

Two New and Highly Apomorphic Species of the *Lasioglossum* Subgenus *Evyllaes* (Hymenoptera: Halictidae) from Central America

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ABSTRACT Two new and apomorphic members of the *Lasioglossum* subgenus *Evyllaes* from Panama and Costa Rica are described. These species inhabit cloud forest habitats in Central America, an area and habitat not normally associated with high species diversity for bees in the genus *Lasioglossum*.

KEY WORDS systematics, taxonomy, zoogeography, phylogeny

THE GENUS *Lasioglossum* Curtis includes 1,144 described species from all continents of the world, except Antarctica (Michener 2000). The subgeneric groupings within *Lasioglossum* are numerous and are treated by some authors as separate genera (see Krombein et al. 1979, Moure and Hurd 1987) because they comprise such speciose and behaviorally diverse taxa. However, other authors treat *Lasioglossum* as a genus consisting of many subgenera (Ebmer 1987, 1995; Michener 1990; Michener et al. 1994). In this article, we refer to the genus *Lasioglossum* and its numerous subgenera, primarily because, although *Lasioglossum* s.l. is most likely monophyletic, the groupings within *Lasioglossum* (e.g., *Evyllaes* Robertson, *Lasioglossum* s.s., *Ctenonomia* Cameron) are potentially paraphyletic and even possibly polyphyletic (*Paralictus* Robertson).

Evyllaes is one of the more speciose subgenera of *Lasioglossum*. There are >100 described species and the greatest species diversity is in the Palearctic region (Michener 1979). Recent molecular studies (Danforth 1999) indicate that *Evyllaes* is massively paraphyletic with respect to the following weak-veined subgenera: *Dialictus* Robertson, *Paralictus*, *Sphecodogastra* Ashmead, *Sudila* Cameron, *Hemihalictus* Cockerell, and most likely *Acanthalictus* Cockerell (Packer, personal communication). This result is not contradicted by any morphological evidence—there are no unique and unreversed synapomorphies uniting all the species of *Evyllaes*.

The vast majority of *Evyllaes* are small, black (and occasionally weakly metallic) bees with few remarkable morphological features, as is true for other species of *Lasioglossum* s.l. Exceptions include the extreme head allometry exhibited by members of *Sudila* (Sakagami et al. 1996), enlarged heads in some female *Paralictus* (Wcislo 1997, 1999), male dimorphism in members of *Chilalictus* Michener (Houston 1970;

Knerer and Schwarz 1976; Kukuk and Schwarz 1987, 1988; Walker 1995), and the enlarged ocelli and compound eyes of nocturnal *Sphecodogastra* (Kerfoot 1967a, b; McGinley 1999). In this article we describe 2 highly apomorphic species of *Evyllaes* for the purposes of including one of them in a molecular analysis of *Lasioglossum* subgeneric relationships (Danforth 1999). These species are bizarre enough to warrant subgeneric status, but given that the higher classification of *Lasioglossum* is at the moment unclear, adding new subgenera in the absence of a well-resolved cladogram for the group will only serve to further confuse things. The species described below are further distinguished by the fact that they occur in Central America, which is not considered to be a region of high species diversity for any subgenera of *Lasioglossum* (Michener 1979).

The 2 species described below have been compared with species listed in Michener's (1954) treatment of the bees of Panama.

Materials and Methods

For examination of internal anatomy, specimens were cleared in hot 10% NaOH, washed in deionized water, and stored in depression slides immersed in glycerol. Specimens used for SEM were cleaned in a sonicator and critical-point dried before mounting. Scanning electron micrographs were produced with a Zeiss DSM 960 scanning electron microscope. For the morphological descriptions below, we followed the format and character numbering scheme of McGinley (1986). For descriptions of surface sculpture we use terms as defined in Harris (1979).

Results

Entries listed in bold are apomorphic features that serve to distinguish these 2 species from all other species of *Evyllaes*.

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Lasioglossum (Evylaeus) gattaca

Type Material. The female holotype is in the Cornell University Insect collection. The specimen is labeled PANAMÁ, Prov[incia] Chiriquí[.] road fr[om] Santa Clara to Volcan, 1.9 km WNW Rio Chiriquí Viejo, 1550 m[.] 8° 49' 07" N, 82° 40' 29" W[.] 3-vii-1996, WT Wcislo/HOLOTYPE *Lasioglossum (Evylaeus) gattaca* BN Danforth & WT Wcislo [red label].

Thirteen paratypes (9♀, 4♂) from localities listed in *Specimens Examined* were deposited in the Cornell University Insect Collection, the Museo de Invertebrados "Graham Fairchild," Universidad de Panamá, and the Smithsonian Tropical Research Institute.

Etymology. The specific epithet refers to the genetic code.

