Revision of the Species of *Lytopylus* from Area de Conservación Guanacaste, Northwestern Costa Rica (Hymenoptera, Braconidae, Agathidinae)

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Revision of the species of Lytopylus from Area de Conservación Guanacaste, northwestern Costa Rica (Hymenoptera, Braconidae, Agathidinae)

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Abstract
Thirty two new species of Lytopylus (Agathidinae) are described with image plates for each species: Lytopylus alejandromasisi sp. n., Lytopylus alfredomainieri sp. n., Lytopylus anamariamongeae sp. n., Lytopylus angelagonzalezae sp. n., Lytopylus cesarmonai sp. n., Lytopylus eddyisanchezii sp. n., Lytopylus elietectantiumae sp. n., Lytopylus ericchapmani sp. n., Lytopylus gahyunae sp. n., Lytopylus gisukei sp. n., Lytopylus guillermopereirai sp. n., Lytopylus gustavoinumii sp. n., Lytopylus hartmanguidoi sp. n., Lytopylus hernanbravoi sp. n., Lytopylus hokwoni sp. n., Lytopylus ivanniasandotalae sp. n., Lytopylus johanvalerioi sp. n., Lytopylus josecortesi sp. n., Lytopylus luisgaritai sp. n., Lytopylus mariamartachavarriae sp. n., Lytopylus miguelviquezi sp. n., Lytopylus motorbasegawai sp. n., Lytopylus okchuna sp. n., Lytopylus pablocobbi sp. n., Lytopylus robertofernandezi sp. n., Lytopylus rogerblancoi sp. n., Lytopylus salvadorlopezi sp. n., Lytopylus sangevoni sp. n., Lytopylus sarahmeierottae sp. n., Lytopylus sergiobermudezi sp. n., Lytopylus sigifredomarini sp. n., and Lytopylus youngcheae sp. n.

A dichotomous key and a link to an electronic, interactive key are included. All specimens were reared from Lepidoptera larvae collected in Area de Conservación Guanacaste (ACG) and all are associated with ecological information including host caterpillar, collection date, eclosion date, caterpillar food plant, and locality. Neighbor-joining and maximum likelihood analyses of the barcode region of the mitochondrial cytochrome c oxidase subunit I gene (COI DNA barcode) were conducted to aid in species delimitation.

Keywords
Costa Rica, DNA barcoding, host use, parasitoid wasps, species limits, taxonomy
Introduction

Agathidinae contains approximately 1,200 described species (Yu et al. 2012), making it a moderately species-rich subfamily of Braconidae. All members of Agathidinae are koinobiont endoparasitoids of Lepidoptera larvae (Sharkey 2006) meaning that they are internal parasitoids that enter early instar host larvae and their hosts continue to develop before being consumed in the last instar or prepupal parasitoid stage. Over most of its history, *Lytopylus* was considered a junior synonym of *Bassus* Fabricius, *Microdus* Nees, or *Agathis* Latreille. Sharkey et al. (2016) removed the genus from synonymy and synonymized *Agathellina* Enderlein, 1920, *Ditropia* Enderlein, 1920, and *Austroearinus* Sharkey, 2006, under it, thereby including six species in the genus, i.e., *Lytopylus azygos* Viereck, 1905, *Agathellina columbiana* Enderlein, 1920, *Austroearinus chrysokeras* Sharkey, 2006, *Austroearinus melanopodes* Sharkey, 2006, *Bassus rufomarmoratus* Muesebeck, 1927, *Ditropia strigata* Enderlein, 1920, *Lytopylus unicolor* (Schrottky, 1902). Only one species of *Lytopylus* has a published host association: *L. unicolor* (Shenefelt 1970) is a parasitoid of the potato tuber-worm *Phthorimaea operculella* (Zeller 1873) in the Gelechiidae.

Although this article appears to be the second taxonomic revision of *Lytopylus* Forster, 1862 from Area de Conservación Guanacaste (ACG), the revision by Sharkey et al. (2011) employed the name *Lytopylus* in error and later Sharkey et al. (2016) transferred all of species described under *Lytopylus* in that paper to *Aerophilus* Szépligeti, 1902.

This work focuses on specimens of *Lytopylus* reared from Lepidoptera larvae collected by Drs Janzen and Hallwachs and the team of ACG parataxonomists since 1978 in the ACG (Janzen et al. 2009, Janzen and Hallwachs 2011, 2016). All are associated with ecological information including host caterpillar, collection date, eclosion date, caterpillar food plant, and locality. COI mitochondrial DNA barcodes for most specimens are deposited in the Barcode of Life Datasytem (BOLD) (http://www.boldsystems.org) (Hebert et al. 2003) and are equally available at http://janzen.sas.upenn.edu. The sequence data are publicly available through the Public Data Portal of BOLD (http://www.boldsystems.org/index.php/Public_BINSearch?searchtype=records).

We include an image plate for each species, a traditional identification key and a digital web-based interactive key; both have illustrations of morphological characters (https://www.dropbox.com/s/j9xongce1qrav5j/Revised%20Lytopylus%20Interactive%20key.zip?dl=0). A diagnoses and descriptions are provided for thirty-two new species and one previously described species.

