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TAXONOMIC REVISION OF THE GENUS *Timulla* ASHMEAD, 1899 OF PANAMA (HYMENOPTERA: MUTILLIDAE)

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ABSTRACT

The males of *Timulla chrysea* Mickel, 1938, *Timulla continua* Mickel, 1938, and *Timulla segesta* Mickel, 1938, and the female of *Timulla tumidula* (Cameron, 1894) are described and illustrated. *Timulla chrysea* and *T. tumidula* are reported for first time from Panama. The following synonyms are presented: *Timulla orthona* (Cameron, 1894), male, is a junior synonym of *Timulla lilea* (Cameron, 1894), female; *Timulla talus* (Cameron, 1894), male, is a junior synonym of *Timulla subrobusta* (Cameron, 1894), female. Observations on mating behavior for *Timulla runata* Mickel and *Timulla cordillera* Mickel, 1938 are described. Flight seasonality of *Timulla labdace* Mickel, 1938 is discussed. Keys and a checklist for the 16 species of *Timulla* from Panama are presented.

KEY WORDS

Timulla, Mutillinae, Trogaspidiini, taxonomy, Neotropical.

REVISIÓN TAXONÓMICA DEL GÉNERO *Timulla* ASHMEAD, 1899 DE PANAMÁ (HYMENOPTERA: MUTILLIDAE)

RESUMEN

Los machos de *Timulla chrysea* Mickel, 1938, *Timulla continua* Mickel, 1938 y *Timulla segesta* Mickel, 1938 y la hembra de *Timulla tumidula* (Cameron, 1894) son descritos e ilustrados. Se registran por primera vez para Panamá a *Timulla chrysea* y *T. tumidula.* Las siguientes sinonimias son presentadas: *Timulla orthona* (Cameron, 1894), macho, es junior sinónimo de *Timulla lilea* (Cameron, 1894), hembra; *Timulla talus* (Cameron, 1894), macho, es junior sinónimo de *Timulla subrobusta* (Cameron, 1894), hembra. Observaciones sobre el comportamiento de apareamiento para *Timulla runata* Mickel y *T. cordillera* son descritos. Estacionalidad de vuelo en *Timulla labdace* Mickel, 1938 es discutido. Se incluye una clave y listado para las 16 species of *Timulla* presentes en Panamá.

PALABRAS CLAVES

Timulla, Mutillinae, Trogaspidiini, taxonomy, Neotropical.

INTRODUCTION

Timulla Ashmead is the only American genus of the tribe Trogaspidiini (Mutillinae), according to the phylogeny and list presented by Brothers & Lelej (2017), which also includes 44 Old World genera. *Timulla* includes about 180 valid species (Bartholomay *et al.*, 2017) and many Neotropical species are known from a single sex. Mickel (1938) recorded 18 species of *Timulla* from Panama, all based on a single sex. Cambra & Quintero (1992, 1993) presented new records of distribution, sexual associations, and synonyms that left a total of 16 *Timulla* species in Panama.

This work presents a taxonomic revision for *Timulla* from Panama, which includes information on flight seasonality, mating behavior, taxonomy, new distribution records, and an identification key for species in Panama, which are now all known from both sexes.

MATERIAL AND METHODS

The study site for flight seasonality of *Timulla labdace* Mickel, 1938 was the field station of the Smithsonian Tropical Research Institute

(STRI) on Barro Colorado Island (BCI). Information on the study site and sampling methods are presented in Cambra *et al*. (2018). The morphological characters used to prepare the key for *Timulla* species from Panama are the same as those used by Mickel (1938) for the species of the Neotropical region.

Photographs of specimens were made with an Olympus Though digital camera; small morphological structures of the specimens through a Leica M 165c stereo microscope. Further image processing was accomplished by using ArcSoft Photo Studio.

The following acronyms are used for morphology: T2, T3, etc., for second, third, etc. metasomal terga; S for metasomal sterna. In the material examined sections, the specimens are deposited in Instituto Nacional de Biodiversidad, Heredia, Costa Rica (INBio), Museo de Invertebrados G. B. Fairchild, University of Panama, Panama (MIUP), Florida State Collection of Arthropods, USA (FSCA), and Entomological Museum of Utah State Univeristy, USA (EMUS).

RESULTS AND DISCUSSION

Key to species of *Timulla* Ashmead from Panama

Males

1. Posterior margin of T7 emarginate medially (Fig. 1) …….. 2
−. Posterior margin of T7 not emarginate medially (Figs 3−4) …….... 4

2. Scutellum with a median, longitudinal, smooth, polished area on the anterior half (Fig. 8); enclosed area of propodeum elevated posteriorly into a distinct tubercle; tegula mostly glabrous and asetose except along anterior and internal margins…..…….. ***centroamericana***
−. Scutellum evenly convex, punctate throughout; enclosed area of propodeum not elevated posteriorly into a tubercle; tegula punctate throughout and usually covered with setae ...…….……. 3

3. Median impunctate area of T7 terminating at a transverse carina (Fig. 1); postero-inner angle of mesocoxa produced into a slight

tubercle ……..… ***prominens prominens***

−. Median impunctate area of T7 terminating at an inverted V-shaped carina; postero-inner angle of mesocoxa not produced into a tubercle ……..……..... ***absentia***

4. Median impunctate area of T7 extending to posterior margin, not interrupted by an elevation of any kind (Fig. 4) …….. 5

−. Median impunctate area of T7 terminating before posterior margin in some sort of elevated prominence (Figs 2−3, 5) ……. 6

5. Anterior margin of clypeus more or less straight; metasomal segments 1, 6, and 7 dark mahogany red to black, other segments orange ……... ***chrysea***

−. Anterior margin of clypeus emarginate; entire metasoma orange ……... ***bradleyi***

6. Median impunctate area of T7 terminating in a prominent polished tooth or tubercle (Fig. 2); scutellum evenly convex, punctate throughout ……...… 7

−. Median impunctate area of T7 not terminating in a polished tooth or tubercle; scutellum evenly convex, punctate throughout or with a median longitudinal smooth polished area ...…….. 8

7. Median impunctate area of T7 terminating in a tubercle; T7 posterior margin with small denticle medially (Fig. 2); median posterior elevated margin of clypeus without tuberculate process; T7 orange ……..... ***lilea***

−. Median impunctate area of T7 terminating in a pointed tooth; T7 posterior margin with broad projection medially; median posterior elevated margin of clypeus reflexed to form a short tuberculate process; T7 dark mahogany red to black …….…….. ***segesta***

8. Scutellum evenly convex, punctate throughout …….…….... 9

−. Scutellum with a median longitudinal smooth polished area …… 11

9. Median impunctate area of T7 terminating into the arms of a Y-shaped carina, with the dorsal “arms” of the Y short …… ***nisa***

−. Median impunctate area not terminating into the arms of a Y-shaped carina ….…… 10

10. Median impunctate area of T7 terminating at a short, arcuate, transverse carina; posterior elevated margin of clypeus evenly arcuate (Fig. 7); S8 with flattened, glabrous lateral swellings, not posteriorly terminating into an elevated tubercle ……..... ***subrobusta***
−. Median impunctate area of T7 terminating at a blunt bituberculate prominence; posterior elevated margin of clypeus subrectangular with postero-lateral angles reflexed (Fig. 6); S8 with prominent lateral ridges posteriorly terminating into an elevated tubercle ……..……...……..……..… ***porcata***

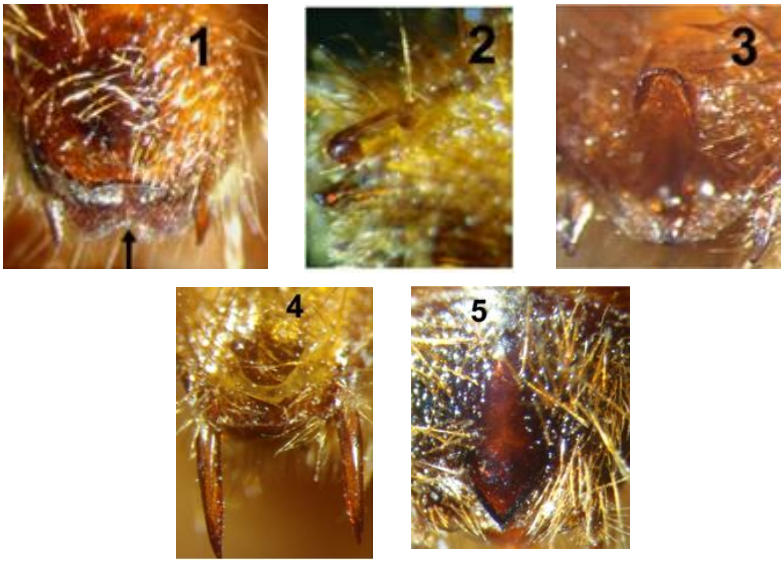
11. Median impunctate area of T7 terminating into the arms of a Y-shaped carina, with the stem of the Y short (Fig. 5); S8 with a prominent median tumid elevation posteriorly, the elevation mostly covered with upright setae; enclosed area of propodeum elevated posteriorly into a distinct tubercle ……..……... 12
−. Impunctate area of T7, viewed posteriorly, terminating into a sharp arcuate or ∩-shaped carina (Fig. 3); S8 without a median tumid elevation posteriorly; enclosed area of propodeum not elevated posteriorly into a tubercle ……..…….... 14

12. S6 with large posterolateral tubercles; posterior elevated area of clypeus transverse, twice as broad as high ……...…..... ***labdace***
−. S6 without distinct posterolateral tubercles; posterior elevated area of clypeus arcuate, about two thirds as high as broad …….....……..… 13