Distribution. Panamanian localities for *L. (E.) gattaca* and *L. (E.) hartmanni* (new species, described herein) are in the western part of the isthmus, a mountainous region formed by the Serranía del Tabasará and by the Cordillera de Talamanca that continues into Costa Rica (see Myers 1969). End-to-end these east-to-west ranges form the continental divide with unbroken highlands up to the ≈1,200 m contour in Panama, with isolated peaks up to 3,475 m (Volcán Barú) in Panama and 3,819 m in Costa Rica (Cerro Chirripó); in Panama they slope north to the Atlantic lowlands, and south through foothills to the Pacific ocean. The highlands contain montane rain forest or cloud forest, except on the higher peaks, with premontane moist or wet forest at lower elevations; temperatures are cool and equable, as typical of midlevel altitudes in the tropics. Long histories of human disturbance, especially at lower elevations, have significantly influenced the biota of much of the region (see Bennett 1968). These anthropogenic disturbances probably benefit sweat bees because halictids are generally scarce in mature rain forest (Michener 1954; W.T.W., unpublished data).

The type locality is in the Chiriquí Viejo river valley on the Pacific slope of the Talamanca range. The forest is seasonal because of a several-month dry season. In this region there are now extensive areas cleared of forest to create pastures used for dairy farming, small-scale agriculture, extensive sun- or shade-coffee cultivation on the slopes; scattered areas of forest remain on steeper slopes or along streams. The bees were collected on yellow composites blooming along the main road to the town of Volcán. Another specimen was collected flying over an earthen road running through a shade-coffee finca that is adjacent to La Amistad International Park, ≈20 km from the type locality.

Diagnosis. This species [as well as *L. (E.) hartmanni*] is distinguished from other species of *Evylaeus* by the following combination of apomorphic features: frons with 2 bulbous protuberances (located between the antennal bases and ocelli), vertex strongly carinate (Fig. 1a), elongate and coarsely striate dorsal surface to the propodeum (Fig. 1b), mesopleuron with conspicuous horizontal striae and 2 small protuberances located ventrally, basitarsal segment of foreleg with

apical acute projection extending beyond the apex of the 2nd tarsal segment (Fig. 2h), and, in males, sternum IV and V with paired patches of posteriorly directed branched hairs (Fig. 3 b and c). *L. (E.) gattaca* can be distinguished from *L. (E.) hartmanni* by characters listed in the diagnosis of *L. (E.) hartmanni*. The easiest way to distinguish the 2 species is by the color of the female metasoma: in *L. (E.) gattaca* the metasoma is reddish, whereas in *L. (E.) hartmanni* the metasoma is black to dark brown.

Description. Female: (1) Length 9.0–9.5 mm; (2) wing length 7.0–7.6 mm; (3) metasomal width 2.2–2.32 mm.

Structure. (4) Head slightly elongate (length/width ratio 1.04–1.08; Fig. 2g). (5) Gena width greater than eye width (gena 1.3 times eye in width); (6) rounded posteriorly (not produced, as in some subgenera of *Lasioglossum*, such as *Sudila*). (7) Supraclypeal area evenly rounded; (8) strongly protuberant below antennal bases. (9) Clypeus projecting ≈0.5 times its length below compound eyes; (10) surface flat; (11) without median sulcus. (12) Frontal carina well-developed between antennal bases. (13) Frons (between antennal bases and ocelli) with 2 distinct protuberances (Fig. 1a); distance between compound eye and lateral ocellus 1.2 times distance between lateral ocellus and vertex; (14) vertex strongly carinate (scoop-shaped in dorsal view) (Fig. 1a); width of vertex (from posterior margin of lateral ocellus to vertex) 0.28 mm; (15) lateral ocelli joined posteriorly by weakly impressed line. (16) Inner margins of compound eyes concave; converging slightly below (Fig. 2g). (17) Hypostomal carina well-developed; (18) anterior angle obtuse; (19) anterior carina nearly perpendicular to longitudinal carina. (20) Epistomal sulcus with anterior tentorial pits located laterad of clypeus (below junction of subantennal suture and epistomal sulcus). (21) Scape reaching 0.83 distance to vertex; conspicuously convex outward; (22) pedicel slightly longer than wide, longer than flagellomere 1; (23) flagellomere 1 slightly shorter than flagellomere 2. (24) Labrum with distal process fringed by stout, recurved setae; (25) basal elevation transverse and well-developed; (26) basal lateral depressions absent; (27) distal keel acutely pointed and lamellate; (28) distal lateral projection weakly developed between setae; (29) fimbrial setae elongate and recurved. (30) Mouthparts as in typical *Lasioglossum*: glossa shorter than prementum, maxillary palpi 6-segmented, labial palpi 4-segmented. (31) Mandible with small, subapical inner tooth.

