s): USA: North Carolina: Dare Co.: Kill Devil Hills, 01–10.Sep.1959, D.G. Shappirio (4♂–UMMZ). **Oklahoma:** Latimer Co.: Aug. 2002, K. Stephan, “FIT” (1♂–TAMU–TAMU–ENTO X1074853). **Texas:** Atascosa Co.: Poteet, 8 mi. N, 14.Oct.1994, A.W. Hook, J.L. Neff, & O. Hernandez (1♀–UTIC); Poteet, 12 mi. N, 14.Oct.1994, A.W. Hook, J.L. Neff, & O. Hernandez (2♀–UTIC); Somerset, 7 mi. S, 27.Jun.1995, J.E. Wappes (1♀–TAMU–TAMU–ENTO X1087280). **Bexar Co.:** 30.Aug.1931, H.B. Parks (1♀–TAMU–TAMU–ENTO X1042949); 04.Oct.1931, H.B. Parks (1♀–TAMU–TAMU–ENTO X1041251). **Kenedy Co.:** Sarita, 19.Sep.1974, Gillaspay & Party (1♀–UAIC); 30.Aug.1975, Gillaspay & Party (1♀–UAIC).

Material examined (*Timulla dubitata fugitiva*) (16♂ and 1♀). Non-type(s): USA: North Carolina: Dare Co.: Kill Devil Hills, 01–10.Sep.1959, D.G. Shappirio (2♂–UMMZ). **Oklahoma:** Latimer Co.: Aug.1986, K. Stephan (3♂–FSCA); Sep.1986, K. Stephan (1♂–FSCA); Aug.1987, K. Stephan (2♂–FSCA); Aug.1988, K. Stephan (2♂–FSCA); Sep.1988 (1♂1♀ [*in copula*]–FSCA; 1♂–FSCA); Aug.1989, K. Stephan (1♂–FSCA); Jul. 2002, K. Stephan,

“FIT” (1♂–OMNH–OMNH-84696); Aug. 2002, K. Stephan, “FIT” (1♂–TAMU–TAMU-ENTO X1086410). **Texas:** Willacy Co.: Raymondville, 17.Apr.1952, Michener, Beamers, Wille, & LaBerge, “taken on *Monarda citriodora*” (1♂–SEMC).

Material examined (*Timulla dubitata dubitata/fugitiva intermediate*) (3♂). Non-type(s): USA: North Carolina: Dare Co.: Kill Devil Hills, 01–10.Sep.1959, D.G. Shappirio (3♂–UMMZ).

Material examined (*Timulla murcia*) (1♀). Holotype: MEXICO: [Coahuila]: Santa Rosa [de Múzquiz], 07.Dec.1894, C.H.T. Townsend (1♀–CUIC–HOLOTYPE Cornell U. no. 1810).

In total, 558♂ and 851♀ of *Timulla dubitata* (Smith, 1855) were examined (AMNH, AUEM, BPBM, CASC, CMNH, CNC, CSCA, CSUC, CUIC, DEBU, DGMC, EMUS, ENMU, FMNH, FSCA, GCWC, INHS, KSUC, LSAM, MCZ, MEM, MSUC, NCSM, NMNH, OMNH, OSAC, OSEC, OSUC, PCYU, PMAE, ROME, SDMC, SEMC, SFAC, SHSU, TAMU, UAAM, UAIC, UCDC, UCFC, UCRC, UGCA, UMMZ, UMRM, UNSM, UTIC, VTEC, WIRC).

***Timulla euterpe* (Blake, 1879)**

(Fig. 5 and 6)

Mutilla Euterpe Blake 1879: 249. Type ♀ (UMSP).

Timulla (Timulla) compressicornis Mickel 1937a: 59, pl. II, fig. 10. Holotype ♂ (NMNH). **New synonym.**

Remarks. The male-based species *Timulla compressicornis* Mickel, 1937 is closely related to *Timulla barbiger*a (Bradley, 1916), as both males lack a ventrobasal mandibular tooth and have a Y-shaped pygidial process with the arms of the Y as long as or longer than the stem. The female-based species *Timulla euterpe* (Blake, 1879) is closely related to the female of *T. barbiger*a, as females of both species have a remarkably similar mesosomal shape in dorsal view and a highly-reduced scutellar scale. Both *T. compressicornis* and *T. euterpe* share an overlap in distribution in the eastern United States and are only known from a single sex (Mickel 1937a). Since the publication of Mickel (1937a), both sexes have been collected in Gainesville, Florida and in Kill Devil Hills, North Carolina. Based on the close relationship in morphology with *T. barbiger*a and the two species known from a single opposite sex—*T. compressicornis* and *T. euterpe*—coupled with their overlap in distribution in the eastern United States, *Timulla compressicornis* Mickel, 1937 is here considered a **new synonym** of *Timulla euterpe* (Blake, 1879).

Lastly, three male specimens with a nearly entirely black head (vertex partly dark red) and a nearly entirely black mesosoma (pronotum with lateral dark red spot in one specimen) were discovered among the material examined (Fig. 6). Males typically have an orange-red front, vertex, pronotum, mesoscutum, and the scutellum anteriorly, with the remainder of the mesosoma being black (Fig. 5). These two types of color forms of *T. euterpe* are more or less similar to the color forms present in other species which were formalized with subspecies designations by Mickel (1937a) (i.e., *T. dubitata*, *T. hollensis*, *T. ocellaria*, and *T. vagans*). Discovery of *T. euterpe* males with a nearly entirely black head and mesosoma provides additional evidence that the subspecies of Mickel (1937a) are merely color forms within a species.