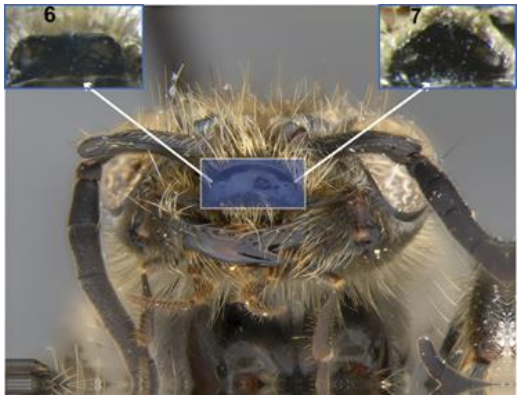
13. Metasomal segment seven black ……..……...….. ***tumidula***
−. Metasomal segment seven orange-red …….....…… ***connexa***

14. Elevated portion of T7, viewed posteriorly, defined dorsally by a sharp, triangular, arcuate carina ….…….....… ***runata***
−. Elevated portion of T7, viewed posteriorly, defined by a rounded ∩-shaped carina ...…….……. 15

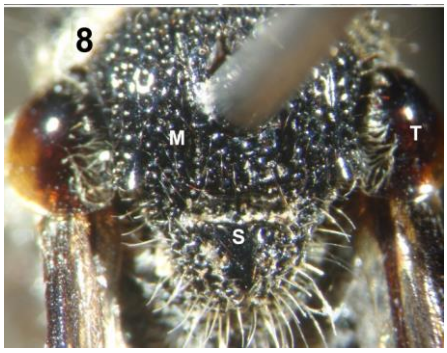
15. Legs entirely black ….…….……... ***continua***
−. Meso- and metatarsi orange-red ……...……...……... ***heterospila***



Figs. 1–5. *Timulla* males, tergum seven.1. *T. prominens*, dorsal view (arrow indicating T7 posterior emargination), 2. *T. lilea*, lateral view, 3. *T. heterospila*, posterior view, 4. *T. bradleyi*, dorsal view, 5. *T. tumidula*, dorsal view.



Figs. 6–7. *Timulla* males clypeus, frontal view. 6. *T. porcata*, 7. *T. subrobusta*.



Figs. 8. *T. runata*, male, dorsal view. Mesoscutum (M), tegula (T) and scutellum (S)

Females

1. Pygidium longitudinally striate; head black (Fig. 20) ……..……..……..… ***prominens prominens***
−. Pygidium not longitudinally striate, sculptured otherwise; head black or reddish ……... 2

2. Head reddish, concolorous with mesosoma (Figs 9, 14−15) …….. 3
−. Head black, contrasting with reddish mesosoma (Figs 10−12) ….. 5

3. Posterior margins of T1 and T2 with incomplete white pubescent bands: band of T1 widely interrupted medially with black, band of T2 composed of median rhomboidal spot that is laterally flanked by white pubescent bands (Fig. 15) ……..……. ***heterospila***
−. Posterior margins of T1 and T2 with complete white pubescent bands …… 4

4. Pygidium with basal half rugose and apical half glabrous; sides of propodeum with large, close punctures throughout; T2 with posterior transverse white band almost uniform in width (Fig. 14); T3–T5 with lateral, longitudinal, white pubescent bands ……..……... ***continua***
−. Pygidium longitudinally rugose from base to apical margin (or

nearly so), with granulate sculpturing between rugae; sides of propodeum almost impunctate, with few small scattered punctures; T2 with posterior transverse white band strongly sinuate (Fig. 9); T3–T5 black, without lateral white pubescent bands ……..…….…. ***absentia***

5. Legs orange-red (Figs 11, 17, 21−23) ……..……... 6
−. Legs entirely black or dark mahogany red (except *T. bradleyi* often with basal third of femur reddish, remainder of leg black) (Figs 12−13, 18−19) ……..…….... 11

6. Lateral white pubescent stripes on T2 continuous from anterior to posterior margins (Fig. 21) ……..…… ***runata***
−. Lateral white pubescent stripes on T2 confined to anterior half to two-thirds of T2 (Figs. 17, 22−23) …...……... 7

7. Posterior face of propodeum with a median, longitudinal stripe or blotch of black integument (Fig. 17) …….. 8
−. Propodeum uniformly reddish (Figs 18−20) ….…….. 9

8. Pleura and most of coxae red; non-white setae covering most of T2–T5 black and sometimes obscurely coppery-red when viewed at certain angles ……..... ***lilea*** (in part)
−. Pleura partly black, and coxae entirely black to dark red; non-white setae covering most of T2–T5 conspicuously coppery-red when viewed at certain angles (Fig. 23) ..……. ***subrobusta***

9. Propodeum broader than pronotum in dorsal view ……..… ***segesta***
−. Pronotum and propodeum equally broad in dorsal view …..…… 10

10. Lateral white pubescent stripes of T2 linear (Fig. 11); T2 with posterior transverse white band uniform in width; lateral white pubescent spots of T5 widely separated, not confluent medially at posterior margin of tergum; pygidium finely rugose posteriorly …..…….…… ***centroamericana***
−. Lateral white pubescent stripes of T2 elongate-ovate (Fig. 17); T2 with posterior transverse white band broad at sides, narrowing towards middle and medially expanded forward at a short angle;

lateral white pubescent spots of T5 confluent medially at posterior margin of tergum; pygidium weakly granulate posteriorly……..…….…..…. ***lilea*** (in part)

11. Lateral white or golden pubescent stripes on T2 continuous from anterior to posterior margins ……. 12
−. Lateral white pubescent stripes on T2 not reaching posterior margin of T2 ……..…...… 13

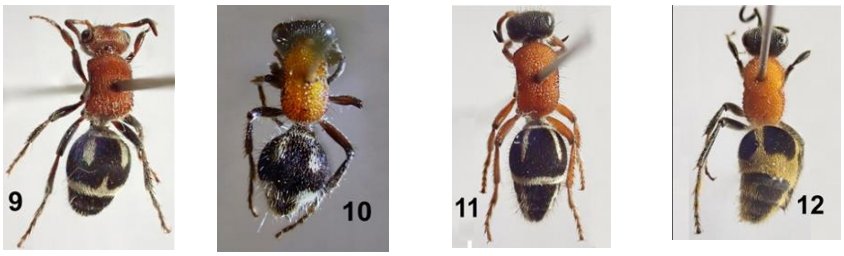
12. At least basal half of pygidium rugose; posterior marginal pubescent bands of T1–T2 and lateral pubescent stripes on T2 white, with the posterior band of T2 linear and uniform in width (Fig. 18) ……..… ***nisa***
−. Pygidium granulate throughout; posterior marginal pubescent bands of T1–T2 and lateral pubescent stripes on T2 golden, with the posterior band of T2 wide and non-uniform in width (Fig. 12) ……..……..…… ***chrysea***

13. Posterior marginal white pubescent band of T2 interrupted medially with black setae (Fig. 10); T3–T5 with transverse white setal bands that reach lateral margins of terga; pronotum as broad as propodeum ……..…… ***bradleyi***
−. Posterior marginal white pubescent band of T2 complete (Figs 16, 19,24); T3–T5 with lateral setae black near margins, usually with sublateral white setal spot on T3–T5 (except *T. tumidula*); propodeum broader than pronotum …….…….……. 14

14. Lateral white pubescent patches on T3 and T4 absent (Fig. 24) ……..… ***tumidula***
−. Lateral white pubescent patches on T3 and T4 present (Figs 13, 16, 19) …….. 15

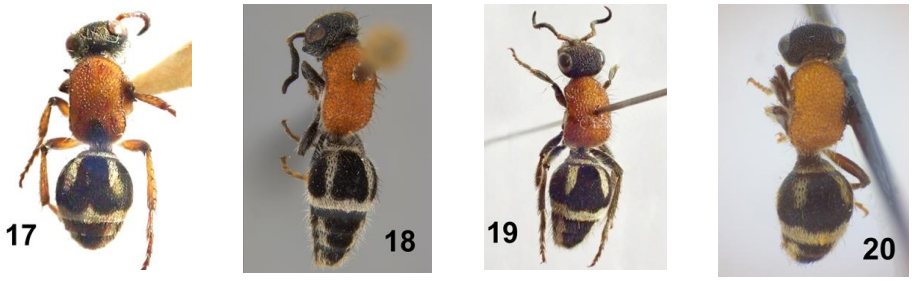
15. Pleura partly black; posterior face of propodeum with a median blotch of black integument ……..… ***connexa***
−. Pleura reddish; propodeum uniformly reddish ……..…… 16

16. Sides of propodeum with small, scattered punctures …… ***porcata***
−. Sides of propodeum with large, close punctures throughout …….. ***labdace***



Figs. 9–12. *Timulla* females. 9. *T. absentia*, 10. *T. bradleyi*, 11. *T. centroamericana*, 12. *T. chrysea.*

Figs. 13–16. *Timulla* females. 13. *T. connexa*, 14. *T. continua*, 15. *T. heterospila*, 16. *T. labdace.*



Figs. 17–20. *Timulla* females. 17. *T. lilea*, 18. *T. nisa*, 19. *T. porcata*, 20. *T. prominens.*

Figs. 21–24. *Timulla* females. 21. *T. runata*, 22. *T. segesta*, 23. *T. subrobusta*, 24. *T. tumidula.*

Checklist of *Timulla* from Panama

Timulla absentia Mickel, 1938
female (Fig. 9)
Cambra & Quintero (1993), male description.