(32) Pronotal lateral angle obtuse; (33) lateral ridge absent; (34) lateral sulcus weak. (35) Mesoscutal lip rounded; (36) only weakly elevated above pronotum; (37) mesoscutal line deeply impressed to 0.66 length of mesonotum; (38) parapsidal line 0.26 length of mesonotum. (39) Median scutellar impression weak. (40) Dorsal surface of propodeum 2.2 times metanotum in length (Fig. 1b); (41) centrally depressed; (42) posterior margin defined by an acute carina (Fig. 1b); (43) propodeal triangle inconspicuous; (44) lateral carinae well-defined, extending 0.66 distance to dorsal

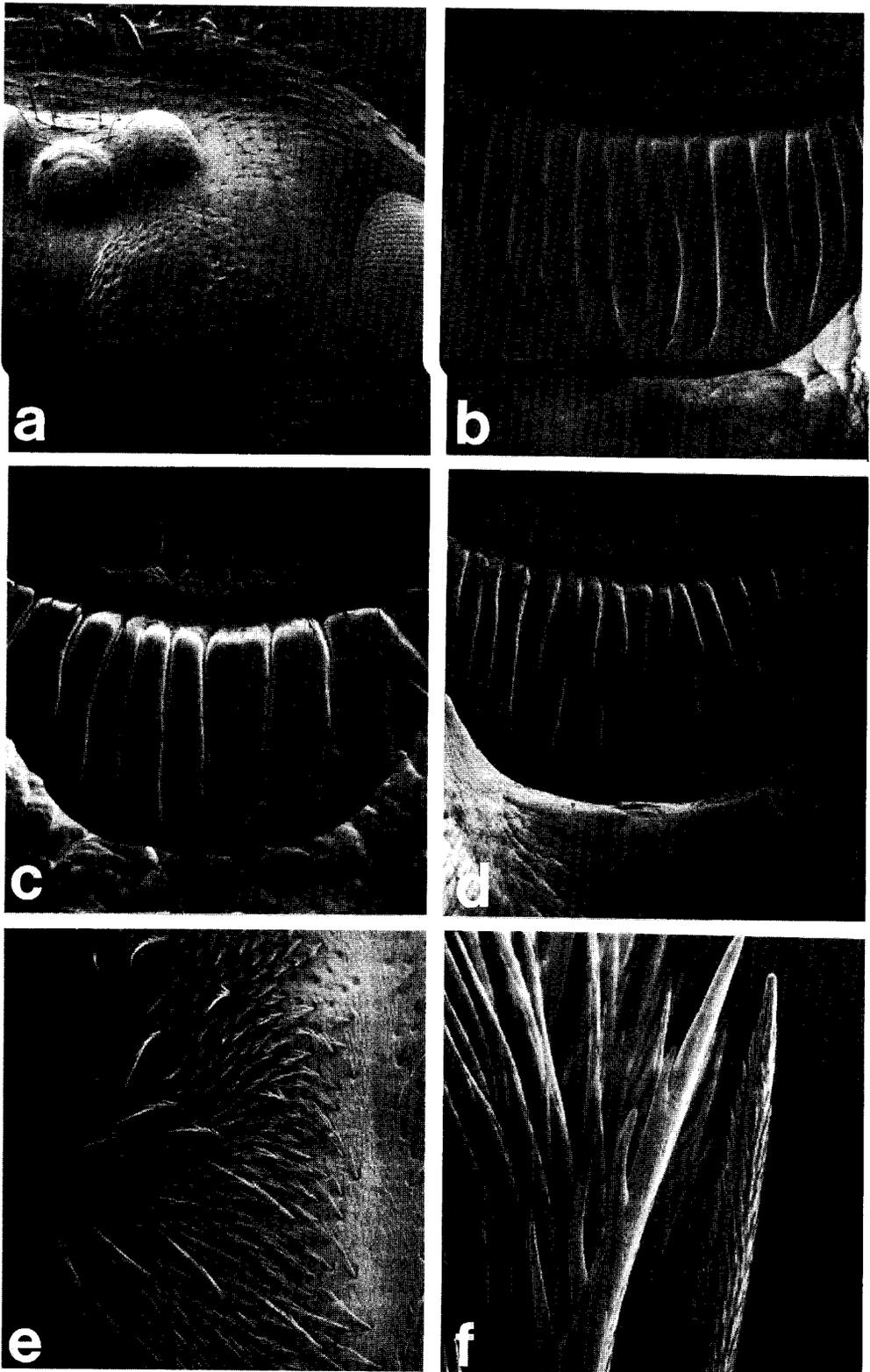


Fig. 1. Scanning electron micrographs. (a) *L. (E.) gattaca* (♀) head capsule; (b) *L. (E.) gattaca* (♀), dorsal surface propodeum; (c) *L. (E.) gattaca* (♂), dorsal surface propodeum; (d) *L. (E.) hartmanni* (♀), dorsal surface propodeum; (e) *L. (E.) gattaca* (♀) dorsal surface mesoscutum; (f) *L. (E.) gattaca* (♀) inner hind tibial spur.