Material examined (*Timulla compressicornis*) (3♂). Holotype: USA: Louisiana: Cameron Par.: Johnson Bayou, 24.Aug.1906, J.D. Mitchell (1♂–NMNH–TypeNo. 50951 U.S.N.M.). **Non-type(s): USA: Florida:** Alachua Co.: Gainesville, 13.Jul.1948, P.W. Fattig (1♂–CUIC–PARATYPE Cornell U. No. 1514.2). **North Carolina:** Dare Co.: Kill Devil Hills, 01–10.Sep.1959, D.G. Shappirio (1♂–UMMZ).

Material examined (*Timulla compressicornis* with mostly black head and mesosoma) (3♂). Non-type(s): USA: Maryland: Calvert Co.: American Chestnut Land Trust, Warrior’s Rest Sanctuary, 38.536633°N 76.519667°W, 08–21.Jul.2008, M. Gates et al., “beach” “Malaise trap” (1♂–EMUS). **South Carolina:** Barnwell Co.: Aiken, 30–40 mi. S at Fourmile Branch, 16.Jul.1974, F. Howell & R. Matthews, “Savannah R. Proj.” “Malaise trap A” (1♂–DGMC; 1♂–EMUS).

Material examined (*Timulla euterpe*) (2♀). Non-type(s): USA: Florida: Alachua Co.: Gainesville, 16.May.1926, M.D. Leonard (1♀–CUIC). **North Carolina:** Dare Co.: Kill Devil Hills, 05.Jul.1950, K.V. Krombein (1♀–NMNH).

In total, 54♂ and 34♀ of *Timulla euterpe* (Blake, 1879) were examined (AMNH, AUEM, CUIC, DGMC, EMUS, FSCA, GCWC, INHS, LSAM, MCZ, MEM, MSUC, NCSM, NHMD, NMNH, OSAC, SEC, SFAC, TAMU, TTUZ, UCDC, UCFC, UGCA, UMMZ, UTIC, WIRC).

***Timulla hollensis* (Melander, 1903)**

Mutilla Sayi var. *hollensis* Melander 1903: 324. Holotype ♂ (MCZ).

Timulla (Timulla) hollensis melanderi Mickel 1937a: 101. Holotype ♂ (CUIC). **New synonym.**

Remarks. Mickel (1937a) described the male-based subspecies *Timulla hollensis melanderi* Mickel, 1937 and in the remarks for it noted: “Exactly like subsp. *hollensis* except the thorax entirely black, and the vertex and posterior part of scutellum with pale pubescence.” I have been unable to find any structural differences between these two subspecies either. Further, they both occur in the northeastern United States, and there is no geographic distinction between them. Both subspecies have been collected in Prince George’s County, Maryland. Based on their identical morphology and geographic overlap, *Timulla hollensis melanderi* Mickel, 1937 is here considered a **new synonym** of *Timulla hollensis* (Melander, 1903).

Additionally, Mickel (1937a) noted that the location of the type of *Mutilla sayi hollensis* Melander, 1903 was unknown to him. I located the holotype among non-type material at the Museum of Comparative Zoology (MCZ) labeled with the unique specimen identifier MCZ-ENT 00585864.

Material examined (*Timulla hollensis hollensis*) (2♂). **Holotype: USA: Massachusetts: Barnstable Co.:** Woods Hole, 13.Aug.1899 (1♂–MCZ–MCZ-ENT 00585864). **Non-type(s): USA: Maryland: Prince George’s Co.:** 09–17. Aug.2007 (1♂–UCDC–USGS–DRO 283478).

Material examined (*Timulla hollensis melanderi*) (2♂). **Holotype (*Timulla hollensis melanderi*): USA: Maryland: Baltimore Co.:** Baltimore, 09.Jul. (1♂–CUIC–HOLOTYPE Cornell U. no. 1518.1). **Non-type(s): USA: Maryland: Prince George’s Co.:** Bowie, 03.Sep.1996, R.D. Hennessey (1♂–EMUS).

In total, 54♂ and 0♀ of *Timulla hollensis* (Melander, 1903) were examined (AMNH, CASC, CMNH, CSUC, CUIC, DEBU, DGMC, EMUS, FMNH, FSCA, GCWC, MCZ, MEM, MSUC, NMNH, OSAC, OSUC, OMAE, SEMC, UCDC, UMMZ).

***Timulla neobule* Mickel, 1937**

Timulla (Timulla) neobule Mickel 1937a: 44. Holotype ♂ (NMNH).

Timulla (Timulla) nicholi Mickel 1937a: 47. Holotype ♀ (UMSP). **New synonym.**

Remarks. In his remarks for the female-based species *Timulla nicholi* Mickel, 1937, Mickel (1937a) stated: “This is probably the female of *neobule*. Mr. Nichol has collected both species at the same time and place, and the evidence gained by the process of elimination indicates that *nicholi* and *neobule* are probably opposite sexes of the same species.” The specimens Mickel (1937a) was referring to were collected in Mesa, Arizona. Additional specimens of both *T. nicholi* and *Timulla neobule* Mickel, 1937 have been collected in Bard, California by H. Ray on upland cotton, *Gossypium hirsutum* Linnaeus, 1758. Only three species of *Timulla* are known from California, all in the extreme southern part of the state: *Timulla neobule*, *T. nicholi*, and *T. tyro* Mickel, 1937 (Mickel 1937a; pers. obs.). The last species, *T. tyro*, was described by Mickel from both sexes, leaving *T. neobule* and *T. nicholi* as the only species of *Timulla* in California known from a single sex.