Material examined. **NICARAGUA:** Rivas Dist., Playa La Flor, 1−8 ago 1999, van den Berghe, 5♀, 1♂ (MIUP). **COSTA RICA, Guanacaste** Prov.: Playa Naranjo, Sta. Rosa, P.N. Guanacaste, mar 1991, E. Alcazar, 1♂ (INBio); Est. Biol. Nancite, P.N. Sta. Rosa, O m, sep 1990, E. Alcazar, 1♂ (INBio); Bahia Junquillal, 4 may 1995, F. Quesada, 1♂ (INBio). **Puntarenas** Prov.: Est. Sirena, 0−100 m, P.N. Corcovado, 21 mar −21 abr 1992, Z. Fuentes, 6♂ (INBio, MIUP); abr 1992, G. Rodriguez, 4♂ (INBio, MIUP); Punta Catedral, P.N. Manuel Antonio, 80 m, Quepos, jul 1992, G. Varela, 2♀ (INBio, MIUP); ago 1992, G. Varela, 1♂ (INBio). **PANAMA: Los Santos** Prov.: Playa de Guanico Abajo, 27 nov 1988, R. Rodriguez, D. Quintero, & R. Cambra, 2♀ (EMUS). **Veraguas** Prov.: P.N. Coiba, Isla Coibita, 6−11 mar 1998, R. Cambra, A. Santos, 11♀, 9♂ (MIUP); Santa Catalina, N7.6243° W81.2421°, 181', 12 feb 2012, F.D. Parker & T.D. McIntyre, 2♀ (EMUS).

Distribution: Nicaragua (first record for this country), Costa Rica, and Panama (Chiriqui, Veraguas, Los Santos, Herrera, Panama) (Mickel, 1938; Cambra & Quintero, 1993).

Timulla bradleyi Mickel, 1938; male
(Fig. 4, 10, 30, 38)
Cambra & Quintero (1993), female description.

Material examined. **COSTA RICA**, **Alajuela** Prov.: Sect. San Ramon de Dos Rios, 620 m, 3−24 abr 1995, M. Chinchilla, 1♂ (INBio); Bijagua, 20 km S Upala, 12 may 1991, 1♂ (INBio). **Cartago** Prov.: Turrialba, Exp. Stat., 20 ago 1989, 1♂ (INBio). **Guanacaste** Prov.: Est. Pitilla, 700 m, 9 km S. Sta. Cecilia, mar 1991, C. Moraga, 1♂ (INBio); 4−25 nov 1991, Igual col., 1♂ (IMIUP); may 1994, P. Rios, 1♂ (INBio). **Heredia** Prov.: El Ceibo, P.N. Braulio Carrillo, 400-600 m, ene 1990, C. Chavez, 1♂; feb 1990, C. Chavez, 4♂ (INBio, MIUP). **Limon** Prov.: Sector Cerro Cocori, Fca. de E. Rojas, 150 m, mar 1993, E. Rojas, 2♂; ene 1992, E. Rojas., 1♂; may 1991, 2♂; 9−30 nov 1992, 2♂; dic 1992, 1♂; abr 1992, 1♂; abr 1993, 2♂; sep 1993, 1♂; dic 1992, 1♂ (INBio, MIUP); Sector Cerro Cocori, 30 km al N de Cariari, A.C. Tortuguero, 100 m, feb 1994, E. Rojas, 1♂; Limon, 1♂ (INBio). **Puntarenas** Prov: Est. Sirena, 0−100 m, P.N. Corcovado, jun 1991, G. Fonseca, 1♂; mar 1992, same coll., 1♂; ene 1990, 1♂; ene 1992, 1♂; feb 1990, 1♂; 21 mar−21 abr 1992, Z. Fuentes, 2♂; dic 1993, G. Fonseca, 1♂; mar 1993, G.Fonseca, 1♂; abr 1995, B. Gamboa, 1♂ (INBio, MIUP). Rancho Quemado, 200 m, Peninsula de Osa, mar 1992, F. Quesada, 1♂; nov 1991, same coll., 1♂; dic 1991, 1♂; dic 1992, M. Segura, 1♂; 12−24 may 1993, A. Gutierrez, 1♂; 10−31 mar 1992, A.L. Marin, 1♂; 1−20 dic 1993, 1♂; 4−27 jul 1994, 2♂; 12 mar− 3 abr 1994, 2♂; 4−25 may 1994, 1♂; 4−25 ene 1994, 1♂; 6−12 feb 1994, 1♂; 14−28 jul 1993, A. Gutierrez, 1♂ (INBio, MIUP); Corcovado National Park, Osa Peninsula, 16−25 mar 1977, D. Enezen, 1♂ (INBio); Send. a Rio Claro, P.N. Corcovado, ene-mar 1992 (trp. Malaise), 1♂ (INBio); Est. Agujas, 375m, 22 ago 1996, M. Lobo, 2♂ (INBio, MIUP); Fila Madre, 3 km SO de Cerro Rincon, 710 m, 25 may 1995, A. Azofeifa, 2♂ (INBio, MIUP); Qbda. Piedras Blancas, 400 m, 10−14 ago 1997, M. Lobo, 1♂ (INBio). **PANAMA: Bocas del Toro** Prov.: P. Int. La Amistad, Wekso-Teribe, 17−24 oct 1999, A. Santos, 1♂ (MIUP). **Darien** Prov.: P. Nac. Darien, Estac. Rancho Frio, Pirre, 20 mar−5 abr 1999, Cambra & Santos, 1♀, 4♂ (MIUP).

Distribution: Costa Rica and Panama (Bocas del Toro, Cocle, Colon, Darien) (Mickel, 1938; Cambra & Quintero 1993).

Timulla centroamericana (Dalla Torre, 1897); female
(Figs 11, 27, 35)

Timulla proclivis Mickel, 1938; male: Cambra & Quintero (1993), synonymy.

Material examined. **PANAMA: Chiriquí** Prov.: 8 km S Boquete: N8.6986° W82.4505°, 2693', 15–29 feb 2012, F.D. Parker & T.D. McIntyre, pantrap, 1♀ (EMUS); 15–29 feb 2012, pan traps, 1♂ (EMUS). **Coclé** Prov.: Antón: Juan Díaz, 7 feb 1989, J. Castañeda, 1♀ (EMUS). **Veraguas** Prov.: Santa Fe, Alto de Piedra, 24 mar 1999, L. De Gracia, C. Vega, 2♀ (MIUP).

Distribution: Panama (Chiriqui, Veraguas, Los Santos, Colon, Panama), Colombia, and Ecuador (Mickel, 1938; Cambra & Quintero, 1993).

Comments: Each female specimen from Santa Fe in Veraguas is mounted on a pin with a female of *Auplopus* sp. (Pompilidae). One has the following information on the label: "carrying in flight the Mutillidae"; the other: "attacking the Mutillidae". Cambra *et al*. (2018) mentioned a female wasp of *Microbembex monodonta* (Crabronidae) carrying in flight a female of *Dasymutilla araneoides*. The Crabronidae are widely recognized hosts of Mutillidae (Callan, 1942; Quintero & Cambra, 1996), and Pompilidae might be as well. The act of carrying a mutillid wasp in flight by Pompilidae and Crabronidae could be a defense mechanism, with the potential host trying to move the parasitoid away from its nesting area.

Timulla chrysea Mickel, 1938; female
(Fig. 12)

Male description. Body length 13.0 mm. *Color.* Integument of head, mesosoma and legs black; first segment and last two segments of metasoma dark mahogany red to black, other segments orange; tibial spurs white. Setae of head, mesosoma, and legs golden except

mesonotum mostly dark brown to black; metasoma with golden setae. *Head*. Median area of clypeus concave, anterior margin straight, posterior elevated margin evenly arcuate; mandible ventral margin excised, forming a large basal tooth; ocelli small, distance between eye margin and lateral ocellus 3.0 × diameter of lateral ocellus. *Mesosoma*. Scutellum with a median longitudinal smooth polished area on anterior half; enclosed area of propodeum not elevated posteriorly; tegula mostly impunctate and glabrous except anterior and inner margins with micropunctures and setae. *Metasoma.* Median impunctate area of T7 extending to posterior margin, not interrupted by elevation of any kind; S1 with median longitudinal carina; S7 without lateral tubercles; S8 without basal lateral tubercle, with oblique weak ridge in apical half, without median tumid elevation posteriorly.

Material examined. **COSTA RICA**, **Alajuela** Prov.: R. San Lorencito, 900 m, R. F. San Ramon, 5 km N de Colonia Palmareña, 13−18 jun 1993, 2♂ (INBio, MIUP). **Cartago** Prov.: P.N. Tapanti, 1150 m, mar 1994, G. Mora, 1♂ (INBio); Quebrada Segunda, P.N. Tapanti, 1150 m, may 1994, G.Mora, 1♂ (INBio); Grano de Oro, Chirripo, Turrialba, 11−20, jul 1993, P. Campos, 1♂; mar 1993, P. Campos, 1♀ (INBio, MIUP); Monum. Nac. Guayabo, 1100 m, oct 1994, G. Fonseca, 1♂ (INBio). **Guanacaste** Prov.: R. San Lorenzo, 1050 m, R.F. Cord. Guanacaste (Tenorio), jul 1991, C. Alvarado, 1♀ (INBio). **Puntarenas** Prov.: Fila Cruces, Finca llama, 1200 m, 6 may 1996, I. Chacon, 1♀ (INBio). **PANAMA: Chiriqui** Prov.: Fortuna, Div. Cont. 17 may 1996, Turnbow, 1♀ (MIUP); abr 1999, R. Cambra, 2♀, 1♂; 28 ago 1987, R. Rodriguez, 1♂ (MIUP).