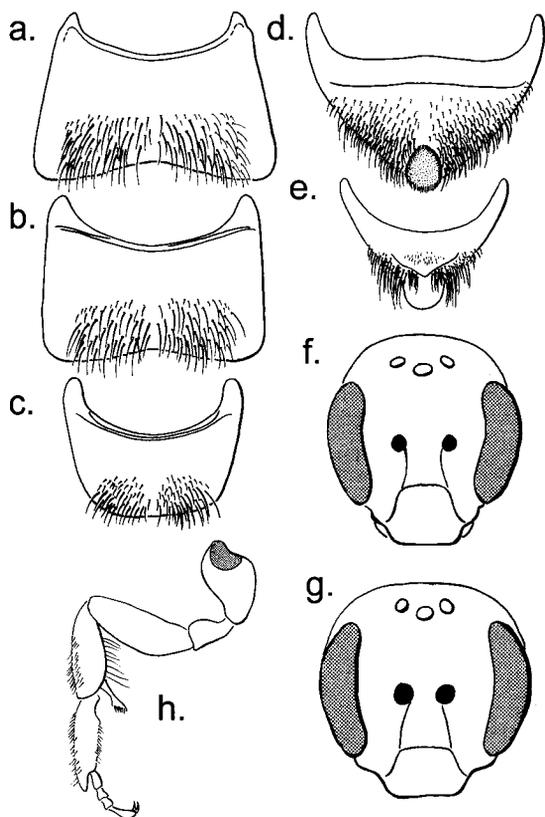


Fig. 2. *L. (E.) gattaca* (♀). (a) S3, ventral view; (b) S4, ventral view; (c) S5, ventral view; (d) T5, dorsal view; (e) T6, dorsal view; (f) head capsule (♂, frontal view); (g) head capsule (♀, frontal view); (h) foreleg (♀, inner view).

surface. (45) Inner hind tibial spur with 4 teeth (Fig. 1f); basal tooth exceptionally long and acutely pointed (Fig. 1f).

(46) Lateral edge of metasomal tergum II straight.

Sculpture. (47) Face weakly imbricate with widely scattered obscure punctures; laterally, along inner margins of compound eyes, impunctate; (48) area between antennal bases and ocelli densely punctate. (49) Punctures becoming more obscure along vertex, especially between compound eyes and lateral ocelli; (50) vertex behind ocelli conspicuously convex with pronounced transverse striations; Fig. 1a). (51, 52) Supraclypeal area imbricate with weak punctures. (53, 54) Clypeus strongly imbricate with obscure punctures. (55) Hypostoma finely strigate, impunctate.

(56) Mesoscutum dull; (57) densely punctate with punctations separated by <1 diameter (Fig. 1e). (58) Scutellum likewise densely punctate. (59) Metanotum punctate. (60) Preepisternum striate; (61) mesopleuron with horizontal striae; small tubercles located ventrally (as in *Sudila*, and some other subgenera); (62) metapleuron weakly striate. (63) Dorsal surface of propodeum coarsely striate, marked by 14–18 linear carinae extending the full length of the dorsal surface (Fig. 1b); (64) surface microscopically imbricate (Fig. 1b).

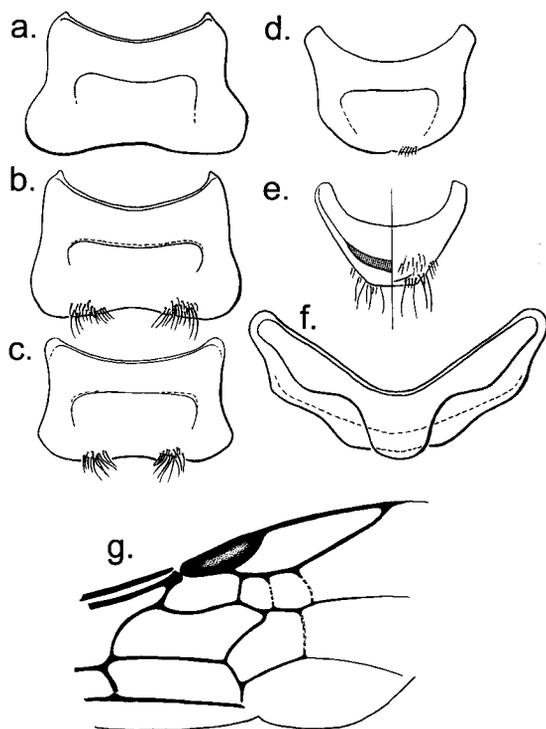


Fig. 3. *L. (E.) gattaca* (♂). (a) S3, ventral view; (b) S4, ventral view; (c) S5, ventral view; (d) S6, ventral view; (e) T7, dorsal (right) and ventral (left) views; (f) S7 and S8, ventral view; (g) forewing (♀), showing weak end 1st r-m, 2nd r-m, and 2nd m-cu veins.

(65) Metasomal tergum I shiny; (66) punctures exceedingly fine and widely scattered.

Coloration. (67) Head and thorax black, abdomen reddish to pale honey colored. (68) Clypeus black. (69) Flagellum dark above, pale brown below.

(70) Tegulae black. (71) Wing membrane light brown to yellow, wing veins and stigma light yellow. (72) Legs black, tarsal segments light brown.

