

STUDIES ON *TIMULLA* ASHMEAD
(HYMENOPTERA: MUTILLIDAE): NEW DISTRIBUTION
RECORDS AND SYNONYMIES, AND DESCRIPTIONS OF
PREVIOUSLY UNKNOWN ALLOTTYPES

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Abstract.—Sex associations permitted us to find and describe the previously unknown allotypes of: *Timulla nisa* Mickel, 1938, male; *T. absentia* Mickel, 1938, male; *T. bradleyi* Mickel, 1938, female. Eleven names are synonymized: *Timulla porcata* (Cameron), 1894 (*T. bituberculata* Mickel, 1938, NEW SYNONYM, male and *T. phiala* Mickel, 1938, NEW SYNONYM, female); *T. centroamericana* (Dalla Torre), 1897 (*T. proclivis* Mickel, 1938, NEW SYNONYM, male); *T. heterospila* (Gerstaecker), 1874 (*T. thura* (Cameron), 1894, NEW SYNONYM, male); *T. mexicana* (Cameron), 1894 (*T. amulae* (Cameron), 1894, NEW SYNONYM, male); *T. runata* Mickel, 1938 (*T. buscki* Mickel, 1938, NEW SYNONYM, male); *T. connexa* (Cameron), 1894 (*T. selene* Mickel, 1938, NEW SYNONYM, female); *T. adrastis* Mickel, 1938 (*T. pilatrix* Mickel, 1938, NEW SYNONYM, female); *T. taygete* Mickel, 1938 (*T. aureata* Mickel, 1938, NEW SYNONYM, female); *T. cordillera* Mickel, 1938 (*T. mulfordi* Mickel, 1938, NEW SYNONYM, female); *T. labdace* Mickel, 1938 (*T. raui* Mickel, 1938, NEW SYNONYM, female). Eight new distribution records are presented: *T. heterospila* (Gerstaecker), Venezuela, previously known from Panama and Colombia; *T. mexicana* (Cameron), Costa Rica, previously known from Mexico and Honduras; *T. adrastis* Mickel, Costa Rica, previously known from Mexico and Guatemala; *T. rufogastra* (Lepeletier), 1845, Panama, previously known from Colombia through French Guiana and Trinidad; *T. sieberi* Mickel, 1938, Perú, previously known only from Brazil, from the holotype and one paratype; *T. brancoensis* Mickel, 1938, Perú, previously known only from the holotype from Brazil; *T. prominens prominens* (Cameron), 1894, Panama, previously known from Mexico through Costa Rica; *T. daedala* (Cameron), 1894, Nicaragua, previously known only from holotype specimen collected in Yucatán, Mexico.

Key Words.—Insecta, sex associations, systematics, *Timulla* distributions, sex pheromones, Mutillinae

Timulla Ashmead, 1899 (Mutillinae), the largest and most cosmopolitan genus within the Mutillidae (Cambra & Quintero 1992), is widely distributed in the Americas, from Argentina to British Columbia, Canada, and the Caribbean islands (Mickel 1937a, 1938). The strongly sexually dimorphic species of *Timulla* have prompted descriptions of numerous species based on a single sex. Of a total of 172 Neotropical species and three subspecies of the subgenus *Timulla*, of *Timulla* (Mickel 1938, Nonveiller 1990), both sexes are known for only 27. In the present contribution, part of a series on the taxonomy, distribution, ecology and mating behavior of *Timulla*, we make 13 new sex associations, placing 11 names as junior synonyms (for five species previously known only from their males, and six only from their females), and describing the allotypes of three species (two males and one female). We also present new distribution records for eight species of *Timulla*.

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METHODS AND MATERIALS

Methods.—Diagnostic characters used to recognize the species were those used by Mickel (1938) in his revision of the Neotropical species of *Timulla*. Male genitalia were not used by Mickel (1938) to separate species. Instead, he used and illustrated many very reliable diagnostic characters present on the surface of the last tergum. Morphological terminology used in descriptions of previously unknown allotypes follows Mickel (1938), except for wing terminology, and the use of tergum (terga) and sternum (sterna) instead of tergite(s) and sternite(s), which follow Bohart & Menke (1976).

Male and female conspecificity was established by finding one, or several, of the following: phoretic pair(s) in nature (i.e., airborne male carrying female in his mandibles); experimental attraction, in nature, of flying male(s) by pheromones released from a caged female (in *Timulla*, we have not been able to find the opposite [e.g., males attracting females, in either nature or the laboratory]); finding individual(s) of both sexes in the field in close proximity and later obtaining, in a closed container, positive experimental mating(s) of at least one of the assorted pair(s). Erroneous heterospecific sexual associations are not known for *Timulla* (unpublished data); we have determined this by experimental attraction of males, in nature, using caged females (males fly upwind to caged females—otherwise, the male captured might be one just coincidentally flying by). Only after conspecific sex association, can the following take place: courtship by the male (quite elaborate in some species [unpublished data], see Fig. 1) and copulation (Fig. 2) if the female submits (courted females often refuse mating by flexing the distal part of the abdomen forward so that the male cannot have access to the genitalia) (unpublished data).