Distribution: Costa Rica and Panama (Chiriqui). First record for Panama.

Comments. *Timulla chrysea* and *T. bradleyi* are the only two Panamanian males with the median impunctate area of T7 extending to posterior margin, not interrupted by an elevation of any kind. These species differ in clypeal morphology and metasomal coloration as presented in the key above. Females of these species have similar mesosomal morphology, but are easily differentiated by metasomal setal pattern and color.

Timulla connexa (Cameron, 1894); male
(Fig. 13)

Timulla selene Mickel, 1938; female: Cambra & Quintero (1993), synonymy.

Material examined. **COSTA RICA**, **Alajuela** Prov.: Fca. Josephina, 2 km S. Pital, 5−27 nov 1988, F. Parker, 2♀. **Cartago** Prov.: Turrialba, Exp. Stat., 20 ago 1989, F. Parker, 1♀ (INBio). **Limon** Prov.: Est. Hitoy Cerere, 100−200 m, Res. Biol. Hitoy Cerere, 30 jul−20 jun 1992, F. Quesada, 1♂; jul 1991, G. Carballo, 1♂; sep 1990, G. Carballo, 1♂ (INBio, MIUP). **San Jose** Prov.: Est. Bijagual, 600 m, N. de Bijagualito, 500 m, abr 1995, J. Saborio, 1♂ (INBio); Cerro Bares, 1756 m, Zona Protectora, cerro Turrubares, abr 1990, R. Zuñiga, 1♂ (INBio); Amubri, A.C. Amistad, 70 m, 4−30 abr 1994, G. Gallardo, 1♂; 3−28 feb 1995, G. Gallardo, 1♂ (INBio, MIUP). **Puntarenas** Prov.: Rancho Quemado, 200 m., Peninsula de Osa, may 1992, F. Quesada, 1♂; sep 1992, M. Segura, 1♂; abr 1992, K. Flores, 1♂; oct 1992, F. Quesada, 1♂ (INBio, MIUP); Est. Sirena, P.N. Corcovado, 1−100 m, abr 1994, G.Fonseca, 1♂ (INBio); Estacion Quebrada Bonita, R.B. Carara, may 1994, J. Saborio, 1♂; ene 1994, R. Guzman, 1♀ (INBio, MIUP); Est. Rio Bonito, 100 m, 7−15 jul 1997, E. Fletes, 1♂ (INBio); Est. Agujas, 300 m, 11−27 jul 1996, A. Azofeifa, 1♂; 17−21 nov 1997, M. Lobo, 1♂; 1−7 dic 1997, A. Azofeifa; mar 1996, A. Azofeifa, 1♂; 4−8 ago 1997, M. Lobo, 1♂ (INBio, MIUP); Fila Madre, 3 km SO de Cerro Rincon, 710 m, 25 may 1995, A. Azofeifa, 1♂ (INBio); Qbda. Piedras Blancas, 400 m, 10−14 ago 1997, M. Lobo, 1♂ (INBio). **PANAMA: Bocas del Toro** Prov.**:** Wekso-Teribe, 17−24 oct 1999, A. Santos, 1♂ (MIUP). **Veraguas** Prov.: Santa Fe, Altos de Piedra, 13−17 nov 1999, A. Santos, 1♀, 1♂ (MIUP). **Colon** Prov.: Santa Rita, 20−21 dic 1990, R. Cambra, 1♂ (MIUP). **Panama** Prov.: Cerro Campana, 14 jul 1990, R. Cambra, 1♂ (MIUP).

Distribution: Costa Rica and Panama (Bocas del Toro, Chiriqui, Veraguas, Cocle, Colon, Panama). (Cameron, 1894; Mickel, 1938; Cambra & Quintero, 1993).

Comments: Mickel (1938) indicated that the females of *T. connexa* (as *T. selene*) and *T. porcata* were similar and that they may belong to a

single species. When Cambra & Quintero (1993) discovered the sexual associations for these taxa, the males were found to be distinctive in various structural features, as indicated in the key above. Therefore, Mickel's treatment of *T. connexa* and *T. porcata* as separate species is supported by our work.

Timulla continua Mickel, 1938; female
(Fig. 14)

Timulla rufogastra: Cambra & Quintero (1986: 310), not Lepeletier, 1845.

Timulla rufogastra: Bartholomay *et al.* (2017: 138), not Lepeletier, 1845.

Male description. Body length 12.5 mm. *Color.* Integument of head, mesosoma and legs black; metasoma orange; tibial spurs white. Setae of head, mesosoma, and legs white except mesonotum mostly black; metasoma with golden setae. *Head*. Median area of clypeus concave, anterior margin straight, posterior elevated margin evenly arcuate; mandible ventral margin excised, forming a large basal tooth; ocelli small, distance between eye margin and lateral ocellus 3.2 × diameter of ocellus. *Mesosoma*. Scutellum gibbose, with a median, longitudinal, smooth, polished area on anterior half; enclosed area of propodeum not elevated posteriorly; tegula mostly impunctate and glabrous except anterior and inner margins with micropunctures and setae. *Metasoma.* Posterior margin of T7 not emarginate medially; elevated portion of T7, viewed from rear, defined by a ∩-shaped carina; S1 with median longitudinal carina; S6 without lateral tubercle; S7 with basal lateral tubercle; S8 with oblique weak ridge, without median tumid elevation posteriorly.

Material examined. **COSTA RICA: Limón**: Parque Nacional de Cahuita, rainforest, 3–4 ago 1981, H.V. Weems, Jr. & G.B. Edwards, 1♀ (FSCA); **San José** Prov.: San Isidro del General, feb 1993, F.D. Parker, 3♂ (EMUS). **PANAMA: Chiriquí** Prov.: 8 km S Boquete: 15–29 feb 2012, F.D. Parker & T.D. McIntyre, malaise, 1♂ (EMUS); 3 ene 2012, F.D. Parker, pantrap, 1♂ (EMUS). **Colon** Prov.: Punta Galeta, STRI marine station, 18 may 2003, A. Aiello (captured mating pair at leaf, 5:30 pm); Viento Frio, 12 may 1995, R. Cambra, 1♀, 6♂ (MIUP).

Distribution: Costa Rica and Panama (Colon and Darien).

Comments: The sex association is based on coincidental distribution and capture of one mating couple. Cambra & Quintero (1993) reported *Timulla rufogastra* (Lepeletier, 1845) from Panama, based on 14 male specimens collected in Darien Province. Now, we recognize these specimens as the opposite sex of *T. continua*. Males of *T rufogastra* and *T. continua* are similar in morphology, but differ in the shape of the clypeus; *T. rufogastra* has the posterior elevated margin of the clypeus weakly reflexed medially, forming a small tubercle, while *T. continua* has the posterior margin evenly arcuate. Bartholomay *et al*. (2017) reported males of *T. rufogastra in copula* with females of *T. eriphyla* Mickel, 1938 and synonymized these taxa. The three males reported from Costa Rica in the latter reference as *T. rufogastra* are actually *T. continua*. Females of *T. eriphyla* have not been collected in Panama nor in Costa Rica, which supports the absence of *T. rufogastra* from these countries.

Timulla heterospila (Gerstaecker, 1874); female
(Fig. 15)

Timulla thura (Cameron, 1894); male: Cambra & Quintero (1993), synonymy.

Material examined. **PANAMA: Cocle** Prov.: Nata, 9 ene 1994, M. Gonzalez, 1♀ (MIUP). **Panama** Prov.: Capira, Cermeño, 1 ene 1995, M. Castro, 1♀ (MIUP).
Distribution: Panama (Veraguas, Los Santos, Cocle, Panama), Colombia, and Venezuela (Mickel, 1938; Cambra & Quintero, 1992, 1993).

Timulla labdace Mickel, 1938; male
(Figs 16, 31, 39)

Timulla raui Mickel, 1938; female: Cambra & Quintero (1993), synonymy.

Material examined. **PANAMA: Colón** Prov.: Quebrada Bonita, NW Madden Dam, 23 oct 1957, W.J. Hansen, 1♂ (EMUS); Santa Rita Ridge, 15 km E Colón, 10–12 jun 1997, Peck, 1♂ (EMUS). **Darien**

Prov.: P. Nac. Darien, Estac. Rancho Frio, Pirre, 20 mar−5 abr 2000, Cambra & Santos, Malaise traps, 25♂ (MIUP). **Panama** Prov.: 34 specimens collected in Barro Colorado Island with ten Malaise traps from the years 2001 to 2006 (Saavedra, 2014) (MIUP); see tables 1 and 2.

Distribution: Panama (Panama, Colon, Darien) and Colombia (Mickel, 1938; Cambra & Quintero, 1993).

Comments. Relatively few specimens (34 males, Tables 1−2) of *T. labdace* were captured in Barro Colorado Island (BCI) during five years of sampling with ten Malaise traps. The largest number of specimens were collected in the months of September (10 specimens) and January (9). The low number of specimens could be related to two factors: 1) the Canal Area of Panama is the southern limit of distribution of this species, or 2) Barro Colorado is a very small artificial island (54 km^2), formed during the construction of the Panama Canal, with probable limitation of hosts. In other localities, however, the species is more common. In the area of Cana, Darién, 28 specimens were collected, with a Malaise trap and manual collections (two people), from April 4−12 (see Cambra & Quintero, 1993). Additionally, the data presented here, 25 males captured with 5 Malaise traps, indicate the abundance of this species in Darién in the months of March and April, which, strangely, are two months in which no specimens were captured during 5 years of sampling on BCI.