Vestiture. (73) Pubescence of head between vertex and antennae simple, erect; (74) hairs jet black.

(75) Pubescence of thorax black; (76) mesoscutal hairs dense, erect, and finely branched (Fig. 1e). (77) Scopal hairs of hind leg arising from coxa, trochanter and ventral surface of femur; hairs finely branched, jet black; hind tibial hairs all black, densely plumose.

(78) Metasomal tergum I and (79) metasomal terga II–IV virtually hairless dorsally, with elongate, black hairs on lateral margins (projecting ventrally). (80) Acarinarium seemingly present but not well developed and without mites in all the specimens studied. (81) Metasomal sterna I–V clothed in erect, black finely branched setae (Fig. 2 a–c).

Male. Similar to female except as follows, and for characters that are unique to females: (1) length 8.0–8.5 mm; (2) wing length 6.65–6.75 mm; (3) metasomal width 1.70–1.80 mm.

Structure. (4) Head length/width ratio 1.11–1.14 (Fig. 2f). (5) Gena narrower, subequal to eye in width.

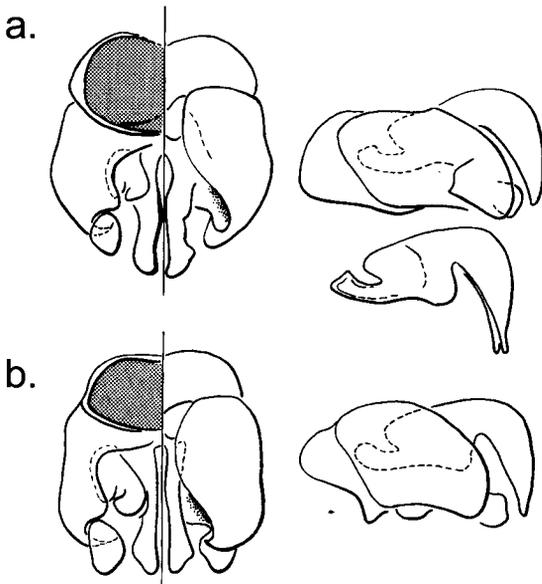


Fig. 4. (a) *L. (E.) gattaca*, genital capsule in ventral (left), dorsal (right) and lateral (far right) views (aedeagus removed for clarity); (b) *L. (E.) hartmanni*, genital capsule in ventral (left), dorsal (right) and lateral (far right) views.

(10) Clypeal surface gently rounded. (21) Scape shorter, reaching only 0.5 distance to vertex. (24) Distal process of labrum absent; (25) basal area evenly rounded; (26) basal lateral depressions absent; (27–29) distal keel, lateral depression, and fimbrial setae lacking. (30) Mandible relatively short, not reaching opposing mandibular base; (31) simple, subapical tooth absent. (40) Dorsal surface propodeum 2.0 times metanotum (Fig. 1c). (45) Inner hind tibial spur finely serrate.

Sculpture. (56) Mesoscutum shiny; (57) lateral punctures closely spaced, those located centrally more widely spaced (punctures separated by greater than a puncture diameter).

Coloration. (67) Head, thorax, and abdomen black, thorax with weak metallic blue sheen. (68) Clypeus lacking yellow maculation, entirely dark. (71) Wing membrane brownish, slightly darker than in female (especially beyond basal vein).

Vestiture. (75) Pubescence of thorax light brown to white (paler than in female); (76) mesoscutal hairs small, less dense than in female, inconspicuously branched. (77) Hind tibial hairs small, pale and only weakly branched.

(81) Metasomal sterna I–III clothed in pale, erect setae (unlike the erect, black, heavily branched setae of females). (82) Sternum IV and (83) sternum V with paired patches of posteriorly directed branched hairs (Fig. 3 b and c); sternum VI with marginal fringe of erect, nearly unbranched hairs (Fig. 3d).

Terminalia. (84) Sternum VII and (85) VIII as in Fig. 3f. (86) Gonobase short; (87) gonostylus as in Fig. 4a; (88) ventral retrorse lobes lacking; (90) volsella as in Fig. 4a.

Flight Records. In these areas of Chiriquí, a dry season usually lasts from approximately mid-December to mid-April, although rain falls in every month, and the intensity of the dry season varies greatly from year to year. Increasing rainfall occurs during the wet season from around May through November; between July and August there is a poorly defined, brief period of reduced rainfall (veranillo). At La Fortuna, a site ≈ 40 km to the east at a comparable elevation, annual precipitation averages $\approx 2,660$ mm. Low clouds and light mist (bajareque) are common. In general, bees are more abundant during the dry season and early wet season, excluding the corbiculate Apidae (W.T.W, unpublished data). Phenological studies are lacking, and the ovaries of none of the specimens were examined, so precise statements about seasonal activity are not possible. At comparable elevations elsewhere in the neotropics, some species of *Lasioglossum* s.l. are most active during the dry season, whereas others are aseasonal (e.g., Michener et al. 1979, Wcislo et al. 1993).