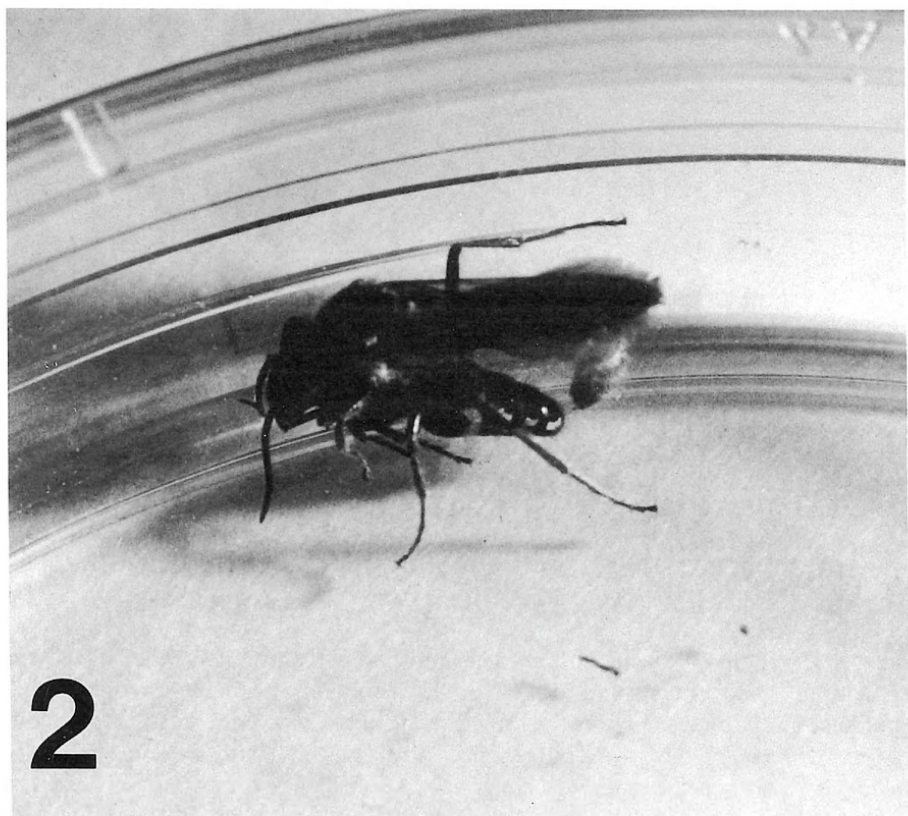
Materials.—Females were captured with forceps, and males (in phoretic pairs) were captured with entomological nets (kept alive for experimental matings) and Malaise traps (killed in alcohol). Sex association experiments were carried out in the laboratory, in 15 cm diameter glass petri dishes, at about 27° C. The 11 × 13 × 5 cm cages, used to enclose females for the experimental attraction of conspecific males, were built of wood, and each had two lateral openings covered with fine metallic mesh, to allow air circulation. Care was taken to wash each cage after every experimental run, to remove female pheromones remaining in the cage that might give erroneous results if the cage were used later with another species.

Institutional Abbreviations.—Specimens studied (and deposited, as indicated) were from the British Museum (Natural History) [BM(NH)]; Cornell University Insect Collection, Ithaca (CUIC); U.S. National Museum of Natural History, Smithsonian Institution (NMNH); Museum National d'Histoire Naturelle, Paris (MNHN); Insect Collection, Dept. of Entomology, University of Minnesota, St. Paul (ICUM); U.S.D.A. Bee Biology and Systematic Laboratory, Utah State University, Logan (BLCU); Museo de Invertebrados "G. B. Fairchild", Panama (MIUP); Zoologisches Museum, Humboldt Universitat, Berlin (ZMHB).

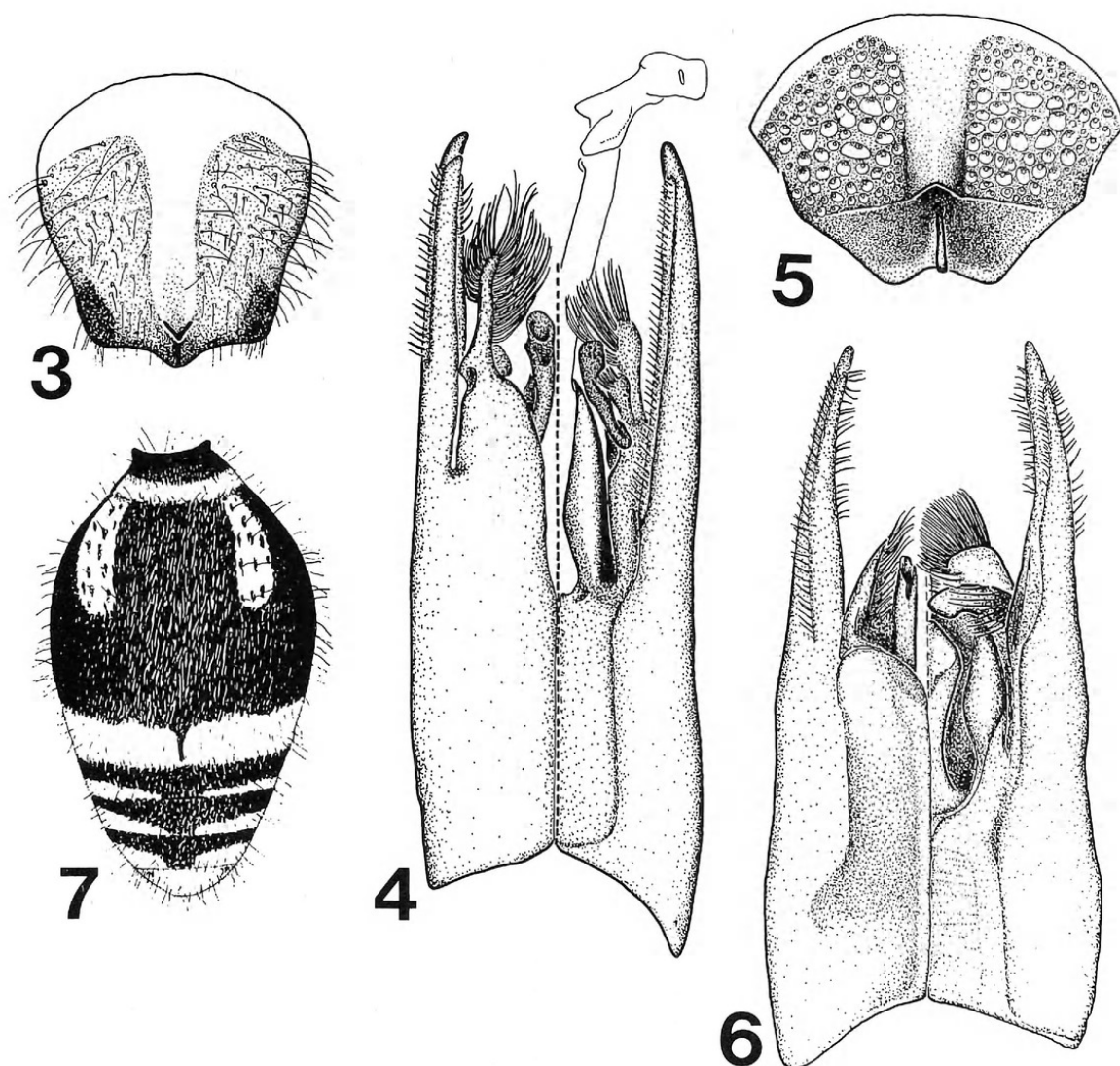
ALLOTYPE DESCRIPTIONS

Timulla (Timulla) nisa Mickel, 1938
(Figs. 1–4)

Timulla nisa Mickel, 1938: 592–593. Type locality: PANAMA. Ancon, [ex] Canal



Figures 1–2. *Timulla nisa*, living pair. Figure 1. Courtship; female hangs from male's mandibular clasp, her legs folded. Figure 2. Mating, winged male about to insert genitalia into receptive female.