Both of these species (*T. neobule* and *T. nicholi*) are members of the *Timulla vagans* species-group which is diagnosed by the following combination of characters. Males have a prominent dorsal carina of the scape that often is densely setose apically, the mandible is ventrobasally armed with a tooth, the mesocoxae are armed with a triangular process, and the pygidial process is Y-shaped with the arms of the Y as long as or longer than the stem and the cuticle is concave between these arms. Females are diagnosed in having a transverse scutellar scale present and the pygidial plate is primarily granulate in sculpture.

Based on the overlap in distribution and shared membership in the *T. vagans* species-group, *Timulla nicholi* Mickel, 1937 is here considered a **new synonym** of *Timulla neobule* Mickel, 1937.

Material examined (*Timulla neobule*) (9♂). **Holotype: MEXICO: Sinaloa:** Los Mochis, 15.Jul.1922 (1♂–NMNH–USNMENT 01545829). **Non-type(s): USA: Arizona: Maricopa Co.:** Mesa, 11.Oct.1925, A.A. Nichol (1♂–EMUS). **California: Imperial Co.:** Bard, 20.Aug.1965, H. Ray, “ex *Gossypium hirsutum*” (1♂–SDMC); 27.Aug.1965, H. Ray, “ex *Gossypium hirsutum*” (1♂–CSCA; 1♂–SDMC); 30.Aug.1965, H. Ray, “ex *Gossypium hirsutum*” (1♂–CSCA); 03.Sep.1965, H. Ray, “ex *Gossypium hirsutum*” (1♂–SDMC); 16.Sep.1965, H. Ray, “ex *Gossypium hirsutum*” (1♂–CSCA); 27.Sep.1965, H. Ray, “ex *Gossypium hirsutum*” (1♂–SDMC).

Material examined (*Timulla nicholi*) (9♀). **Holotype:** USA: Arizona: Maricopa Co.: Mesa, 11.Oct.1925, A.A. Nichol (1♀-UMSP-Type specimen no. 87 Univ. of Minn.). **Non-type(s):** USA: California: Imperial Co.: Bard, 03.Sep.1965, H. Ray, "ex *Gossypium hirsutum*" (1♀-SDMC); 07.Sep.1965, H. Ray, "ex *Gossypium hirsutum*" (1♀-AMNH); 08.Sep.1965, H. Ray, "ex *Gossypium hirsutum*" (5♀-CSCA; 1♀-SDMC).

In total, 31♂ and 33♀ of *Timulla neobule* Mickel, 1937 were examined (AMNH, ASUHIC, CASC, CSCA, DGMC, EMEC, EMUS, MCZ, NMNH, SDMC, UAIC, UCDC, UCRC, UMSP, UNSM).

***Timulla ocellaria* Mickel, 1937**

Timulla (Timulla) ocellaria ocellaria Mickel 1937a: 91. Holotype ♂ (UMSP).

Timulla (Timulla) ocellaria rufidorsa Mickel 1937a: 93, pl. III, fig. 14. Holotype ♂ (NMNH). **New synonym.**

Remarks. Mickel (1937a) described the male-based subspecies *Timulla ocellaria rufidorsa* Mickel, 1937 and in the remarks for it noted: "Exactly like *ocellaria* subsp. *ocellaria* except the prothorax and the mesonotum ferruginous with pale pubescence, and the tegulae dark ferruginous." I have been unable to find any structural differences between these two subspecies either. Further, they both occur in the central/mid-eastern United States, and there is no geographic distinction between them. Both subspecies have been collected at the same time and location in Fort Knox, Kentucky and Tuttle, Oklahoma by the same collectors. Based on their identical morphology and overlap in geographic distribution, *Timulla ocellaria rufidorsa* Mickel, 1937 is here considered a **new synonym** of *Timulla ocellaria* Mickel, 1937.

Timulla ocellaria is one of the few nocturnal species of *Timulla* and males have very large ocelli (Mickel 1937a; pers. obs.). Remarkably, I have not seen any mating pairs of *T. ocellaria* among collections despite examining more than 900 males collected at lights.

Material examined (*Timulla ocellaria ocellaria*) (5♂). **Non-type(s):** USA: Kentucky: Hardin Co.: Fort Knox, 03.Jul.1953, R.D. Alexander (2♂-OSUC-OSUC 0098506, OSUC 0098509; 1♂-UAIC; 1♂-UMMZ). **Oklahoma:** Grady Co.: Tuttle, 02.Jul.2006, B. Baldwin, "UV Light" (1♂-EMUS).

Material examined (*Timulla ocellaria rufidorsa*) (20♂). **Holotype:** USA: Oklahoma: Bryan Co.: Durant, 01.Jul.1910, Hunter, "at light" (1♂-NMNH-USNMENT 01545802). **Non-type(s):** USA: Kentucky: Hardin Co.: Fort Knox, 03.Jul.1953, R.D. Alexander (1♂-OSUC-OSUC 0098523; 1♂-UMMZ). **Oklahoma:** Grady Co.: Tuttle, 02.Jul.2006, B. Baldwin, "UV Light" (17♂-EMUS).

In total, 944♂ and 0♀ of *Timulla ocellaria* Mickel, 1937 were examined (AMNH, CASC, CNC, CSCA, CSUC, CUIC, DGMC, EMEC, EMUS, FHSM, FMNH, FSCA, GCWC, INHS, LSAM, MCZ, MEM, MSUC, NMNH, OMNH, OSAC, OSEC, OSUC, PMNH, PERC, SEMC, TAMU, UAAM, UAIC, UCDC, UCMC, UCRC, UGCA, UKIC, UMMZ, UMRM, WIRC).