Table 1. Specimens of *T. labdace* collected by year in B.C.I.

2001	2002	2003	2004	2005	2006	TOTAL
0	14	2	4	8	6	34

Table 2. Specimens of *T. labdace* collected by month (six years) in B.C.I.

En	Fe	Ma	Ab	Ma	Jun	Jul	Ag	Se	Oc	No	Di
9	1	0	0	4	4	2	0	10	0	2	2

Timulla lilea (Cameron, 1894); female
(Figs 17, 28, 36)

Mutilla orthona Cameron, 1894: 288−289. Male, San Felix, Chiriqui, Champion, British Museum Natural History. **NEW SYNONYMY.**
Timulla orthona: Mickel (1938).

Material examined. **COSTA RICA**, **Alajuela** Prov.: Sector San Ramon, 800 m, 11−15 abr 1994, M. Zumbado, 1♂ (INBio); Bijagua, 20 km S Upala, 10 ene 1991, 1♂; 29 ene 1991, 1♂; 24 feb 1990, 1♂; 17 mar 1991, 1♂; 26 mar−12 abr 1991, 1♂; 28 mar 1991, 1♂; 2 abr 1991, 1♂; 15 abr 1991, 1♂; 29 abr 1991, 1♂; 16 may 1991, 1♂; 1 may 1990, 1♂; 1−3 may 1990, 2♂; 1−10 may 1990, 1♂; 11−15 may 1990, 1♂; jun 1990, 13♂; 15−18 jul 1990, 3♂; 1−12 ago 1990, 1♂; 27 sep−18 oct 1990, 2♂; 21−23 ago 1990, 1♂; 14−16 ago 1990, 1♂ (INBio, MIUP); Finca Los Lagos, 76 km N Fortuna, 10 ago 1989, 1♂ (INBio); Sector Colonia Palmareña, 9 km SO de Bajo Rodriguez, 700 m, 28 feb− 11 mar 1997, G. Carballo, 2♀ (INBio, MIUP). **Cartago** Prov.: Ref. Nac. Fauna Silv. Tapanti, 1250 m, oct 1991, G. Mora, 2♂; sep 1991, G. Mora, 1♂; nov 1991, G. Mora, 1♂ (INBio, MIUP); Monumento Nacional Guayabo, A. C. Amistad, 1100 m, jun 1994, G.Fonseca, 1♂ (INBio); Grano de Oro, Chirripo, Turrialba, 1120 m, feb 1993, P. Campos, 1♂; 8−31 ago 1992, P. Campos, 1♂ (INBio, MIUP). **Guanacaste** Prov.: Est. Cacao 1000−1400 m, SW ladera Volcan Cacao, sep 1989, R. Blanco, 1♂ (INBio); Rio San Lorenzo, 1050 m, Tierras Morenas, Z. Prot. Tenorio, jul 1992, G. Rodriguez, 2♂; may 1994, G. Rodriguez, 1♀ (INBio, MIUP); Est. Pitilla, 700 m, 9 km S. Sta. Cecilia, P.N. Guanacaste, 21 mar− 6 abr 1993, C. Moraga, 1♂ (INBio); EJN, 14 km S Cañas, 1−12 mar 1990, 1♂ (INBio). **Limon** Prov.: Est. Hitoy Cerere, Res. Biol. Hitoy Cerere, Rio Cerere, 200 m, sep 1990, G. Carballo, 1♂; Amubri, A.C. Amistad, 70 m, 4−30 abr 1994, G. Gallardo, 2♂; jul 1996, G. Gallardo, jul 1996, 1♂; ago 1996, 1♂; 2−30 mar 1996, 3♂ (INBio, MIUP). **Puntarenas** Prov.: Fca. Cafrosa, Est. Las Mellizas, P.N. La Amistad, 1300 m, mar 1991, M. Ramirez, 1♂; Est. Sirena, 0−100m, P.N. Corcovado, ene 1992, G. Fonseca, 2♂; oct 1991, G. Fonseca, 1♂; abr 1991, G. Fonseca, 1♂; dic 1991, G. Fonseca, 1♂; sep 1990, Saborio, 1♀; nov 1990, Saborio, 1♀ (INBio, MIUP); Rancho Quemado, 200 m, Peninsula de Osa, dic 1991, F. Quesada, 1♂; 11−28 oct 1993, A. Gutierrez, 1♀; Rey Curre, 100 m,

2−28 feb 1993, S. Rojas, 1♂ (INBio, MIUP); Albergue Cerro de Oro, 200 m, 5−9 may 1995, B. Gamboa, 1♂ (INBio). **San Jose** Prov.: San Isidro, 9 mi S., 31 dic 1988, 1♂ (INBio). **PANAMA: Bocas del Toro** Prov.: P. Int. La Amistad, Wekso-Teribe, 17−24 oct 1999, A. Santos, 11♂ (MIUP). **Veraguas** Prov.: Dist. Bahia Honda, 28 may−2 jun 2002, Cambra & Santos, 2♀, 1♂ (MIUP).

Distribution: Nicaragua, Costa Rica, Panama (Bocas del Toro, Chiriquí, Veraguas, Panama, Darien), and Colombia (Mickel, 1938; Cambra & Quintero, 1992, 1993).

Comments: The sex association is based on coincidental distribution. We have not collected specimens of *T. lilea* in the Provinces of Panama and Darien, despite abundant sampling in those Provinces. Mickel (1938) mentioned that he examined female specimens of *T. lilea* collected in Darien and Western Colombia and indicated that these specimens have the black integument on the posterior area of propodeum almost obsolete. Those specimens he mentioned could actually be *T. segesta*, which can be difficult to separate from *T. lilea*.

Timulla nisa Mickel, 1938; female
(Fig. 18)

Cambra & Quintero (1993), male description.

Material examined. **COSTA RICA**, **Chiriquí** Prov.: Boquete, 14–21 ene 2012, F.D. Parker, 1♂ (EMUS); **Puntarenas** Prov.: Vuelta Campana, R. Terraba, 100−500 m, Rey Curre, 12−14 mar 1993, M. Camacho, F. Mejia, A. Mora, 1♀ (INBio, MIUP). **PANAMA: Veraguas** Prov.: Dist. Bahia Honda, 9−11 ago 2001, A. Santos, 1♀, 3♂ (MIUP). **Los Santos** Prov.: Tonosi, Res. Forestal La Tronosa, 29 jul−1 ago 2006, R. Cambra, 1♀, 10♂ (MIUP).

Distribution: Costa Rica, Panama (Chiriquí, Veraguas, Los Santos, Panama, Coclé), Colombia, Venezuela, and Trinidad (Mickel, 1938; Cambra & Quintero, 1992, 1993).

Timulla porcata (Cameron, 1894); female
(Figs 6, 19, 26, 34)

Timulla bituberculata Mickel (1938), male. Cambra & Quintero (1993), synonymy.

Timulla phiala Mickel (1938), female: Cambra & Quintero (1993), synonymy.

Material examined. **COSTA RICA**, **Guanacaste** Prov.: Est. Murcielago, 8 km SW de Cuajiniquil, P.N. Guanacaste, 100 m, ago 1993, E. Araya, 1♂; 19 sep 1994, F. Quesada, 1♂; Est. Sta. Rosa, 300 m., P.N. Guanacaste, 13−28 jun 1992, 1♂; 3−12 jun 1992, 1♂; ene 1991, 1♂; ene 1991, M. Zumbado, 1♂, 1♀ (phoretic pair, mounted in same pin) (INBio, MIUP); Est. Maritza, 600 m, W ladera volcan Orosi, ago 1990, 1♀, 2♂; jun 1990, R. Blanco, 1♂; 28 feb−10 mar 1992, D. Garcia, 1♂; 27 feb−10 mar 1992, R. Vargas, 1♀; 27 feb−10 mar 1992, M. Segura, 1♂, 1♀ (phoretic pair, mounted in same pin) (INBio, MIUP); Fca. Jenny, 30 km N de Liberia, P.N. Guanacaste, 5−26 ago 1993, E. Araya, 1♂; 16−20 may 1994, 1♀; 8−20 mar 1994, 1♀; 7−28 jun 1994, 1♀; mar-abr 1989, 3♂, 1♀; oct 1988, 1♀; 16 oct−10 nov 1991, 2♀; ene 1992, E. Araya, 2♀; 2−24 ene 1995, E. Araya, 1♀ (INBio, MIUP); Playa Naranjo, Sta. Rosa, P.N. Guanacaste, dic 1990, E. Alcazar, 1♀; mar 1991, E. Alcazar, 1♀ (INBio, MIUP); 3 km NO de Nacaome, 100 m, P.N. Barra Honda, dic 1992, M. Reyes, 1♀; abr 1993, M. Reyes, 1♂, 1♀ (INBio, MIUP); Est. Las Pailas, 800 m, P.N. Rincon de la Vieja, 15 jul−14 sep 1992, J. Sihezar, 3♀; 5−24 ago 1994, D. Garcia, 1♂, 1♀ (phoretic pair, mounted in same pin); 6 ene−13 abr 1993, igual col., 1♀; 15 sep−12 nov 1992, 1♀; 9−25 feb 1993, D. Garcia, 1♀; 24 ago−14 sep 1992, 1♂; 1−22 jul 1992, 2♂; 24−30 abr 1994, K. Taylor, 2♂; 7−23 ene 1994, 1♀; sep 1993, 1♀; 12−23 ene 1994, 1♂ (INBio, MIUP); Los Almendros, P.N. Guanacaste, 8−20 nov 1993, E.Lopez, 2♀; 5−12 jul 1994, 1♂; 8−26 jun 1994, 1♂; 11−30 jun 1993, 1♂; 8−26 jun 1994, 1♂; 10−30 mar 1993, 1♂; 23 oct−13 nov 1992, E. Lopez, 2♀; 28 jul−14 ago 1992, E. Lopez, 1♀; 24 ago−14 sep 1992, 1♂ (INBio, MIUP); Est. Cacao, 1000−1400 m, ladera SO volcan Cacao, jun 1990, 1♂ (INBio); Est. Agua Buena, 220 m, P.N. Guanacaste, 8−23 abr 1993, E. Lopez, 1♂ (INBio); Ojo de Agua, Guapote, 270−280m, ene 1992, E. Araya, 2♀ (INBio, MIUP); Tierras Morenas, 700 m, jul 1993, G. Rodriguez, 1♂ (INBio); Sta. Cruz, 22