Figures 3–7. Allotypes. Figure 3. *Timulla nisa*, male tergum 7. Figure 4. *Timulla nisa*, male genitalia, dorsal view (right half), ventral (left half). Figure 5. *Timulla absentia*, male tergum 7. Figure 6. *Timulla absentia*, male genitalia, dorsal view (right half), ventral (left half). Figure 7. *Timulla bradleyi*, female abdomen, dorsal.

Zone. Holotype female deposited NMNH, No. 52132, examined; Cambra & Quintero 1992: 468–469.

Allotype. — Male, designated here (deposited MIUP), “Cerro Cara de Iguana, El Valle de Antón, Coclé Province, 2–3 Oct 1988, R. Cambra.”

Description. — *Allotype, male*. Head, thorax, legs and first abdominal segment black, remainder of abdomen ferruginous; head, thorax and legs covered with pale pubescence, except mesonotum with sparse, black pubescence; abdomen beneath clothed with sparse, pale pubescence, except distal portion of final sternum, with sparse, fulvous pubescence; terga clothed with fulvous pubescence. Head, mandibles deeply excised beneath and with conspicuous tooth beneath near base; posterior, elevated margin of glabrous clypeal area, evenly arcuate; scape distinctly bicarinate beneath; antennal scrobes carinate above; ocelli small, distance between eye margin and lateral ocelli equal to $3 \times$ greatest diameter of latter; parapsidal furrows present and deep on posterior two-thirds of mesonotum; scutellum evenly convex, not gibbous, punctate throughout; enclosed area of propodeum elevated posteriorly into a distinct tubercle; tegula glabrous, impunctate, except for anterior and inner margins and postero-inner quadrant, all with fine punctures and sparse, pale pubescence. Abdomen, second tergum with sparse, moderate punctures on the disk, becoming closer laterally. Median impunctate area of last tergum

(Fig. 3) terminating in very short, almost obsolete arms of Y-shaped carina; posterior margin of last tergum not emarginate medially; sixth sternum without posterolateral tubercles; seventh sternum with pair of weak, posterolateral tubercles; last sternum with pair of weak, lateral ridges on anterior one-half, ridges not elevated posteriorly in dentiform tubercles. Legs, postero-mesal angles of intermediate coxae tuberculate; calcaria pale. Wings, proximal one-third subhyaline, distal two-thirds fuscous; submarginal cell II receiving first recurrent vein distinctly beyond middle; submarginal cell III present but less distinct than II and receiving second recurrent vein at three-fifths distance from base to apex. Body length, 11.5 mm.

Discovery of the male of Timulla nisa.—Numerous females, which we identified as *T. nisa*, and males, not matching the description of any previously known species of *Timulla*, were collected in close proximity to each other. The subsequent courtship and mating of one pair (Figs. 1, 2), when placed together in a closed container, confirmed their conspecificity. The male specimen of that pair, is designated here as the allotype of the species. Males of *T. nisa* will key to *T. taygete* Mickel in couplet 38 of Mickel's keys (1938: 539), a species distributed from Mexico to Guatemala, Honduras, Belize and Costa Rica. It differs from *T. taygete* in having the enclosed area of the propodeum elevated posteriorly into a distinct tubercle, and the postero-inner angles of the intermediate coxae tuberculate.

Distribution.—Panama, Colombia, Venezuela, and Trinidad, in lowland and premontane rain forests.

Material Examined.—COLOMBIA. Valle Restrepo, Campo Alegre (1100 m), 10 Feb 1984, O. Cepeda, 1 female (MIUP); Risaralda, Ucomari, Oct 1990, 1 female (MIUP).

Timulla (Timulla) absentia Mickel, 1938
(Figs. 5, 6)

Timulla absentia Mickel, 1938: 653–654. Type locality: COSTA RICA (no additional data). Holotype female deposited Museo Civico di Historia Naturale, Genoa, Italy; Cambra & Quintero 1992: 467.

Allotype.—Male, designated here (deposited MIUP), "Playa Venado, Veracruz, [Panama Province], Panama, 8 Nov 1988, R. Cambra" (female and allotype male mounted in same pin).

Description.—*Allotype, male.* Head, thorax and legs integument, black, clothed with pale pubescence, except for mesonotum with sparse, black pubescence; abdomen integument entirely ferruginous, clothed with sparse, pale pubescence, terga clothed with sparse, fulvous pubescence. Head, mandibles deeply excised beneath and with conspicuous tooth beneath near base; posterior elevated margin of glabrous clypeal area, subarcuate, with a very slight angle medially; scape distinctly bicarinate beneath; antennal scrobes carinate above; ocelli small, distance between eye margins and lateral ocelli equal to $3.5 \times$ greatest diameter of latter. Thorax, parapsidal furrows obsolete on anterior one-third of mesonotum; scutellum evenly convex, not gibbous, punctate throughout; enclosed area of propodeum not elevated posteriorly to form a distinct tubercle, sides converging towards tip to form distinct angle; tegula glabrous, impunctate, except anterior and inner margins and postero-mesal quadrant, all with fine punctures and sparse, pale pubescence. Abdomen, second tergum with sparse, moderate punctures on disk, becoming closer laterally, and the broad, posterior margin with distinct, very small punctures; median impunctate area of last tergum (Fig. 5) terminating in an inverted V-shaped carina; posterior margin of last tergum emarginate medially; sixth sternum with pair of weak posterolateral tubercles; seventh sternum with pair of distinct, posterolateral tubercles; last sternum with pair of lateral ridges on anterior one-half, ridges elevated posteriorly forming dentiform tubercles. Legs, postero-mesal angles of intermediate coxae not tuberculate; calcaria pale. Wings, proximal three-fourths are subhyaline, distal fourth forming broad fuscous margin; submarginal cell II receiving first recurrent vein very slightly before middle; submarginal cell III present but less distinct than II and receiving second recurrent vein distinctly beyond middle. Body length, 9.5 mm.