***Timulla subhyalina* Mickel, 1937**

Timulla (Timulla) subhyalina Mickel 1937a: 97, pl. III, fig. 16. Holotype ♂ (UMSP).

Timulla (Timulla) dubitiformis Mickel 1937a: 102. Holotype ♀ (NMNH). **New synonym.**

Remarks. Mickel (1937a) described the male-based subspecies *Timulla subhyalina* Mickel, 1937 from specimens from the north-central/northwestern United States and Canada. Additionally, Mickel (1937a) described the female-based species *Timulla dubitiformis* Mickel, 1937 from the central and eastern United States. In his remarks for the latter species, *T. dubitiformis*, Mickel (1937a) noted: "This female has an exceptionally wide distribution and no male of which the female is unknown has a similar distribution. I am of the opinion that one or all of the group of males including *rufosignata*, *tolerata*, *subhyalina*, *hollensis* subsp. *hollensis*, *hollensis* subsp. *melanderi*, and *sayi* represent the male sex. All of these have a more limited distribution than *dubitiformis*, and I have attempted without success to find some basis for separating the latter into geographical groups which could be correlated with the above males. The situation may be that the males have differentiated into geographical groups, while the females have remained stable; this has been found to be true of certain other species of Mutillidae both in the United States and the Philippine Islands. All that can be said at present is that the male will probably prove to be among those mentioned above." The male-based species that Mickel (1937a) referred to above, including *Timulla kansana* Mickel, 1937 and *T. ocellaria*, form a species-group which share the following

combination of characters: the clypeus is pentagonal and weakly concave, a ventrobasal mandibular tooth may be present or absent, the ocelli may or may not be enlarged, the mesosternal area is weakly armed with an obscure tubercle, and the pygidial process is Y-shaped with the arms of the Y short in length. This species-group is here referred to as the *Timulla ocellaria* species-group.

Krombein (1953) associated females that keyed to *T. dubitatiformis* with the male-based species *Timulla rufosignata* (Bradley, 1916) from Kill Devil Hills, North Carolina. Krombein (1953) differentiated the newly-recognized female of *T. rufosignata* from *T. dubitatiformis* as follows: “The four females taken in 1952 and the six females captured in 1948 and 1950 are conspecific, key to *dubitiformis* in Mickel’s key, and fall within the range of variation he ascribes to that species. They are quite constant in coloration, sculpture, vestiture, and differ from “*dubitiformis*” females of the metropolitan Washington area in having the last three tergites with ferruginous integument, the scutellar scale evanescent or absent, and the posterior surface of the propodeum more coarsely sculptured, with a few longitudinal ridges and a tendency toward the development of small asperites on the upper third. The Kill Devil Hills series differs from the type of *dubitiformis* from Boulder, Colorado in the same particulars.”

Mickel (1937a) attempted to find some distinction between specimens across the broad geographic distribution of *T. dubitatiformis* that could correspond with the more limited distributions of males of the *T. ocellaria* species-group. I attempted to do the same and in the end, I was unsuccessful like Mickel despite examining 286 *T. dubitatiformis* specimens. The characters that Krombein (1953) ascribes to the females he associated with *T. rufosignata* fall within the variation of *T. dubitatiformis* throughout its distribution. There is no apparent geographic pattern with the characters that Krombein (1953) emphasized. Krombein’s association, however, does confirm the relationship between *T. dubitatiformis* and members of the male-based *T. ocellaria* species-group. The type locality of *T. dubitatiformis* is Boulder, Colorado, and the only male-based species of the *T. ocellaria* species-group that occurs in Colorado is *T. subhyalina*. Further, the only other species of *Timulla* that occur in Colorado are *T. barbiger*, *T. grotei*, *T. oajaca*, *T. suspensa* and *T. vagans*, all of which are known from both sexes (Mickel 1937a; pers. obs.). To the northwest, the only species of *Timulla* that occur in Washington state are *T. dubitatiformis* and *T. subhyalina*. Based on shared membership in the *T. ocellaria* species-group and overlap in distribution, *Timulla dubitatiformis* Mickel, 1937 is here considered a **new synonym** of *Timulla subhyalina* Mickel, 1937.

This taxonomic action generates a challenge in that although I consider the holotype of *T. dubitatiformis* to be a synonym of *T. subhyalina*, not all *T. dubitatiformis* females *sensu* Mickel (1937a) can now be considered conspecific with *T. subhyalina* as they belong to other male-based species of the *T. ocellaria* species-group. I have labeled all *T. dubitatiformis* females (*sensu* Mickel (1937a)) that I have examined in collections as ‘*Timulla dubitatiformis*’ despite awareness of this name eventually being synonymized. Due to their apparent morphological uniformity, assigning the name ‘*Timulla ocellaria* species-group’ for females of the former species *T. dubitatiformis* is the suggested approach moving forward post-synonymy. All members of the *T. ocellaria* species-group are now effectively known for both sexes with the recognition that the former female-based species *T. dubitatiformis* is in reality a morphologically-conservative complex of species (with the males being *Timulla hollensis* (Melander, 1903), *T. kansana* Mickel, 1937, *T. ocellaria* Mickel, 1937, *T. rufosignata* (Bradley, 1916), *T. sayi* (Blake, 1871), *T. subhyalina* Mickel, 1937, and *T. tolerata* Mickel, 1937).

Material examined (*Timulla dubitatiformis*) (2♀). **Holotype:** USA: Colorado: Boulder Co.: Boulder, 26.May.1908, T.D.A. Cockerell (1♀–NMNH–USNM 01546530). **Non-type(s):** USA: Washington: Whitman Co.: Pullman, 08.Jul.1976, P.J. Landolt (1♀–FSCA).