ene 2000, 1♂, 1♀ (INBio, MIUP). **Heredia** Prov.: La Ribera de Belen, 960 m, 9 oct 1994, M. Zumbado, 1♀; dic 1992, M. Zumbado, 1♀ (INBio, MIUP). **San Jose** Prov.: Escazu, 2−14 may 1988, 1♂ (INBio). **NICARAGUA:** Managua Dist., Laguna de Xiloa, 24 dic 1993, V. den Berghe, 1♀; Granada, 8♂ (MIUP). **GUATEMALA:** Escuintla, 6 may 1982, E. Morales, 1♂ (MIUP). **HONDURAS**: Fco. Morazan, 32 km E. El Zamorano, 7♀ (MIUP); Fco. Morazan, San Antonio del Oriente, El Zamorano, R. Cave, 2♂ (MIUP); E.A.P., 30 km E. Tegucigalpa, 12♀ (MIUP). **EL SALVADOR**: CAPREX, 4 may 1998, 1♀ (MIUP).

Distribution: Mexico to Panama (Mickel, 1938; Cambra & Quintero, 1992, 1993).

Comments: The sites in Panama where *T. porcata* has been found (from the border with Costa Rica to the Province of Coclé in the central part of the isthmus) and its absence from Darien, despite intense sampling, support Mickel's (1938) assertion that the record of a male from Colombia was mislabeled.

Timulla prominens prominens (Cameron, 1894); male, female (Figs 1, 20, 32, 40)

Cambra & Quintero (1993): record for Panama.

Material examined. **COSTA RICA: Alajuela** Prov.: Bijagua, 20 km S. Upala, 22 abr 1991, 1♂, 1♀ (phoretic pair on same pin) (INBio). **Guanacaste** Prov.: Fca. Jenny, 30 km N. de Liberia, P.N. Guanacaste, mar-abr 1989, 2♂ (INBio, MIUP). **Limon** Prov.: Est. Hitoy Cerere, 100 m, R. Cerere, Res. Biol. Hitoy Cerere, ene 1993, G. Carballo, 1♀ (INBio). **MEXICO:** Chiapas, Chajul Biological St., 16° 7' N, 90° 57' W, 17 abr 1993, orillas rio Lacantun, R. Brooks, 1♀ (MIUP). **EL SALVADOR**: Amatecamp, 17 dic 1997, 1♀ (MIUP). **PANAMA**: **Bocas del Toro** Prov.: PILA, Wekso-Teribe, 17−24 oct 1999, A. Santos, 1♂ (MIUP).

Distribution: Mexico, Guatemala, El Salvador, Nicaragua, Costa Rica and Panama (Bocas del Toro) (Mickel, 1938; Cambra & Quintero, 1993).

Timulla runata Mickel, 1938; female
(Figs 8, 21)

Timulla buscki Mickel, 1938; male: Cambra & Quintero (1993), synonymy.

Material examined. **COSTA RICA**, **Puntarenas** Prov.: Est. Sirena, 0−100 m, P.N. Corcovado, abr 1992, G. Rodriguez, 1♂ (INBio). **PANAMA: Panamá** Prov.: Chilibre, 23 abr 1989, M. Gutierrez, 1♀ (EMUS); **Veraguas** Prov.: P. Nac. Coiba, Isla Coiba, 1 ago 1998, R. Cambra, 1♀ (MIUP); 23−27 ene 1994, J. Nieves, 3♂ (MIUP); P. Nac. Coiba, Isla Coibita, 30 jul 1998, R. Cambra, 1♀ (MIUP); 6−11 mar 1998, Cambra & Santos, 1♂ (MIUP). **Los Santos** Prov.: Tonosi, R. Forestal La Tronosa, El Cortezo, 3-6 may 2006, Cambra & Santos, 1♂ (MIUP); Tonosi, R. Forestal La Tronosa, Buenos Aires, 29 jul-1 ago 2006, Cambra & Miranda, 1♀ (MIUP).

Distribution: Costa Rica and Panama (Chiriquí, Los Santos, Veraguas, Coclé, Colon, Panama) (Mickel, 1938; Cambra & Quintero, 1992, 1993).

Timulla segesta Mickel, 1938; female
(Fig. 22)

Male description. Body length 13.2 mm. *Color.* Integument of head, mesosoma and legs black; metasoma orange except first and last segment dark mahogany red to black; tibial spurs white. Setae of head mesosoma and legs white except mesonotum black; metasoma with golden setae. *Head*. Median area of clypeus concave, anterior margin straight, posterior elevated margin not evenly arcuate, reflexed medially forming a tubercle; mandible ventral margin excised, forming a large basal tooth; ocelli small, distance between eye margin and lateral ocellus 3.2 × diameter of lateral ocellus. *Mesosoma*. Scutellum evenly convex, punctate throughout; enclosed area of propodeum not elevated posteriorly; tegula mostly impunctate and glabrous except anterior and inner margins with micropunctures and setae. *Metasoma.* Posterior margin of T7 not emarginate medially; elevated portion of T7 terminating in a very prominent pointed tooth; S1 with median

longitudinal carina; S6 without lateral tubercle; S7 with basal lateral tubercle; S8 with oblique ridge, without median tumid elevation posteriorly.

Material examined. **PANAMA: Darien** Prov.: P. Nac. Darien: Estac. Cruce de Mono, 11−28 feb 1993, R. Cambra, 3♀, 2♂ (MIUP); Estac. Rancho Frio, Pirre, 20 mar−5 abr 2000, Cambra & Santos, 2♂; 7−16 nov 2000, Cambra & Santos, 1♀ (MIUP).

Distribution: Panama (Darien, Las Cruces trail: Mickel, 1938).

Comments: One male specimen of *T. segesta*, collected in Estac. Rancho Frio, is only 5 mm in length. It is the smallest male specimen examined of the genus *Timulla* in Panama; other males within the genus generally range from 9 to 17 mm in body length.

Timulla segesta is closely related to *Timulla lilea*. The female of *T. segesta* has the mesosoma slightly but distinctly broader posteriorly than anteriorly in dorsal view, while in *T. lilea* the mesosoma is not at all broader posteriorly than anteriorly. The males of *T. segesta* and *T. lilea* are the only species in Panama with the median impunctate area of T7 terminating in a very prominent, polished tooth or tubercle. The males of these species differ in both structure and color, as presented in the key above.

Timulla subrobusta (Cameron, 1894); female
(Figs 7, 23, 29, 37)

Mutilla talus Cameron, 1894: 282−283; male, Bugaba, Chiriqui, Champion, British Museum Natural History. **NEW SYNONYMY.**

Material examined. **COSTA RICA**, **Guanacaste** Prov.: Est. Las Pailas, 800 m, P.N. Rincon de la Vieja, 9−25 feb 1993, D. Garcia, 1♀; 8−26 may 1994, K. Taylor, 1♂ (INBio, MIUP); Est. Maritza, 600 m, W ladera volcan Orosi, 1 ago−1 oct 1992, malaise, 1♀ (INBio)**;** Est. Pitilla, 700 m, 9 km S Sta. Cecilia, mar 1991, C. Moraga, 2♂; feb 1990, C. Moraga, 1♂; may 1988, 1♂; nov1988, 1♂; 21 mar−21 abr 1989, 1♂; feb 1993, C. Moraga, 1♂; ene 1989, 1♂; sep 1988, 1♂; nov 1988, C. Chaves, 1♂ (INBio, MIUP); Est. Sta. Rosa, 300 m, P.N.