Variation.—Body length varies, in males from 8–12 mm ($n = 4$), in females from 4–8.5 mm ($n = 50$).

Discovery of the male of Timulla absentia.—One phoretic pair was captured in Playa Venado. We identified the female as *T. absentia*. The male was undescribed and the specimen is designated here as the allotype of that species. The allotype male will key to *T. tyro* in couplet 8 of Mickel's key (1938: 537) which ranges from Arizona and California through Mexico. It differs from *T. tyro* in having the inverted carina on the final abdominal tergum V-shaped (U-shaped in *T. tyro*) and the legs entirely black (tibiae and tarsi are ferruginous in *T. tyro*).

Distribution.—Costa Rica and Panama. In Panama this species is confined to open land at sea level, and is rather common on sandy beaches of the Pacific coast.

Material Examined.—See allotype.

Timulla (Timulla) bradleyi Mickel, 1938
(Fig. 7)

Timulla bradleyi Mickel, 1938: 632–633. Type locality: COSTA RICA. LIMÓN PROVINCE: Suretka. Holotype male deposited CUIC; Cambra & Quintero 1992: 467.

Allotype.—Female, designated here (deposited MIUP), “El Copé, Coclé Province, Div. Continental (900 m), 22 Sep 1990, R. Cambra.”

Description.—*Allotype, female.* Head, abdomen and legs black, except tip of scape and basal one-third of femur, ferruginous; thorax ferruginous; head clothed with sparse, pale pubescence, except vertex with sparse, black pubescence; thorax clothed with sparse, pale pubescence, except dorsum clothed with sparse fuscous pubescence; legs clothed with sparse pale pubescence; abdomen beneath clothed with sparse, pale pubescence, thick at posterior margins of sterna; abdominal terga for most part, black pubescent, pale pubescent markings as follows: first tergum with narrow, complete, posterior marginal band; second tergum with pair of anterior, longitudinal stripes not extending to transverse midline, and a posterior marginal band narrowly interrupted medially with black; terga 3–5 each with pair of transverse spots extending along the posterior margin to the posterolateral angle (Fig. 7). Head, antennal scrobes carinate above; front and vertex with large, deep punctures. Thorax, not broader posteriorly than anteriorly, lateral margins of dorsum of thorax shallowly emarginate at mesonotal area; scutellar scale present; lateral margins of posterior face of propodeum not denticulate; sides of propodeum with moderate close punctures posteriorly; second tergum with large, distinct punctures visible through the pubescence. Abdomen, pygidial area microgranulate, almost smooth; second sternum with large, distinct, closely set punctures. Body length, 8.5 mm.

Discovery of the female of Timulla bradleyi.—After two years of intense collecting of mutillids in El Copé, near the Continental Divide (approx. altitude, 900 m), Coclé Province, Panama, *T. bradleyi* was the only species of *Timulla* whose female was unknown to us. In 1990, we were fortunate to collect a series of males of *T. bradleyi* in close proximity to females not previously described; one of these females, placed in an entomological net, attracted a male, later identified as *T. bradleyi* (the male flew upwind toward the female, confirming their conspecificity). That female specimen is designated here as the allotype of the species. The female of *T. bradleyi* keys to *T. manni* Mickel in couplet 98 of Mickel's keys (1938: 551), a species known from Bolivia, Argentina, and Chile. It differs from *T. manni*, and all the species of the genus, in the following combination of characters: pale pubescent bands on terga three to five not reaching anterior margins and inter-

rupted medially, pygidial area microgranulate, posterior pale pubescent band of second tergum narrowly interrupted medially with black.

Distribution.—Costa Rica and Panama, in premontane rain forests.

Material Examined.—COSTA RICA. *CARTAGO PROVINCE*: Turrialba, CATIE, 26–29 Jun 1986, G. Bohart, W. Hanson, 3 males (BLCU); Turrialba Experim. Station, 20 Aug 1989, F. D. Parker, 1 male (BLCU). PANAMA. *COCLÉ PROVINCE*: El Copé, 21 Feb 1990, R. Cambra, 3 males (MIUP); 14 Jun 1990, D. Quintero & A. Mena, 3 males (MIUP); 1–2 Sep 1990, R. Cambra, 12 males (MIUP); 9–10 Oct 1990, R. Cambra, 1 female (MIUP).

NEW SYNONYMY, INCLUDING THREE SPECIES WITH
NEW DISTRIBUTION RECORDS

Timulla (Timulla) porcata (Cameron), 1894
(Figs. 8, 9)

Mutilla porcata Cameron, 1894: 275–276 (in part, not variety from Caldera, Chiriquí). Type locality: PANAMA. *CHIRIQUÍ PROVINCE*: Volcan de Chiriquí, 760–1220 m. Holotype female deposited BM(NH), examined. *Timulla porcata*: Mickel 1938: 656; Cambra & Quintero 1992: 469.

Timulla bituberculata Mickel, 1938: 634–635. Type locality: MEXICO. *OAXACA*: Tuxtepec. Holotype male deposited NMNH, No. 52147, examined. NEW SYNONYMY.

Timulla phiala Mickel, 1938: 663–664. Type locality: COSTA RICA. (no additional data). Holotype female deposited MNHN, examined. NEW SYNONYMY.