Material examined (*Timulla subhyalina*) (5♂). **Non-type(s):** USA: Colorado: Sedgwick Co.: Julesburg, 20–27. Aug.2001, Irwin & Parker, “MT” (4♂–EMUS). **Washington:** Whitman Co.: Colton, 10 mi. S, 16.Sep.1982, W.J. Hanson (1♂–EMUS).

In total, 286♀ of *Timulla ocellaria* species-group females (i.e., *Timulla dubitatiformis* (*sensu* Mickel 1937a)) were examined (AMNH, ASUHC, AUEM, BPBPM, CASC, CMNH, CNC, CSUC, CUC, DEBU, DGMC, EMEC, EMUS, FHSM, FMNH, FSCA, GCWC, INHS, KSUC, LSAM, MCZ, MEM, MSUC, MTEC, NCSM, NMNH, OMNH, OSAC, OSEC, PMAE, PMNH, PERC, SDMC, SDSU, SEMC, TAMU, UAAM, UCMC, UGCA, UKIC, UMMZ, UMRM, UNSM, UTIC, WFBM, WIRC, WSU).

In total, 143♂ of *Timulla subhyalina* Mickel, 1937 were examined (AMNH, CMNH, CNC, CSCA, CSUC, CUIC, DGMC, EMUS, FHSM, FMNH, FSCA, GCWC, INHS, MCZ, MEM, MSUC, MTEC, NMNH, OSAC, OSEC, PMAE, PMNH, PERC, SDSU, UAIC, UCDC, UCMC, UCRC, UGCA, UMRM, UNSM, WFBM, WIRC, WSU).

***Timulla suspensa* (Gerstaecker, 1874)**

Mutilla suspensa Gerstaecker 1874: 299. Type ♀ (ZMHB).

Timulla (Timulla) suspensa sonora Mickel 1937a: 84, pl. III, fig. 15. Holotype ♀ and allotype ♂ (NMNH). **New synonym.**

Timulla (Timulla) suspensa jonesi Mickel 1937a: 90. Holotype ♂ (UMSP). **New synonym.**

Remarks. Mickel (1937a) described the subspecies *Timulla suspensa sonora* Mickel, 1937 based on a relatively large series of specimens with several pairs collected *in copula*. He differentiated it from the nominal subspecies, *Timulla suspensa suspensa* (Gerstaecker, 1874), as follows in the remarks for *T. suspensa sonora*: “I have compared female specimens of this subspecies with the holotype of *suspensa* Gerstaecker and find the only difference is in the color of the legs, in subspecies *suspensa* black, and in subspecies *sonora* ferruginous; in pattern of pubescence, sculpture and puncturation of body the two are identical; the color of the abdomen of the female varies from distinctly black to distinctly ferruginous; the series before me includes many intergrades between the two...” The male of *T. suspensa suspensa* is unknown. Female leg coloration was emphasized by Mickel (1938) for the Neotropical *Timulla* as a species-level character, although it was not always reliable, with females of some species having both bright red legs in some individuals and dark mahogany red legs in others, such as in the Mexican species *Timulla obscurella* Mickel, 1938 (Mickel 1938; pers. obs.). There is no geographic distinction between *T. suspensa sonora* and *T. suspensa suspensa*, as both are known from southeastern Arizona (Mickel 1937a). Based on their identical morphology and geographic overlap, *Timulla suspensa sonora* Mickel, 1937 is here considered a **new synonym** of *Timulla suspensa* (Gerstaecker, 1874).

A second subspecies was described by Mickel (1937a), namely *Timulla suspensa jonesi* Mickel, 1937, based on three males from Douglas, Arizona and five males from southern Texas, with the holotype being from Douglas, Arizona; the female is unknown. Mickel (1937a) differentiated the males of *T. suspensa jonesi* and *T. suspensa sonora* as follows: “Closely related to the male of subsp. *sonora* but differs in having the second abdominal sternite entirely ferruginous, the somewhat more dense, pale pubescence of the pronotum, and the slightly less reflexed postero-lateral angles of the clypeal glabrous area.” Variation within clypeal shape has been observed within species of *Timulla* (e.g., *Timulla rufogastra* (Lepelletier, 1845) in Mickel (1938)), as well as cuticle coloration in both males and females as discussed for other subspecies treated in this paper. Additionally, two of the specimens of *T. suspensa jonesi* were collected by W. W. Jones in Douglas, Arizona and one specimen by F. H. Snow at San Bernardino Ranch in Douglas, Arizona. Both of these collectors also collected specimens of the subspecies *T. suspensa sonora* at the same locality and month as *T. suspensa jonesi* (Mickel 1937). Thus, the subspecies are sympatric in Arizona.

However, five of the paratypes of *T. suspensa jonesi* were collected in south Texas (Mickel 1937a). I consider these Texas paratypes to belong to an undescribed species (Waldren in prep.). Further, I have females associated with these south Texas males which are distinctly different from females of *T. suspensa* in having the anterior whitish setal patches of T2 limited to the basal half of the sclerite rather than longitudinally spanning the entire length of T2 as in *T. suspensa*. Based on their identical morphology and geographic overlap in Douglas, Arizona, *Timulla suspensa jonesi* Mickel, 1937 is here considered a **new synonym** of *Timulla suspensa* (Gerstaecker, 1874).

Material examined (*Timulla (Timulla) suspensa jonesi* (Texas specimens are an undescribed species)) (2♂).

Paratype(s): USA: Texas: Bexar Co.: 23.Sep.1934, H.B. Parks (1♂–TAMU–TAMU-ENTO X1043037); **Victoria Co.:** Victoria, 19.Jun.1913, J.D. Mitchell (1♂–NMNH–ParatypeNo. 53395 U.S.N.M.).