Guanacaste, abr 1991, G. Fonseca, 1♂; ene 1992, G. Fonseca, 1♂ (INBio, MIUP); 3 km NO de Nacaome, 100 m, P.N. Barra Honda, 3−30 may 1993, M. Reyes, 1♂ (INBio); Est. Palo Verde, 10 m, P.N. Palo Verde, 25 mar−21 abr 1992, A. Gutierrez, 1♂ (INBio). **Puntarenas** Prov.: Est. Quebrada Bonita, 50 m, Res. Biol. Carara, jul 1992, Saborio, 1♀; abr 1993, Saborio., 1♀; jul 1993, R. Guzman, 1♀; nov 1993, J. Saborio, 1♀; dic 1994, J. Saborio, 1♀; abr 1992, J.Saborio, 1♀; abr, 1995, R. Guzman, 1♀ (INBio, MIUP); Rancho Quemado, 200 m, Peninsula de Osa, 12−24 may 1993, A. Gutierrez, 1♂ (INBio); Est. Carara, 200 m, Res. Biol. Carara, feb 1990, R. Zuñiga, 1♂ (INBio); Sector Laguna Meandrica, 100 m, Res. Biol. Carara, jun 1990, R. Zuñiga, 1♂ (INBio); Est. Quebrada Bonita, R.B. Carara, 50 m, abr 1994, 3♂; may 1994, R. Guzman, 1♂; mar 1994, 1♂; may 1993, J. Saborio, 1♂; may 1994, J. Saborio, 2♂; ene 1995, R. Guzman, 1♂ (INBio, MIUP); P.N. Manuel Antonio, Quepos, 80 m, may 1991, R. Zuñiga, 1♂ (INBio); Est. Sirena, P.N. Corcovado, 1−100 m, abr1994, G.Fonseca, 1♂ (INBio). **Alajuela** Prov.: Bijagua, 20 km S Upala, 20 ene−12 feb 1991, 2♂; 16 ene 1991, 1♂; 5 feb 1991, 1♂; 19 feb 1991, 1♂; 5 mar 1991, 2♂; 12 mar 1991, 1♂; 19 mar 1991, 1♂; 2 abr 1991, 1♂; 5 abr 1991, 1♂; 8 abr 1991, 1♂; 12 abr 1991, 1♂; 17 abr 1991, 1♂; 18 abr 1991, 2♂; 27 abr 1991, 1♂; 29 abr 1991, 2♂; 12 may 1991, 1♂; 11−15 may 1990, 1♂ (INBio, MIUP); Finca Josephina, 2 km S. Pital, 5−27 nov 1988, 3♂; 5−28 sep 1988, 1♂ (INBio, MIUP); Sector San Ramon, 620 m, abr 1994, P. Rios, 1♂ (INBio). **Heredia** Prov.: La Selva Res. Stat., 24−30 ago 1988, W. J. Hanson, 1♂ (INBio). **San Jose** Prov.: Cerro Bares, 1756 m, Zona Protectora, Cerro Turrubares, abr 1990, R. Zuñiga, 1♂ (INBio); Est. Bijagual, N. de Bijagualito, 500 m., mar 1995, J. Saborio, 1♂ (INBio). **PANAMA**: **Chiriqui** Prov.: Rio Sereno, Miraflores, 8 feb 1994, A. Rodriguez, 1♀, 1♂ (MIUP).

Distribution: Mexico, Costa Rica, and Panama (Chiriqui) (Mickel, 1938).

Comments: This was the last of the 16 Panamanian *Timulla* species to be recognized from both sexes. The association is based on coincidental distribution and the fact that all other Panamanian species were recognized from both sexes

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Timulla tumidula Mickel, 1938; male
(Figs 5, 24, 33, 41)

Female description. Body length 11.5 mm. *Color.* Integument of head, legs and metasoma black; tibial spurs white; mesosoma red (Fig. 24). Setae of head white except vertex mostly black; mesosoma dorsum with dark red setae; mesopleura with white setae; metasoma posterior marginal white pubescent band of T1 and T2 complete; lateral white pubescent stripes on T2 not continuous from anterior to posterior margins; T3 and T4 with black setae, without lateral longitudinal bands of white pubescence; T5 with lateral white pubescence; sterna with white setae. *Mesosoma* broader posteriorly than anteriorly; scutellar scale present; sides of propodeum with large close punctures; lateral margins of propodeum weakly crenulate, without distinctive teeth. *Metasoma.* Basal two-thirds of pygidial area irregularly rugose; posterior third weakly sculptured.

Material examined. **COSTA RICA**, **Alajuela** Prov.: Sector San Ramon, 800 m, 11−15 abr 1994, M. Zumbado, 1♂; 11−15 abr 1994, 620 m, E. Araya, 1♂ (INBio, MIUP); Sector San Ramon de Dos Rios, 620m, 20 feb− 5 mar 1995, F. Quesada, 1♂; 18 mar− 13 abr 1995, F. Quesada, 1♂, 1♀ (mating pair), 27 Apr− 11 May 1995, F. Quesada, 1♂, 1♀ (mating pair) (INBio, MIUP); Est. San Ramon Oeste, 620m, 3−19 abr 1994, 2♂ (INBio, MIUP); San Cristobal, 600−620m, 3−23 mar 1997, F. Quezada, 1♂ (INBio); Rio San Lorencito, 900 m, Res. For. San Ramon, 5 km N Colonia Palmarena, mar 1990, 1♀ (INBio); Alajuela, 9♂ (INBio, MIUP); Bijagua, 20 km S Upala, 6 ene 1991, 1♂; 8 ene 1991, 1♂; 29 ene 1991, 1♂; 20 ene−12 feb 1991, 4♂; 5 feb 1991, 1♂; 7 feb 1991, 2♂; 12 feb 1991, 2♂; 14 feb 1991, 1♂; 16 feb 1991, 1♂; 5 mar 1991, 1♂; 17 mar 1991, 1♂; 28 mar 1991, 2♂; 2 abr 1991, 1♂; 4 abr 1991, 1♂; 5 abr 1991, 1♂; 12 abr 1991, 1♂; 8 abr 1991, 1♂; 18 abr 1991, 1♂; 17 abr 1991, 1♂; 29 abr 1991, 1♂; 11−15 may 1990, 1♂; 12 may 1991, 1♂; 16 may 1991, 1♂; jun 1990, 3♂; 25 dic 1990, 3♂ (INBio, MIUP). **Cartago** Prov.: Monumento Nacional Guayabo, A.C.A.C. Amistad, 1100 m, jul 1994, G. Fonseca, 1♂; sep 1994, G. Fonseca, 1♂; Cartago, 2♂; Turrialba, Exp. Stat., 20 ago 1989, 2♂ (INBio, MIUP). **Guanacaste** Prov.: Est. Pitilla, 700 m, 9 km S. Sta. Cecilia, 4−25 nov 1991, C. Moraga, 1♀; nov 1989, 1♀; mar 1990,

2♀; may 1989, 1♀; jun 1989, 1♀; ago 1994, C. Moraga, 1♀; 9−20 nov 1993, C. Moraga, 1♀; sep 1993, malaise, 1♀; jun 1994, P. Rios, 1♀, 21 mar−21 abr 1989, 8♂; ago 1988, 3♂; may 1988, 1♂; jul 1988, 1♂; nov 1988, 1♂; jul 1991, P. Rios, 1♂; abr 1991, P. Rios, 1♂; 31 mar−29 abr 1992, K. Taylor, 1♂; mar 1991, C. Moraga, 4♂; abr 1991, 1♂; may 1991, 1♂; dic 1989, 1♂; nov 1989, C. Chaves, 1♂; 18 abr−19 may 1993, P. Rios, 1♂; mar−15 abr 1994, 1♂; may 1995, P. Rios, C. Moraga, 2♂; jul 1995, C. Moraga, P. Rios, 1♂; ago 1994, 2♂ (INBio, MIUP); Est. Maritza, 600 m, W. ladera volcan Orosi, 27 feb−10 mar 1992, 6♂; abr 1995, 1♂ (INBio, MIUP); Est. Las Pailas, P.N. Rincon de la Vieja. A.C. Guanacaste, 800m, 12−23 ene 1994, D. Garcia, 1♂; 5−23 ago 1994, K. Taylor, 1♂; 12 abr−4 may 1994 1995, K. Taylor, 1♂ (INBio, MIUP); Sector Sta. Maria-Pailas, Sendero a Pailas, 815 m, 18 nov 1997, F. Quesada, 1♂ (INBio). **Heredia** Prov.: El Ceibo, P.N. Braulio Carrillo, 400−600 m, oct 1989, R. Aguilar, 2♂; sep 1989, R. Aguilar, 1♂ (INBio, MIUP); La Virgen, Sarapiqui, 220 m, 9−24 abr 1993, M. Ortiz, 1♂ (INBio); Est. Magsasay, P.N. Braulio Carrillo, 200 m, mar 1991, M. Zumbado, 1♂; jul 1991, A. Fernandez, 1♀; ene 1991, M. Barrelier, 1♀ (INBio, MIUP). **Limon** Prov.: Cerro Tortugero, P.N. Tortugero, 100 m, abr 1989, R. Aguilar, 2♀ (INBio, MIUP); Amubri, 70 m, Talamanca, 12−30 sep 1992, G. Gallardo, 1♀ (INBio); Est. Cuatro Esquinas, P.N. Tortuguero, 1♂; jun 1991, J. Solano, 1♀ (INBio); Sector Cocori, 30 km N. de Cariari, Finca E. Rojas, 100−150m, abr 1994, E. Rojas, 2♂; feb 1994, 3♂; ene 1994, 3♂; nov 1993, 1♂; mar 1992, 1♂; 5 jun− 5 jul 1992, 1♂ (INBio, MIUP); Sector Cerro Cocori, Fca. de E. Rojas, 150 m, ene 1993, E. Rojas, 3♂; abr 1994, E. Rojas, 1♀; oct 1993, E. Rojas, 1♀; ene 1992, E. Rojas, 4♂; oct 1991, 2♂; feb 1993, 1♂; may 1993, 3♂; mar 1993, 1♂; 31 ene−21 feb 1992, 2♂; nov 1991, 1♂; abr 1992, 1♂; 28 may−17 jun 1992, 2♂; 31 ago 1992, 1♂; dic 1992, 1♂; nov 1992, 1♂; mar 1992, 1♂; jun 1991, 2♂; 10 sep−14 oct 1992, 1♂; mar 1991, 1♂ (INBio, MIUP); Cerro Tortugero, P.N. Tortugero, 100 m, feb 1992, R. Delgado, 2♂; abr 1989, R. Aguilar, 1♂; dic 1989, J. Solano, 1♂ (INBio, MIUP); Valle La Estrella, R.B. Hitoy Cerere, A.C.A.C. Amistad, 100 m, jul 1994, M. Segura, 1♂ (INBio); Sardinas, Barra del Colorado, 15 m, 4−11 ene 1995, F. Araya, 1♂; 26 mar 1996, F. Araya, 1♂; 23 abr 1996, F. Araya, 1♂ (INBio, MIUP); Amubri, 70 m, 3−28 feb 1995, G. Gallardo, 1♂ (INBio); Limon, 3♂ (INBio, MIUP); 7 mi N. Guacimo, 22 feb−3 mar

1988, 1♂ (INBio). **PANAMA: Bocas del Toro** Prov.: PILA, Wekso-Teribe, 17−24 oct 1999, A. Santos, 4♂, 1♀ (MIUP).