Specimens Examined. 14 (10♀, 4♂). PANAMÁ, Prov[incia] Chiriquí[.] road fr[om] Santa Clara to Volcan, 1.9 km WNW Rio Chiriquí Viejo, 1550 m[.] 8° 49' 07" N, 82° 40' 29" W[.] 3-vii-1996, WT Wcislo (7♀, 3♂). PANAMÁ, Prov[incia] Chiriquí[.] Santa Clara, finca Hartmann, Ojo de Agua[.] 8° 51' 40" N, 82° 44' 64" W[.] 27-II-1997, WT Wcislo (1♀). PANAMÁ, Prov[incia] Chiriquí[.] road fr[om] Santa Clara to Volcan, 6.3 km WNW Rio Chiriquí Viejo, 1550 m[.] 8° 49' 35" N, 82° 41' 57" W[.] 3-vii-1996, L Packer & WT Wcislo (2♀, 1♂)

Lasioglossum (Ecyllaes) hartmanni

Type Material. The female holotype is in the Snow Entomological Museum, University of Kansas. The specimen is labeled: COSTA RICA, Cartago Prov.[ince], Tapanti[.] 12 June 1963, 1250 m. (C.D. & D.R. Michener)/HOLOTYPE: *Lasioglossum (Ecyllaes) hartmanni* BN Danforth & WT Wcislo [red label].

Nine paratypes (7♀, 2♂) from localities listed in *Specimens Examined* were deposited in the Snow Entomological Museum, University of Kansas.

Etymology. This species is named after Sr. Ratibor Hartmann of Santa Clara, Chiriquí, in recognition of his long-standing and enthusiastic support for studies on the natural history of the flora and fauna of Chiriquí and their conservation.

Distribution. The type locality is Tapanti, now protected as a National Park astride the northern slopes of the Cordillera de Talamanca. This area of lower montane and premontane rain forests is on steep terrain that rises from the Orosi Valley, and is cool and extremely wet, with $\approx 6,500$ mm of rain per year; February to April are the drier months. The species occurs north to Volcán Poás National Park, a 2,704 m volcano in the Cordillera Central. The upper elevations of Poás are cool and wet, and frequently enshrouded by clouds. Presumably the species occurs throughout the Cordillera de Talamanca into Panamá, because the

Cerro Colorado locality is in the Serranía del Tabasará, east of the Talamancas.

Diagnosis. This species can be distinguished from *L. (E.) gattaca* by the following features: in females the metasoma is black or dark brown rather than red, the coarsely striate dorsal surface of the propodeum is shorter in relationship to the length of the metanotum (in both males and females; Fig. 1d), and the underlying cuticle is more imbricate. This species is slightly larger than *L. (E.) gattaca*, and there are subtle differences in genitalic morphology, as indicated in Fig. 4 a and b.

Description. This species is morphologically similar to *L. (E.) gattaca* except as follows (apomorphies for these two species are shown in bold): Female: (1) Length 9.5–10.0 mm; (2) wing length 7.0–8.0 mm; (3) metasomal width 2.5–2.6 mm.

Structure. (4) Head slightly elongate (length/width ratio 1.01–1.06). (13) Frons (between antennal bases and ocelli) with 2 distinct protuberances; distance between compound eye and lateral ocellus 1.3 times distance between lateral ocellus and vertex; (14) vertex strongly carinate (scoop-shaped); width of vertex (from posterior margin of lateral ocellus to vertex) 0.30 mm. (21) Scape reaching 0.88 distance to vertex; scape conspicuously convex outward.

(40) Dorsal surface of propodeum 1.8–1.9 times metanotum (Fig. 1d). (45) Inner hind tibial spur with 3–4 teeth; basal tooth exceptionally long and acutely pointed (as illustrated in Fig. 1f).

Sculpture. (50) Vertex behind ocelli with slightly weaker transverse striations (this region also conspicuously convex).

(63) Dorsal surface of propodeum coarsely striate, marked by 18–22 linear carinae extending nearly the full length of the propodeal dorsal surface (Fig. 1d); (64) surface more conspicuously imbricate than in *L. (E.) gattaca* (Fig. 1d).

Coloration. (67) Head and thorax black, abdomen brown to black.

Vestiture. (74) Hairs brown.

(75) Pubescence of thorax brown to black. (77) Scopal hairs arising from coxa, trochanter and ventral surface of femur; hairs plumose and light brown; hind tibial hairs all black, densely plumose.

(78) Metasomal tergum I and (79) metasomal terga II–IV virtually hairless dorsally, with elongate, light brown hairs on lateral margins (projecting ventrally). (81) Metasomal sterna I–V clothed in erect, light brown finely branched setae (apparently serving to carry pollen in 1 specimen) (as illustrated in Fig. 2 a–c).