Material examined (*Timulla (Timulla) suspensa sonora*) (2♂ and 2♀). Holotype: USA: New Mexico: Doña Ana Co.: [Las Cruces], Mesilla Park, Cockerell (1♀–NMNH–USNMENT 01545823). **Paratype(s): USA: Arizona: Cochise Co.:** Douglas, 08.Aug.1928, W.W. Jones (1♂–EMUS). **Non-type(s): USA: Arizona: Cochise Co.:** Sierra Vista, 16 mi. SE, 19.Aug.1972, R.R. Snelling (1♂1♀ [*in copula*]–EMUS).

In total, 482♂ and 491♀ of *Timulla suspensa* (Gerstaecker, 1874) were examined (AMNH, ASUHC, BPBM, CASC, CMNH, CNC, CSCA, CSUC, CUIC, DGMC, EMUS, ENMU, FMNH, FSCA, GCWC, KSUC, MCZ, MEM, MSBA, MSUC, NMNH, NMSU, OSAC, OSEC, OSUC, PCYU, SDMC, SEMC, TAMU, TTUZ, UAIC, UCDC, UCMC, UCRC, UGCA, UMMZ, UTIC, WFBM, WIRC, WSU).

Timulla vagans (Fabricius, 1798)

(Fig. 7 and 8)

Mutilla vagans Fabricius 1798: 282. Type ♀ (NHMD).

Mutilla hexagona Say 1836: 295. Type ♂ (lost or destroyed; refer to Mawdsley (1993)). Junior subjective synonym of *Timulla* (*Timulla*) *vagans* (Fabricius, 1798) according to Mickel (1937a: 66).

Mutilla ornativentris Cresson 1865: 438. Holotype ♀ (ANSP). Junior subjective synonym of *Timulla* (*Timulla*) *vagans* (Fabricius, 1798) according to Mickel (1937a: 66).

Mutilla Briaxus Blake 1871: 277. Type ♂ (ANSP). Junior subjective synonym of *Timulla* (*Timulla*) *vagans* (Fabricius, 1798) according to Mickel (1937a: 66).

Mutilla Canadensis Provancher 1887: 250. Type ♂ (ULQC, missing; refer to Gahan and Rohwer (1918: 103)). Junior primary homonym of *Mutilla canadensis* Blake, 1871 according to Dalla Torre (1897: 84). Junior subjective synonym of *Timulla* (*Timulla*) *vagans* (Fabricius, 1798) according to Mickel (1937a: 66).

Mutilla secunda Dalla Torre 1897: 84. New name for *Mutilla canadensis* Provancher, 1889 due to being preoccupied by *Mutilla canadensis* Blake, 1871 as a junior primary homonym. Junior subjective synonym of *Timulla* (*Timulla*) *vagans* (Fabricius, 1798) according to Mickel (1937a: 66).

Timulla (*Timulla*) *vagans rufinota* Mickel 1937a: 78. Holotype ♂ and allotype ♀ [*in copula*] (NMNH). **New synonym.**

Timulla (*Timulla*) *huntleyensi* [sic]: Mickel 1937a: 10. Misspelling.

Timulla (*Timulla*) *huntleyensis* Mickel 1937a: 82. Holotype ♂ (UMSP). **New synonym.**

Remarks. Mickel (1937a) described *Timulla vagans rufinota* Mickel, 1937 as follows: “Male.—Exactly like *vagans* except the pronotum and mesonotum entirely and the propodeum more or less, ferruginous. Length, 17 mm. Female.—Indistinguishable from *vagans*. Length, 9 mm.” The holotype and allotype are a pair that was collected practicing phoretic copulation, which is how Mickel was able compare the female of *T. vagans rufinota* with those of *T. vagans vagans* despite them being indistinguishable. Additionally, at the time of description, *T. vagans rufinota* was known only from Florida, while *T. vagans vagans* (Fabricius, 1798) was known from states besides Florida (Mickel 1937a). The two subspecies of *T. vagans* are represented in Fig. 7 and Fig. 8. New specimens have been discovered that challenge the geographic distinction between these subspecies. Specimens of both *T. vagans rufinota* and *T. vagans vagans* have been collected in Ames, Iowa and Fort Knox, Kentucky. Further, there is another specimen of *T. vagans rufinota* collected from the vicinity of Spring Green, Wisconsin, which is well inside the range of *T. vagans vagans* and far from the original known distribution of Florida (Mickel 1937a). Based on these subspecies being structurally identical and there being no geographic distinction between them, *Timulla vagans rufinota* Mickel, 1937 is here considered a **new synonym** of *Timulla vagans* (Fabricius, 1798).

Another taxon described by Mickel (1937a), *Timulla huntleyensis* Mickel, 1937, was considered as related to *Timulla grotei* (Blake, 1871) due to their similarity in coloration: both species have the metasomal segments covered with fulvous (*i.e.*, orange-red) setae. Mickel (1937a) differentiated the two species in *T. huntleyensis* having “larger ocelli, the hypopygial carinae dentiform posteriorly, more uniformly punctate second sternite, the black disk of second sternite and pale fuscous pubescence of the head and pronotum.” He also distinguished *T. huntleyensis* from *Timulla suspensa sonora* Mickel, 1937 “in the larger ocelli, darker pubescence of the head and pronotum, the greatly dilated scape with its dense brush of pubescence and the less developed lateral tubercles of the seventh sternite.” Another species, *Timulla vagans* (Fabricius, 1798), also differs from *T. grotei* and *T. suspensa sonora* in all of the characters Mickel used to distinguish *T. huntleyensis* from these two species (except for the black S2). The only apparent difference between *T. huntleyensis* and *T. vagans* is the coloration of the metasomal setae: orange-red in *T. huntleyensis* and blackish in *T. vagans*. Further, *T. huntleyensis* has most of S2 with blackish cuticle and *T. vagans* has S2 with orange-red cuticle.