Distribution: Costa Rica and Panama (Bocas del Toro). First record for Panama.

Comments: The sex association is based on coincidental distribution and the capture of two mating couples (see material examined). *Timulla tumidula* is closely related to *T. connexa* and *T. labdace*. The female of *Timulla tumidula* is recognized by lacking lateral white pubescent patches on T3 and T4, while *T. connexa* and *T. labdace* have lateral white pubescent patches on T3 and T4.

MATING BEHAVIOR IN *Timulla*

Timulla runata Mickel 1938
Female and male from Panama, Veraguas, captured on the banks of the Santa Maria River, 20 km S. of Santa Fe, **August 8**, 1987.

12:45 pm: Both, male and female, were placed in the same transparent plastic box.

12:49 pm: The male grasped the female with his mandibles by the pronotal collar, with the male in position on the female. For 35 minutes the male dragged the female in short flights and actively walking but with short stops. During those 35 minutes the female was passive and her legs flaccid. The male at that time flexed the metasoma four times towards the direction of the female's pygidium in possible copulation attempts but there was no contact. During some of the short stops the male rubbed his pygidium and wings with his hind legs; the female also rubbed her pygidium with her hind legs.

1:24 pm: A stationary stage was started, the male continued to hold the female with his mandibles and began rubbing his hind legs over the fore wings, passing them over the wings and lateral areas of the metasoma close to the felt lines. He also rubbed his pygidium with his hind legs; this occurred in cycles of 3–4 minutes. The male also rubbed his middle and hind legs at the tarsi level. The female rubbed her hind

legs at the level of the felt lines. Later, the male oscillated to the female laterally, towards left and right, holding her with his mandibles. In this phase, the male used his fore legs to help position the female; lateral movements were determined by turns of the male's head. The female kept her metasoma flexed towards the ventral part of her mesosoma; therefore, the male's attempts to make contact with the female pygidium were not successful.

3:00 pm: The female exposed the sting outside her metasoma for about one second and quickly retracted it inside her metasoma; immediately afterward, the female stretched her metasoma forward and the male, having his metasoma ventrally arched forward, made contact with the female's pygidial area to initiate the copulation phase. The female's metasoma was slightly flexed upward to make contact with the genitalia of the male.

3:03 pm: The male produced vibrations of his abdomen up and down. The vibrations were variable, mainly from 40 vibrations in 30 seconds to 60 vibrations in 40 seconds. The vibrations were interrupted for periods of 39 to 56 seconds. The observations of August 8 ended at 6:00 pm, while the male and female remained in copulation.

August 9:
6:00 am: Males and females continued in mating and with the same behavior.

11:00 am: The male released the female, terminating the copulation.

Timulla cordillera Mickel, 1938
Female and male captured in Peru, Madre de Dios, Manu Reserve, Pakitza Station.

July 2, 1993:
2:45 pm: Both wasps, male and female, were placed in the same transparent plastic box.

3:00 pm: The male grasped the female with his mandibles by the pronotal collar, with the male in position above the female. The male

rubbed his antennae on the female's eyes. The male and female groomed their own felt lines with their hind legs. The female remained mostly passive. The male continually moved his fore legs to touch the mesosoma of the female laterally and to preen the antennae. Later, the male oscillated the female laterally, left and right, holding her with his mandibles. In this phase, the male used his fore legs to help position the female; lateral movements are determined by turns of the male's head. The female remained with her antennae pointed backward below the mesosoma. The male did not try to make contact with the pygidium of the female. The male raised his metasoma and rubbed his anterior wings with his hind legs. The female rubbed her antennae with her fore legs for a few seconds. All of the above was repeated constantly during the first 20 minutes after the male grasped the female.

3:20 pm: The male with his fore legs rubbed his vertex and mesonotum, the female remained passive, only rubbing her felt lines with her legs and the male groomed her pygidium with his hind legs.

3:30 pm: The male again oscillated the female laterally, left and right, this time stronger for two minutes; a very audible stridulatory sound was produced (it could not be determined if the sound was produced by the female or the male). The female protruded her sting and there was contact between the pygidium of the male and that of the female. The male, for a few seconds, made lateral movements of his metasoma, maintaining genital contact with the female. The movements were stopped and the copulation started without displacement of the male and the female during that phase.

3:35 pm: The male produced vibrations of his metasoma up and down as described for *Timulla runata*. This repetitive behavior continued to be observed until 9:00 p.m., when the mating observations were stopped.

July 3:
6:40 am: They were still in copulation and immobile; the male only moved the antennae and the metasoma up and down. The female remained with her stinger exposed. This was maintained until 7:35 a.m.

7:35 am: The male, for a few seconds, made lateral movements of his metasoma; the female, with her hind legs, began to push the distal part of the male's metasoma; the male raised the metasoma and both genitalia were released. The female remained with her sting exposed for approximately 8 seconds, then retracted the sting within the metasoma.

July 5:
8:30 am: The male of *Timulla cordillera,* who copulated on July 2, was placed with four females that were collected from July 3–4. The male was not attracted to any of the four females and there was no copulation.

July 6:
8:30 am: One of the four previous females was placed with the male that copulated on July 2. About 5 minutes later we went to collect throughout the day. Upon returning, at 7:00 p.m., to Pakitza Station we observed both specimens in copulation. A person who was at Pakitza Station that day, informed us that at 2:20 p.m. he observed the male copulating with the female; therefore, courtship and mating would have started between 8:35 a.m. and 2:15 p.m.

9:00 pm: They were still in copulation with the same behavior described on July 2.

July 7:
7:30- 12:20 am: The copulation continued, with behavior equal to that described above.

12:20 pm. The male released the female, terminating the copulation.

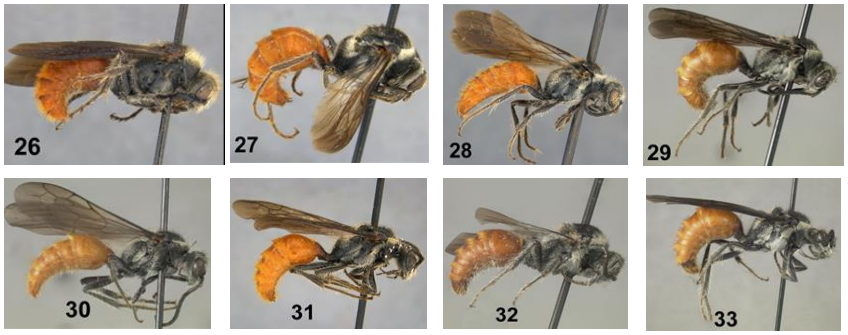
Comments of the mating behavior in *Timulla*

Very little is known about mating behavior in Mutillidae. In the Neotropical region, phoresis has been reported only in the genus *Timulla* (Mickel, 1937; Sheldon, 1970; Cambra & Quintero, 1992). Phoresis in *Ephuta*, a genus present in the Nearctic and Neotropical

region, has been mentioned only for two species from North America (Deyrup & Manley, 1986). In the Nearctic region, phoresis in the Myrmosinae (e.g. *Myrmosa unicolor*, Fig. 25) is also documented.

Field observations on mating behavior in *Timulla* were presented by Fattig (1936), Sheldon (1970), and Bartholomey *et al*. (2017), but none of them made observations about the duration of the copulation. The long time spent in copulation, observed in the laboratory, is unusual for Mutillidae. Copulation in *Timulla runata* lasted about 20 hours; while in *Timulla cordillera* it lasted approximately 16 hours. Experimental mating observations in New World mutillid genera by Brothers (1972) for *Pseudomethoca* and *Dasymutilla*; and Contreras (1993) for *Pertyella*, *Calomutilla* and *Lophomutilla*, showed short duration in copula, between 15 to 180 seconds. Mickel (1937) commented: "for some reason which is not readily apparent, the males and females of the genus *Timulla* are taken more often in copula than the two sexes of any other group of Mutillidae". We conclude that the long duration of courtship and copulation in *Timulla* is the main reason for that genus having the greatest number of sexual associations in the Neotropical Region.

Fig. 25. Myrmosinae, *Myrmosa unicolor* (det. RAC), male and female, captured in copula with Malaise trap.



Figs. 26–33. *Timulla* males, lateral view. 26. *T. porcata*, 27. *T. centroamericana*, 28. *T. lilea*, 29. *T. subrobusta*, 30. *T. bradleyi*, 31. *T. labdace*, 32. *T. prominens*, 33. *T. tumidula*.

Figs. 34–41. *Timulla* males head, frontal view. 34. *T. porcata*, 35. *T. centroamericana*, 36. *T. lilea*, 37. *T.subrobusta*, 38. *T. bradleyi*, 39. *T. labdace*, 40. *T. prominens*, 41. *T. tumidula*.

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