Male. Similar to female except as follows, and for characters which are unique to females: (1) length \approx 9.0 mm; (2) wing length \approx 7.2 mm; (3) metasomal width \approx 1.9 mm.

Structure. (4) Head length/width ratio \approx 1.12. (40) Dorsal surface of propodeum 1.9 times metanotum. (45) Inner hind tibial spur finely serrate.

Coloration. (67) Head, thorax, and abdomen black, thorax with weak metallic blue sheen. (68) Clypeus lacking yellow maculation, entirely dark.

Terminalia. (84) Sternum VII and (85) VIII as in Fig. 3f. (86) Gonobase short; (87) gonostylus as in Fig. 4b; (88) ventral retrorse lobes lacking; (90) volsella as in Fig. 4b.

Flight Records. Activity patterns of *L. (E.) hartmanni* appear to be similar to *L. (E.) gattaca*, with specimens collected at the beginning of the dry season in Panama, and during the early wet season in Costa Rica, where annual patterns of rainfall are roughly similar to those described above for *L. (E.) gattaca* (see Herrera 1986)

Specimens Examined. 10 (8♀, 2♂). COSTA RICA, Cartago Prov. [inca], Tapanti [·] 12 June 1963, 1250 m. (C.D. & D.R. Michener) (5♀). COSTA RICA, Alajuela Prov. [inca], SE slope Volcan Poas. 15 July 1963, 6450 feet [= 1966 m] (Michener & Kerfoot) (2♀, 2♂). PANAMÁ: Chiriqui Prov. [inca], Cerro Colorado, 1400 m by road [·] 20 January 1988 DW Roubik collector (1♀).

Discussion

The phylogenetic affinities of these 2 species to other *Evylaeus* are not at all clear. Morphologically they are highly apomorphic, but none of the apomorphic features are shared with other groups of *Lasioglossum*. These 2 species clearly belong to a monophyletic group of subgenera including *Hemihalictus*, *Sphecodogastra*, *Sudila*, *Evylaeus*, *Dialictus*, and *Paralictus* (referred to as the *Hemihalictus* series by Michener 2000) because they possess weakened 1r-m, 2r-m, and 2m-cu wing veins (Fig. 3g). However, within this group their affinities are not clear. Like *Evylaeus* the females are all black, except for the reddish metasoma of *L. (E.) gattaca*. The weak metallic coloration of males is similar to the North American *Dialictus* or *Sudila*, a subgenus endemic to Sri Lanka, but males of these 2 species do not show strong positive head allometry, which is typical of *Sudila* (however, we did not examine enough male specimens of either species to rule out the possibility of positive head allometry). Additional similarities to *Sudila* include the presence of the tubercle on the ventral surface of the mesopleuron (Sakagami et al. 1996) but this character is also shared with some strong-veined subgenera, such as *Callalictus* Michener, *Parasphecodes* Smith, and *Pseudochilalictus* Michener (B.N.D., unpublished data).

DNA sequence data from the mitochondrial COI gene (Danforth 1999) is inconclusive as far as the placement of *L. (E.) gattaca*. This species, when analyzed along with sequences from >65 species of *Lasioglossum*, came out in a basal lineage of *Evylaeus* closely related to *L. (E.) marginatum* (Brullé) from Europe; however, this sister-group relationship was not well supported. Additional (unpublished data) data from nuclear elongation factor-1 α suggest that *L. (E.) gattaca* may fall into a basal lineage of *Evylaeus*, from which the North American *Dialictus* is derived. This latter conclusion is congruent with the mitochondrial data, because “basal *Evylaeus*” (=acarinat *Evylaeus*) are probably paraphyletic with respect to the North American *Dialictus*. More species of basal *Evy-*

laeus will be needed before strong conclusions can be reached about the phylogenetic affinities of *L. (E.) gattaca* and its sister species *L. (E.) hartmanni*.

The social behavior of these species is not known. Placement within the weak-veined *Lasioglossum* would suggest they are eusocial, but both solitary, *L. (D.) figueresi* Wcislo, and eusocial, *L. (D.) aeneiventre* (Friese), species of weak-veined *Lasioglossum* are known from the neotropics (Wcislo 1990, Wcislo et al. 1993).