The holotype of *T. huntleyensis* was collected in Huntley, Montana on August 23, 1915 along with four males of *T. vagans*. These *T. vagans* males do not differ in structure from *T. huntleyensis*. Additionally, one male of *T. huntleyensis* and two males of *T. vagans* were collected in Harrison, Nebraska on August 13, 1962 from the same

collecting event. Additionally, one male of *T. huntleyensis* and one male of *T. vagans* were both collected from Long Island, New York in 1929. A fourth specimen of *T. huntleyensis* is known from Morrill, Nebraska and a fifth specimen from Burrville, Tennessee. Based on the collection of both *T. huntleyensis* and *T. vagans* males in three different states at the same time and place, on being identical in structure, in having setal color differences similar to that observed in *T. barbiger* (orange-red to black setae), and in having S2 coloration differences similar to that observed in *T. suspensa* (blackish to orange-red cuticle), *Timulla huntleyensis* Mickel, 1937 is here considered a **new synonym** of *Timulla vagans* (Fabricius, 1798).

Material examined (*Timulla huntleyensis*) (5♂). **Holotype:** USA: Montana: Yellowstone Co.: Huntley, 23.Aug.1915 (1♂-UMSP). **Non-type(s):** Nebraska: Scotts Bluff Co.: Morrill, 07.Aug.1930, D.B. Whelan (1♂-UNSM); Sioux Co.: Harrison, 7 mi. N, 13.Aug.1962, J.G. & B.L. Rozen, "collected on *Helianthus*" (1♂-AMNH). **New York:** Unknown: Long Island, 1929 (1♂-INHS-INHS 209,995). **Tennessee:** Morgan Co.: Burrville, 17.Aug.1952, B. Benesh (1♂-FMNH).

Material examined (*Timulla vagans rufinota*) (8♂ and 1♀). **Holotype and allotype:** USA: Florida: Leon Co.: Centerville, 20.Jul., Hubbard, "taken in copulation" (1♂1♀ [*in copula*]-NMNH-USNMENT 01545788). **Non-type(s):** USA: Iowa: Story Co.: Ames, 22.Jul.1962 (5♂-UMRM). **Kentucky:** Hardin Co.: Fort Knox, 15.Jul.1952, R.D. Alexander (1♂-UMMZ). **Wisconsin:** Sauk Co.: Spring Green Prairie/TNC, N of Spring Green, 43.199320°N 90.059220°W, 01-07.Aug.2003, C.M. Brabant, "unbaited Townes Malaise trap in sand/oak barrens" (1♂-WIRC).

Material examined (*Timulla vagans vagans*) (18♂). **Non-type(s):** USA: Iowa: Story Co.: Ames, 05.Aug.1939, W. Buren (2♂-EMUS); 12.Aug.1939, W. Buren (1♂-EMUS); 13.Aug.1939, W. Buren (1♂-EMUS); 01.Aug.1940, W. Buren (1♂-EMUS). **Kentucky:** Hardin Co.: Fort Knox, 21.Jun.1953, R.D. Alexander (1♂-OSUC-OSUC 0098590; 1♂-CASC) 03.Jul.1953, R.D. Alexander (2♂-OSUC-OSUC 0098591, OSUC 0098592). **USA: Montana:** Yellowstone Co.: Huntley, 23.Aug.1915 (4♂-MTEC); 18.Aug.1942, C.R. Hunt, "on potatoes" (1♂-MTEC); 23.Jul.1917 (1♂-WFBM); 23.Aug.1915 (1♂-WFBM). **Nebraska:** Sioux Co.: Harrison, 7 mi. N, 13.Aug.1962, J.G. & B.L. Rozen, "collected on *Helianthus*" (2♂-AMNH). **New York:** Unknown: Long Island, 1929 (1♂-INHS-INHS 210,018).

In total, 1248♂ and 1562♀ of *Timulla vagans* (Fabricius, 1798) were examined (AMNH, AUEM, BPBPM, CASC, CLEV, CMNH, CNC, CSCA, CSUC, CUIC, DEBU, DGMC, EMEC, EMUS, ENMU, ESUW, FHSM, FMNH, FSCA, GCWC, INHS, ISUI, KSUC, LSAM, MCZ, MEM, MSBA, MSUC, MTEC, NCSM, NHMD, NMNH, NMSU, OMNH, OSAC, OSEC, OSUC, PMAE, PMNH, PSUC, PERC, ROME, SDMC, SDSU, SEMC, SFAC, SHSU, TAMU, UAAM, UAIC, UCDC, UCFC, UCMC, UCMS, UCRC, UGCA, UKIC, UMMZ, UMRM, UNSM, UTIC, VTEC, WFBM, WIRC, WSU).