Notes on Synonymy.—New synonymies are based on the finding of two phoretic pairs in Guanacaste. We identified the males of these phoretic pairs as *Timulla bituberculata* Mickel and the females as *T. phiala* Mickel, and we are confident that both names refer to the same species. *Timulla porcata* (Cameron), known only from the holotype female collected in Panama, is nearly identical to *T. phiala*, except for one detail of coloration: the pale pubescent band on the posterior margin of the fifth abdominal tergum is narrowly discontinuous in *phiala* and widely separated by a median band of black hairs in *porcata*. We consider that this small difference in color does not represent a valid species difference and, thus, we place *T. phiala* as a junior synonym of *T. porcata*.

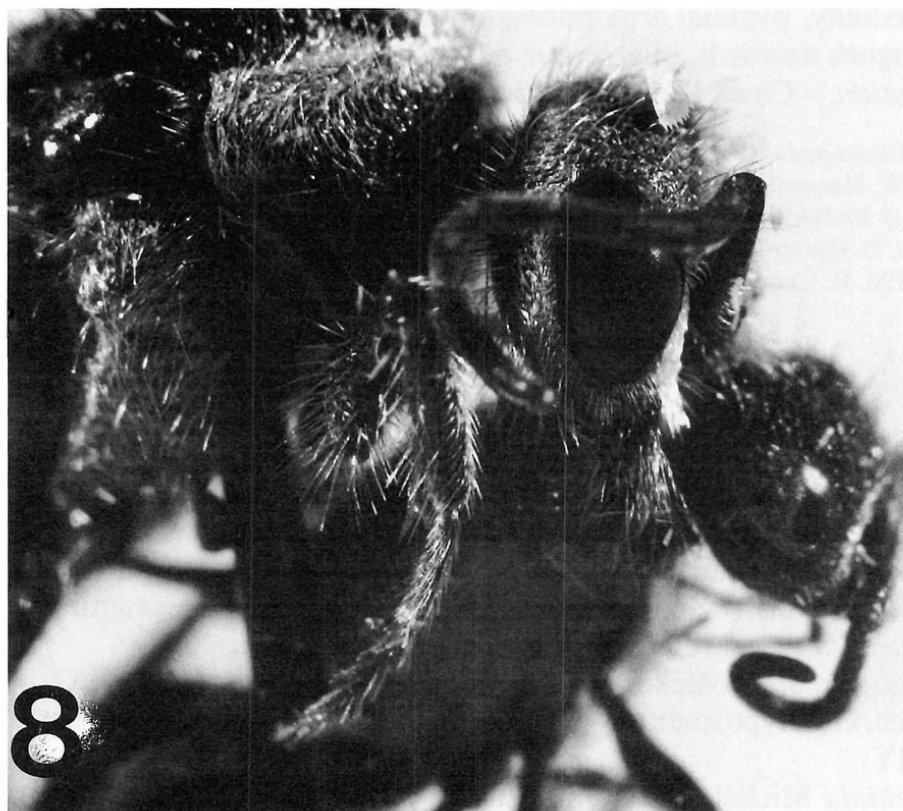
Distribution.—Mexico, Belize, Nicaragua, Costa Rica and Panama, in lowland and premontane rain forests.

Material Examined.—COSTA RICA. *GUANACASTE PROVINCE*: 14 km S of Cañas (Malaise trap), 11–15 Mar 1989 (phoretic pair in same pin), 1–11 Apr 1990 (phoretic pair in same pin), F. D. Parker (BLCU). NICARAGUA. Masaya, Laguna de Apollo, Nov 1991, E. van den Berghe, 3 females. PANAMA. *BOCAS DEL TORO PROVINCE*: Changuinola, 1–15 Jul 1991, R. Rodríguez, 1 female (MIUP); *Coclé Province*: El Valle de Antón, 9 Jan 1991, R. Contreras, 1 male (MIUP); 6 Jul 1991, R. Contreras, 1 female (MIUP).

Timulla (Timulla) centroamericana (Dalla Torre), 1897

Mutilla centralis Cameron, 1894: 271 (nec Burmeister 1875). Syntype locality: GUATEMALA. Paso Antonio, 123 m; PANAMA. *CHIRIQUÍ PROVINCE*: Volcan de Chiriquí, 760–1220 m. Syntype female deposited BM(NH), examined.

Mutilla centroamericana Dalla Torre, 1897: 22 (replacement name); *Timulla*



Figures 8–9. Phoretic pair, pinned. Figure 8. *Timulla porcata*, lateral view. Figure 9. Close-up, male's mandibular clasp of neck of female; arrow, male right mandible.

centroamericana: Mickel, 1938: 665, lectotype designation; specimen from Guatemala apparently was lost from BM(NH); Cambra & Quintero 1992: 467–468.

Timulla proclivis Mickel, 1938: 565–566. Type locality: COLOMBIA. MAGDALENA: Río Frío. Holotype male deposited ICUM. NEW SYNONYMY.

Notes on Synonymy.—Synonymy is based on the capture of two mating pairs in Panama Province: one, resting on the surface of a leaf of maize, in Tocumen, and the other, captured in Capira. We identified the females of these two pairs as *T. centroamericana* (Dalla Torre) and the males as *T. proclivis* Mickel; we are confident that both names refer to the same species, thus *Timulla centroamericana* (Dalla Torre) is a senior synonym of *T. proclivis* Mickel.

Variation.—Body length varies, in males 12–16.5 mm ($n = 20$), in females 6–10.5 mm ($n = 54$).

Distribution.—Panama, Colombia and Ecuador (Mickel 1938, Cambra & Quintero 1992). This species has a wide distribution in Panama, ranging from sea level up to 1100 m, on both the Atlantic and Pacific slopes.

Material Examined.—PANAMA. COLÓN PROVINCE: Santa Rita, 20–21 Dec 1990, R. Cambra, 1 female; PANAMA PROVINCE: Estación Experimental Universidad Panama, Tocumen, 1 Jul 1987, B. Gray, mating pair (MIUP); Capira, 24 Apr 1991, J. Coronado, [mating pair mounted in same pin] (MIUP); Río Perequeté, Corregimiento Playa Leona, La Chorrera, 17 Jan 1992, R. Cambra, 1 male, 2 females (MIUP).

Timulla (Timulla) heterospila (Gerstaecker), 1874

Mutilla heterospila Gerstaecker, 1874: 299. Type locality: COLOMBIA. Bogotá. Holotype female deposited ZMHB, No.19282. *Timulla heterospila*: Mickel 1938: 616–617.