Acknowledgments

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References Cited

- Bennett, C. F. 1968. Human influences on the zoogeography of Panamá. *Ibero-Americana* 51: 1-112.
- Danforth, B. N. 1999. Phylogeny of the bee genus *Lasioglossum* (Hymenoptera: Halictidae) based on mitochondrial COI sequence data. *Syst. Entomol.* 24.
- Ebmer, A. W. 1987. Die europäischen Arten der Gattungen *Halictus* Latreille 1804 und *Lasioglossum* Curtis 1833 mit illustrierten Bestimmungstabellen (Insecta: Hymenoptera: Apoidea: Halictidae: Halictinae) 1. Allgemeiner Teil, Tabelle der Gattungen. *Senckenb. Biol.* 68(1/3): 59-148.
- Ebmer, A. W. 1995. Asiatische Halictidae, 3. Die Artengruppe der *Lasioglossum* carinate-*Evylaeus* (Insecta: Hymenoptera: Apoidea: Halictidae: Halictinae). *Lin. Biol. Beitr.* 27: 525-652.
- Harris, R. A. 1979. A glossary of surface sculpturing. *Occas. Pap. Entomol. State Calif. Dep. Food Agric.* 28: 1-31.
- Herrera, W. 1986. *Clima de Costa Rica*. Editorial Universidad Estatal a Distancia, San Jose.
- Houston, T. F. 1970. Discovery of an apparent male soldier caste in a nest of a halictine bee (Hymenoptera: Halictidae), with notes on the nest. *Aust. J. Zool.* 18: 345-351.
- Kerfoot, W. B. 1967a. Nest architecture and associated behavior of the nocturnal bee, *Sphecodogastra texana*. *J. Kans. Entomol. Soc.* 40: 84-93.
- Kerfoot, W. B. 1967b. The lunar periodicity of *Sphecodogastra texana*, a nocturnal bee (Hymenoptera: Halictidae). *Anim. Behav.* 15: 479-486.
- Knerer, G., and M. Schwarz. 1976. Halictine social evolution: the Australian enigma. *Science (Wash. D.C.)* 194: 445-448.
- Krombein, K. V., P. D. Hurd, D. R. Smith, and B. D. Burks. 1979. *Catalog of Hymenoptera in America North of Mexico* (3 vols.). Smithsonian Institution Press, Washington, DC.
- Kukuk, P. F., and M. Schwarz. 1987. Intranest behavior of the communal sweat bee *Lasioglossum (Chilalictus) erythrurum* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* 60: 58-64.
- Kukuk, P. F., and M. Schwarz. 1988. Macrocephalic male bees as functional reproductives and probable guards. *Pan-Pac. Entomol.* 64: 131-137.
- McGinley, R. J. 1986. Studies of Halictinae (Apoidea: Halictidae), I: revision of New World *Lasioglossum*. *Smithson. Contrib. Zool.* 429:1-294.
- McGinley, R. J. 1999. Studies of Halictinae (Apoidea: Halictidae), II: revision of *Sphecodogastra* Ashmead, floral specialists on Onagraceae. *Smithson. Contrib. Zool.*
- Michener, C. D. 1954. Bees of Panamá. *Bull. Am. Mus. Nat. Hist.* 104: 1-175.
- Michener, C. D. 1979. Biogeography of the bees. *Ann. Mo. Bot. Gard.* 66: 277-347.
- Michener, C. D. 1990. Reproduction and castes in social halictine bees, pp. 77-121. *In* W. Engels [ed.], *Social insects: an evolutionary approach to castes and reproduction*. Springer, New York.
- Michener, C. D. 1999. *Bees of the world, a comprehensive guide*. Johns Hopkins University Press, Baltimore, MD.
- Michener, C. D., R. J. McGinley, and B. N. Danforth. 1994. *The bee genera of North and Central America* (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, DC.
- Michener, C. D., M. D. Breed, and W. J. Bell. 1979. Seasonal cycles, nests, and social behavior of some Colombian halictine bees (Hymenoptera: Apoidea). *Rev. Biol. Trop.* 27: 13-34.
- Moure, J. C., and P. D. Hurd, Jr. 1987. An annotated catalog of the halictid bees of the western hemisphere (Hymenoptera: Halictidae). Smithsonian Institution Press, Washington, DC.
- Myers, C. W. 1969. The ecological geography of cloud forest in Panama. *Am. Mus. Novit.* 2396: 1-52.
- Sakagami, S. F., A. W. Ebmer, and O. Tadauchi. 1996. The halictine bees of Sri Lanka and the vicinity: III. *Sudila* (Hymenoptera, Halictidae) Part 1. *Esakia* 36: 143-189.
- Walker, K. 1995. Revision of the Australian native bee subgenus *Lasioglossum (Chilalictus)* (Hymenoptera: Halictidae). *Mem. Mus. Victoria* 55(parts 1 and 2): 1-423.
- Wcislo, W. T. 1990. A new species of *Lasioglossum* from Costa Rica (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* 63: 450-453.
- Wcislo, W. T. 1997. Invasion of nests of *Lasioglossum imitatum* by a social parasite, *Paralictus asteris* (Hymenoptera: Halictidae). *Ethology* 103: 1-11.
- Wcislo, W. T. 1999. Transvestism hypothesis: A cross-sex source of morphological variation for the evolution of parasitism among sweat bees (Hymenoptera: Halictidae)? *Ann. Entomol. Soc. Am.* 92:2 pp. 239-242.
- Wcislo, W. T., A. Wille, and E. Orozco. 1993. Nesting biology of tropical solitary and social sweat bees, *Lasioglossum (Dialictus) figueresi* Wcislo and *Lasioglossum (D.) aeneiventre* (Friese) (Hymenoptera: Halictidae). *Insectes Soc.* 40: 21-40.

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