Discussion

None of the color-based subspecies proposed by Mickel (1937a) have held up to close examination; only one of his subspecies was based on structure and it was discovered in this study to be a distinct species (*Timulla navasota coahuila*, now *T. coahuila*, **new status**). In each case for the seven color-based subspecies, the nominate subspecies is structurally identical with the non-nominate subspecies and they overlap in geographic distribution. Further, intergrades have been discovered for most subspecies. Each of Mickel's subspecies based on cuticle coloration corresponds to one of two color forms. Color form A involves the pronotum and mesoscutum entirely with orange cuticle (with the front, vertex, gena, scutellum, metanotum, mesopleuron, propodeum, and T1 often partly with orange cuticle) (Fig. 3, 5, 7). Color form B involves the head, mesosoma, and T1 with entirely black cuticle (Fig. 4, 6, 8). The following species exhibit both color forms and had two subspecies consequently recognized by Mickel (1937a): *T. dubitata*, *T. hollensis*, *T. ocellaria*, and *T. vagans*. Additionally, I have examined male specimens of *T. euterpe* and *T. rufosignata* that exhibit color form B when previously they were only known to exhibit color form A (Mickel 1937a) (refer to the *T. euterpe* section above and Fig. 6; the *T. rufosignata* specimens were collected in Pendleton, South Carolina and are housed at PMAE). The existence of both color forms in males of six species in the central and eastern United States suggests that geography-related mimicry is involved.

Mimicry in male mutillids has been little discussed, although Müllerian mimicry has been extensively investigated in females (Wilson et al. 2012, 2015, 2018). Müllerian mimicry in *Timulla* females was covered in Wilson et al. (2015), who grouped members of this genus, along with unrelated mutillids, into four mimicry rings: Eastern, Madrean, Red-headed *Timulla*, and Black-headed *Timulla*. The countries covered in this paper, the United States and Canada, are home to two of these mimicry rings regarding *Timulla*: the Eastern ring and the Red-headed *Timulla* ring. Generally, members of the Eastern ring occur in the central and eastern United States and Canada and involve the female mutillid being orange-red dorsally (Wilson et al. 2012, 2015). Members of the Red-headed *Timulla* ring mostly occur in the central United States and involve the head and mesosoma being orange-red dorsally and the metasoma being black dorsally (Wilson et al. 2015). Some species of *Timulla* have females that exhibit the coloration of both mimicry rings depending on the locality, such as *T. dubitata* and *T. vagans* (Mickel 1937a). Mickel (1937a) recognized these color differences in females, although he did not base subspecies on them due to intergrades being readily apparent.

Examination of 4,012 male *Timulla* specimens has revealed the existence of intergrades between subspecies and also significant geographic overlap between them which had led to the proposed synonymy in this contribution. Several species in the subfamily Sphaerophthalminae, such as *Dasymutilla ursus* (Fabricius, 1793) (= *Dasymutilla vesta* (Cresson, 1865), see Brothers et al. 2022), *Pseudomethoca sanbornii* (Blake, 1871), and *Sphaerophthalma pensylvanica* (Lepeletier, 1845), have males that also exhibit color forms A and B and have a similar distribution to these *Timulla* males (Mickel 1924, 1937a; Schuster 1958; Williams et al. 2012; pers. obs.). Further, each of these sphaerophthalmine species belongs to a separate tribe: Dasymutillini, Pseudomethocini, and Sphaerophthalmini, respectively (Brothers and Lelej 2017; Waldren et al. 2023). The existence of both color forms in species belonging to another subfamily among three tribes in the same geographic location is additional evidence that the Nearctic *Timulla* subspecies are merely cases of intraspecific color variation with a mimicry component. Additional study is needed to better characterize these male-specific mimicry rings in the central and eastern United States. Two subspecies now remain in *Timulla*, both of which are based on cuticular color differences in a single sex and both occur in the Neotropical region: *Timulla mediata pexsa* Mickel, 1938 and *Timulla prominens forreri* (Cameron, 1894). I have examined numerous specimens of both subspecies, and similar to the Nearctic subspecies, neither of these subspecies is supported by structure and geographic distribution. These remaining two subspecies will be evaluated in future studies.

Lastly, in addition to *Timulla*, the other two major genera that Clarence Mickel revised in the United States and Canada were *Dasymutilla* Ashmead, 1899 (Mickel 1928, 1936) and *Pseudomethoca* Ashmead, 1896 (Mickel 1924, 1935a). Mickel also included subspecies in these revisions that were primarily color-based. The remaining *Dasymutilla* subspecies were recently synonymized by Manley et al. (2020, 2022), and the single *Pseudomethoca* subspecies was recently synonymized by Williams (2023). None of Mickel's subspecies in the United States and Canada can be considered genuine subspecies as they are all sympatric and are primarily based on color differences with the existence of intergrades (with the exception being *Timulla coahuila*, **new status**). With the changes to *Timulla* herein, none of Mickel's mutillid subspecies remain valid in the United States and Canada. Rudolf Schuster, one of Mickel's graduate students, revised the two remaining major mutillid groups in the United States and Canada: the genus *Ephuta* Say, 1836 (Schuster 1951, 1956) and the tribe Sphaerophthalmini (Schuster 1947, 1958). Schuster also included subspecies in his revisions; however, his subspecies are primarily based on structural differences rather than coloration. Schuster's subspecies will probably be regarded as full species in the future in contrast to Mickel's color-based subspecies.

Conclusion

Before this study, thirty species and eight subspecies of *Timulla* were known from the United States of America (thirteen from both sexes, eleven from the male only, and six from the female only; Mickel 1937a, 1938; Krombein 1951, 1953, 1979; Pagliano et al. 2020). After the changes proposed herein and the discovery of *T. cyllene* in Arizona, twenty-eight species and zero subspecies are now known from the United States (twenty-five from both sexes, one from the male only, and two from the female only). The three remaining species known from a single sex are *Timulla contigua* Mickel, 1937 (female only; Texas), *Timulla euphrosyne* Mickel, 1937 (female only; Texas),

and *Timulla nitela* Mickel, 1937 (male only; Arizona). Two species of *Timulla* are now known from Canada from both sexes (*T. subhyalina* and *T. vagans*).

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