Mutilla thura Cameron, 1894: 289–290. Type locality: PANAMA (no additional data). Holotype male deposited BM(NH), examined. *Timulla thura*: Mickel 1938: 599. NEW SYNONYMY.

Notes on Synonymy.—Synonymy is based on the experimental attraction, by a caged female of *Timulla heterospila*, of eleven males that we later identified as *T. thura*. On all occasions, the males flew upwind toward the caged female, thus indicating that they had detected the presence of the female not by sight but by pheromones liberated by her into the air. One of the captured males, attracted by the caged female, mated with her in the lab, confirming its conspecificity.

New Distribution Record.—The finding of *T. heterospila* in Venezuela represents a new distribution record, as this species was previously known only from the lowlands of Panama and Colombia. *Timulla heterospila* lives in open and modified habitats, from sea level up to 200 m altitude.

Material Examined.—PANAMA. PANAMA PROVINCE: Capira, 19 Jul 1991, J. Coronado, 1 female (MIUP); 4 Aug 1991, 2 males (MIUP); 21 Aug 1991, 5 males (MIUP); 22 Aug 1991, 2 males (MIUP); 26 Aug 1991, 2 males (MIUP). VENEZUELA: GUARICO [STATE]: Hato Masaguaral (44 km S of Calabozo), 3–10 May 1985, A. Menke & [J. M.] Carpenter, 1 female (NMNH).

Timulla (Timulla) mexicana (Cameron), 1894

Mutilla mexicana Cameron, 1894: 265. Type locality: MEXICO. Oaxaca. Holotype female deposited BM(NH), examined. *Timulla mexicana*: Mickel 1938: 638.

Mutilla amulae Cameron, 1894: 277. Type locality: MEXICO. GUERRERO: Amula. Holotype male deposited BM(NH), examined. *Timulla amulae*: Mickel 1938: 637–638. NEW SYNONYMY.

Notes on Synonymy.—New synonymy is based on the capture of one phoretic pair (we identified the female as *Timulla mexicana* and the male as *T. amulae*),

in Guanacaste, indicating that they are conspecific. We are confident that both names refer to the same species; the name of the male, *T. mexicana*, has page precedence over that of the female, *T. amulae*. Mickel (1938) suggested that *T. amulae* might be the male of *T. mexicana*.

New Distribution Record.—The finding of *Timulla mexicana* in Costa Rica represents a new distribution record, as this species was previously known only from Mexico and Honduras.

Material Examined.—COSTA RICA. GUANACASTE PROVINCE: EJA, 14 km S of Cañas, 15 Apr–6 May 1991, F. D. Parker [mounted in same pin] (BLCU); 17–18 Mar 1990, F. D. Parker, 4 males (BLCU); 18–19 Apr 1990, F. D. Parker, 1 male (MIUP); SAN JOSÉ: Escazú, 18–19 Mar 1988, F. D. Parker, 1 male (MIUP).

Timulla (Timulla) runata Mickel, 1938

Timulla runata Mickel, 1938: 592. Type locality: PANAMA. Gamboa. Holotype female deposited NMNH, No. 52131, examined; Cambra & Quintero 1992: 469.

Timulla buscki Mickel, 1938: 601–602. Type locality: PANAMA. PANAMA PROVINCE: Isla Taboga. Holotype male deposited NMNH, No. 52138, examined. NEW SYNONYMY.

Notes on Synonymy.—One female, that we identified as *Timulla runata*, and one male, identified as *T. buscki*, were captured in close proximity on the open, grassy edge of a gallery forest of the Santa María River. Minutes after their capture, they readily mated, after being placed together inside a plastic container, confirming their conspecificity. In addition, we examined a phoretic pair (we identified the female as *T. runata* and the male as *T. buscki*) from Caballero.

Variation.—Body length, in males 9.5–12 mm ($n = 24$), in females 4.5–7.5 mm ($n = 57$).

Distribution.—Panama and Colombia (Mickel 1938). This species, the most common *Timulla* in Panama (Cambra & Quintero 1992), is widely distributed in the lowlands of Panama, on both the Atlantic and Pacific slopes, from sea level up to 200 m.

Material Examined.—PANAMA. COCLÉ PROVINCE: Caballero, Antón, 30 Jan 1988, R. Rodríguez, 1 male, 1 female (MIUP); VERAGUAS PROVINCE: Santa María River, 20 km S of Santa Fé, 8 Aug 1987, 1 male, 1 female (MIUP).

Timulla (Timulla) connexa (Cameron), 1894

Mutilla connexa Cameron, 1894: 279–280. Type locality: PANAMA. CHIRIQUÍ PROVINCE: Bugaba. Holotype male deposited BM(NH), examined. *Timulla connexa*: Mickel 1938: 629–630 (reports males from Limón, Costa Rica).

Timulla selene Mickel, 1938: 655–656. Type locality: PANAMA. CHIRIQUÍ PROVINCE: Bugaba. Holotype female deposited BM(NH), examined. NEW SYNONYMY.

Notes on Synonymy.—New synonymy is based on the following evidence: (1) Collection of numerous males (that we identified as *Timulla connexa*) and females (that we identified as *T. selene*) at the same time and in close proximity to each other, at El Copé, and their subsequent matings when placed together in the laboratory; (2) Collection of two females, which we identified as *T. selene*, from Alajuela; males (*T. connexa*) were known already from Costa Rica but females

were not. *Timulla connexa* Cameron is a senior synonym of *T. selene* and we are confident that both names refer to the same species.

Variation.—Body length, in males 13.5–18.5 mm ($n = 24$), in females 6.5–10.5 ($n = 17$).

Distribution.—Costa Rica and west of Panama, in premontane, wet rain forests, at elevations ranging from 800 to 1000 m.

Material Examined.—COSTA RICA. ALAJUELA PROVINCE: Finca Josephina, 5–27 Sep 1988, F. D. Parker (BLCU). PANAMA. COCLÉ PROVINCE: El Copé, 24 Sep, 10 Oct 1990, 10 males, 8 females (MIUP).

Timulla (Timulla) adrastis Mickel, 1938

Timulla adrastis Mickel, 1938: 631–632. Type locality: MEXICO. Tuxpan. Holotype male deposited NMNH, No. 52146, examined.

Timulla pilatrix Mickel, 1938: 651. Type locality: MEXICO (no additional data). Holotype female deposited NMNH, No. 52151, examined (additional records for Guatemala). NEW SYNONYMY.

Notes on Synonymy.—New synonymy is based on one phoretic pair captured in Guanacaste; we identified the male in that phoretic pair as *Timulla adrastis* Mickel and the female as *T. pilatrix* Mickel. We are confident that both names refer to the same species. The name of the male has page precedence over that of the female, *T. pilatrix*.

New Distribution Record.—The finding of *Timulla adrastis* in Costa Rica represents a new distribution record, as the species was known previously only from Mexico and Guatemala.

Material Examined.—COSTA RICA [All specimens, except as indicated, were collected by F. D. Parker and deposited BLCU]. ALAJUELA PROVINCE: Bijagua, 20 km S of Upala, 6 Jan 1991, 1 male; same loc., 7 Feb 1991, 2 males; same loc., 16 Feb 1991, 1 male; same loc., 5 Mar 1991, 1 male; same loc., 28 Mar 1991, 2 males; same loc., 2 Apr 1991, 1 male; same loc., 12 Apr 1991, 1 male; same loc., 29 Apr 1991, 1 male; GUANACASTE PROVINCE: 14 km S of Cañas, 21–22 Jan 1989, 1 male, 1 female, mounted in same pin; 14 km S of Cañas, 8–18 Mar 1988, 1 male; same loc., 3–9 Jul 1988, 1 male; same loc., 1 Aug 1988, 1 male; same loc., 28–29 Jan 1989, 2 males; same loc., 9–14 Feb 1989, 1 female; same loc., 18 Feb 1989, 1 male; same loc., 28 Feb 1989, 1 male; same loc., 1–5 Mar 1989, 1 male; same loc., 10 May 1989, 1 male; same loc., 7–10 Oct 1989, 1 male; La Taboga Forest Reserve, 9 km SW of Cañas, 17–27 Feb 1987, W. L. Rubink, 2 males.

Timulla (Timulla) taygete Mickel, 1938

Timulla taygete Mickel, 1938: 639–640. Type locality: MEXICO. YUCATÁN: Chichen Itza. Holotype male deposited ICUM.

Timulla aureata Mickel, 1938: 651–652. Type locality: COSTA RICA. Navarro Farm, near Cartago. Holotype female deposited NMNH, No. 52152, examined. NEW SYNONYMY.

Notes on Synonymy.—New synonymy is based on examination of two phoretic pairs captured by F. D. Parker in Guanacaste. We identified the males in these phoretic pairs as *Timulla taygete* and the females as *T. aureata*, confirming their conspecificity. Mickel (1938) suggested that *T. aureata* might be the female of *T. taygete*. The name of the male, *T. taygete*, has page precedence over that of the female, *T. aureata*.

Distribution.—Mexico, Guatemala, Honduras, Belize, and Costa Rica.

Material Examined.—COSTA RICA. GUANACASTE PROVINCE: 14 km S of Cañas, Costa Rica, 11–31 Jan, 15–24 Feb 1990, two phoretic pairs, each pair mounted in same pin (BLCU).

Timulla (Timulla) cordillera Mickel, 1938

Timulla cordillera Mickel, 1938: 566–567. Type locality: PERU. Río Pichio, Puerto Bormadez. Holotype male deposited CUIIC.

Timulla mulfordi Mickel, 1938: 617. Type locality: BOLIVIA. Río Beni, near the mouth of Río Mapiri. Holotype female deposited NMNH, No. 52140, examined. NEW SYNONYMY.

Notes on Synonymy.—New synonymy is based on the attraction, in Pakitza, by a living female, which we identified as *Timulla mulfordi*, of a male, identified as *T. cordillera*, that flew into the open mouth of a glass vial containing the female and attempted to mate her, confirming their conspecificity. We are confident that both names refer to the same species; the name of the male, *T. cordillera*, has page precedence over that of the female, *T. mulfordi*. In addition, we captured in Pakitza 11 males and 29 females, from 14 Feb to 10 Mar 1992.

Distribution.—Perú and Bolivia (Mickel 1938). This species ranges from the Amazonian forests of Perú, near sea level, to the eastern Andean slopes of Perú and Bolivia, at elevations from 300 to 1200 m.

Material Examined.—PERU. LORETO DEPARTMENT: Explorama Lodge, Yanamono River, 80 km NE Iquitos, 1–2 Nov 1990, D. Quintero & R. Cambra, 4 females (MIUP); MADRE DE DIOS DEPARTMENT: BIOLAT Biological Station, Pakitza, Río Manu, Perú, 8 Mar 1992, R. Cambra, 1 male, 1 female mounted in same pin (MIUP); 14 Feb–10 Mar 1992, 11 males, 29 females (NMNH, ICUM, BLCU, MIUP).

Timulla (Timulla) labdace Mickel, 1938

Timulla labdace Mickel, 1938: 630–631. Type locality: PANAMA. Barro Colorado Island. Holotype male deposited NMNH, No. 52145, examined.

Timulla rauui Mickel, 1938: 656–657. Type locality: PANAMA. Barro Colorado Island. Holotype female deposited NMNH, No. 52153, examined. NEW SYNONYMY.

Notes on Synonymy.—New synonymy is based on the capture of one phoretic pair in Cana (we identified the female as *Timulla rauui* and the male as *T. labdace*), indicating their conspecificity. We are confident that both names refer to the same species; the name of the male, *T. labdace*, has page precedence over that of the female, *T. rauui*.

Distribution.—Lowland tropical rain forests of central and eastern Panama, and in Colombia.

Material Examined.—PANAMA. DARIEN PROVINCE: Cana, Parque Nacional del Darién, 6 Apr 1991, R. Cambra, phoretic pair mounted in same pin (MIUP); 4–9 Apr 1991, R. Cambra, 10 males (MIUP); 5–12 Apr 1991, R. Cambra, 12 males, 1 female; 12 Apr 1991, R. Cambra, 4 females (MIUP).

NEW DISTRIBUTION RECORDS

Timulla (Timulla) rufogastra (Lepeletier), 1845

Mutilla rufogastra Lepeletier, 1845: 629. Syntype locality: “Amer. Mer.” Syntype male deposited Spinola Collection, Torino, Italy, No. 198.1. *Timulla rufogastra*: Mickel 1937b: 174–175 (lectotype designation); 1938: 598 (distribution records).

Variation.—Body length, 9.5–13 mm ($n = 14$), specimens from Panama.

Distribution.—This species was previously known from Colombia (Muzo, Boyacá; Río Frío, Magdalena), Venezuela, Trinidad, and French Guiana (Mickel 1938).

Material Examined.—(The capture from Panama, below, represents a new distribution record.) PANAMA. DARIÉN PROVINCE: Trocha Yaviza-Pinogana, 27–29 Mar 1990, R. Cambra, 14 males (MIUP).

Timulla (Timulla) sieberi Mickel, 1938

Mutilla lineola: Klug 1821: 307 (not Fabr.). Type locality: BRAZIL. Pará. Type female deposited ZMHB, No. 6627.

Timulla sieberi Mickel, 1938: 626–627 (Klug's specimen designated as holotype; one paratype, Brazil, Rio Arrayodos).

Distribution.—This species inhabits humid forest in the Amazonian basin, and was known previously only from Brazil.

Material Examined.—(The capture from Peru, below, represents a new distribution record.) PERU. Loreto Department: Explorama Napo Camp, Río Sucusari (affluent of Napo River), 157 km NE Iquitos, 10 Nov 1990, R. Cambra, 1 female (MIUP).

Timulla (Timulla) brancoensis Mickel, 1938

Timulla brancoensis Mickel, 1938: 623–624. Type locality: BRAZIL. AMAZONAS: Río Branco [Acre State]. Holotype female deposited ZMHB.

Distribution.—This species was known previously only from the holotype from Brazil (the type locality is in northwestern Brazil, some 400 km NE of Pakitza). *Timulla brancoensis* lives in the humid tropical forests of the Amazonian basin.

Material Examined.—(The captures from Peru, below, represent a new distribution record.) PERU. MADRE DE DIOS DEPARTMENT: BIOLAT Biological Station, Pakitza, Río Manu, 26 Feb 1992, R. Cambra, 1 female (MIUP); Malaise trap, 1–6 Mar 1992, R. Cambra, 1 female (MIUP); 5 Mar 1992, D. Quintero, 1 female (MIUP); 4 Mar 1992, R. Cambra, 1 female (MIUP).

Timulla (Timulla) prominens prominens (Cameron), 1894

Mutilla prominens Cameron, 1894: 273. Type locality: GUATEMALA. Capetillo. Holotype female deposited BM(NH), examined. *Timulla prominens*: Mickel 1938: 569–570.

Distribution.—The typical form of this species was known previously from the Isthmus of Tehuantepec, Mexico, through Costa Rica (Mickel 1938), while the only other subspecies, *T. prominens forreri* (Cameron), 1894, is a disjunct endemic of the highlands of Sierra Occidental, in the Mexican Nearctic.

Material Examined.—(The capture from Panama, below, represents a new distribution record.) PANAMA. BOCAS DEL TORO PROVINCE: Changuinola, 1–15 Jul 1991, R. Rodríguez, 2 females (MIUP).

Timulla (Timulla) daedala (Cameron), 1894

Mutilla daedala Cameron, 1894: 269. Type locality: MEXICO: North Yucatán. Holotype female deposited BM(NH), examined. *Timulla daedala*: Mickel 1938.

Distribution.—This species was known previously only from the holotype.

Material Examined.—(The capture from Nicaragua, below, represents a new distribution record.) NICARAGUA. MANAGUA: Laguna de Xilola, 9–10 Nov 1991, E. van den Berghe, 2 females (MIUP).

DISCUSSION

The sex associations of 13 species of *Timulla* presented in this paper number more than the eleven such associations presently known for all of North America. This brings to 40 the number of Neotropical species for which both sexes are known. With this new information, sexes have been associated for 24.8% (40 out of a total of 161) of Neotropical species of *Timulla*. This is still lower than for North America, 28.9%; however, only 38 species and subspecies are known from North America (Krombein 1979), about one-fourth as many as the Neotropics.

The new distribution records have expanded the ranges of several species of *Timulla*. The emerging pattern is one with few sympatric species (maximum number found is three) and numerous species with wide distributions. We need to obtain sex associations for well over 50% of the known species in order to be able to answer two troublesome questions: First, is the size of the geographic distribution of a species of *Timulla* directly correlated with degree of sexual dimorphism? That is, do species with females distinctly smaller than the males (and thus more easily transported to more distant localities in their phoretic flights), have larger ranges than those with less sexual dimorphism?; or, are their geographic distributions correlated to some other factor(s) (i.e., ecology, historical aspects, host distributions, etc.)? Second, do females “pay” males with sex after completing their phoretic flight? Further, if females allow mating to occur in flight, are they immediately dropped from the air by their satisfied males, as may be the case in bethylids and tiphiids?.

Most species of *Timulla*, both in the Neotropics and temperate areas, have males with a common color pattern: orange abdomen, and black head and thorax. This is probably a Batesian mimicry of widespread aculeate wasps, and an anti-predatory strategy by the defenseless sex. Although males of *Timulla* possess similar body coloration, their specific diagnosis is relatively easy because of numerous valid morphological details; contrastingly, females have fewer morphologic diagnostic characters and, in some groups of species, are very similar and difficult to identify.

We have stressed the importance of pheromone attraction and experimental pairing for increasing sex matching records of mutillid species. In addition, it is also important to attempt to obtain information through laboratory experiments of parasitism (useful for rearing unknown conspecific males, and completing, or verifying, sex associations) an effort not successful in our hands with *Timulla* (personal observations). We recommend the illustration of the male genitalia in future descriptions of *Timulla*, as it has valuable species diagnostic characters and it should prove valuable for future cladistic work. The penial valves (ventral face) are distinctly asymmetrical and the illustration of only half of the genitalia (Figs. 4, 6) does not show it.

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