Methods

Species concepts

We use Mayr’s (1969) biological species concept, i.e., a species consists of a group of natural populations that are reproductively isolated from other groups. Because insect taxonomists usually work with dead specimens, delimitation of insect species is based
on methods that indirectly infer reproductive isolation rather than direct observation, i.e., similarity in morphological, molecular (COI DNA sequences), geography, and host use data if recorded.

**Specimen information**

Most specimens, and all holotypes, are deposited in the insect collection in the Biology Department of Utah State University (USU) Logan, Utah. Duplicates are in the Hymenoptera Institute Collection (HIC), Entomology Department, University of Kentucky and those from ACG will eventually be deposited in a major North American Museum. The detailed parasitoid specimen records are available by search of the individual specimen DHJPARxxxxxxx voucher codes on Janzen’s database (http://janzen.sas.upenn.edu/caterpillars/database.lasso). Host caterpillars are uniquely identified by their own voucher code system, which is recognizable by YY-SRNP-XXXXX where “YY” is the two-digit year and “XXXXX” is a unique number within that year. Some of the host caterpillars are incompletely identified, but they also have unique names such as *Dichomeris Janzen512*, which is an interim name for *Dichomeris* species 512 as determined by a biodiversity specialist of the ACG team or a professional taxonomist who provides the proper genus epithet. These names will be updated in the database when the species is blessed with a formal scientific name, but the interim name, in this case *Dichomeris Janzen512*, will remain searchable in that database.

**Morphological analysis**

Morphological characters were recorded using the DELTA Editor (v. 1.02; Dallwitz et al. 1999). The DELTA Editor was used to enter the data for both interactive (web-based) and traditional printed keys (https://www.dropbox.com/s/j9xongce1qav5j/Revised%20Lytopylus%20Interactive%20key.zip?dl=0). Images to illustrate the couplets were taken by a JVC digital camera fixed on microscopes and stacked with the program Automontage. Plates for each species were arranged using Adobe Photoshop Elements 12. The morphological terms mostly follow Sharkey and Wharton (1997) and are coordinated with the Hymenoptera Anatomy Ontology (HAO, Yoder et al. 2010). The minimum number of characters necessary to distinguish a species from all other species in this study is included in a diagnosis for each species. Descriptions, based on the holotype of each species, were automatically generated using DELTA.

**DNA extraction, PCR, and sequencing**

271 COI DNA sequences were sourced from the BOLD database. DNA was extracted by the Centre for Biodiversity Genomics using a glass fibre protocol (Ivanova et al. 2006).
Extracts were resuspended in 30 μL dH₂O, and a 658-bp region near the 5’ terminus of the COI gene was amplified using standard insect primers LepF1 (5’-ATTCAACCAAT-CATAAAGATATTGG-3’) and LepR1 (5’-TAAACTTCTGGATGTCCAAAAAATCA-3’) following the established protocols (Smith et al. 2008). If initial amplification failed, other amplifications were conducted following the established protocols using internal primer pairs, LepF1-C113R (130 bp) or LepF1-C_ANTMR1D (300 bp) and MLepF1-LepR1 (400 bp) to generate shorter overlapping sequences (Smith et al. 2008).

For the specimens which DNA sequences were not available in BOLD, DNA was extracted from individual legs at University of Kentucky (UKY) with Qiagen DNeasy Blood and Tissue Kit following the manufacturer’s animal tissue protocol (Qiagen Inc., Chatsworth, California, USA).

COI was amplified from extracted DNA using the forward primer mlCOIintF (Leray et al. 2013) and reverse primer jgHCO2198 (Geller et al. 2013). Unique 9 bp tags, designed using Barcode Generator (available from http://comailab.genomecenter.ucdavis.edu/index.php/Barcode_generator) were attached to the primers so that each sequence could be traced to its parent specimen by the unique combination of tags. PCR was performed using Takara reagents consisted of 10X buffer, 2.5 μM nucleotides, 1 μM of each primer, 0.125 U Takara Ex Taq, 2 μL template DNA and enough dH₂O for a total reaction volume of 25 μL. We followed the “touchdown” thermal cycling protocol for these primers as outlined in Leray et al. (2013).

COI PCR DNA products, in addition to those from BOLD, were sequenced on an Illumina MiSeq system at the UKY Genomics Core Laboratory.

DNA assembly and phylogenetic analysis

Individual directional reads were downloaded from BOLD (produced by Sanger sequencing) and were edited and assembled using Geneious Pro (v. 6.1.6; Drummond et al. 2010) with the default settings. Edited sequences were stored in the NEXUS file format. The three sequences produced by NGS at UKY were included in the file of edited sequences. NGS sequencing data was assembled using PEAR (Zhang et al. 2013) and demultiplexed using custom Phyton scripts. Among all bidirectional reads from each specimen, the 1st and 2nd most numerous reads were manually retrieved from the output file. The sequences were then queried against the GenBank nucleotide library using NCBI BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and those that were highly similar to Lytopylus specimens were retained. Finally, three COI sequences were exported from the FASTQ file and added to the file of edited sequences. The multiple sequence alignment was assembled on the MAFFT server (http://www.ebi.ac.uk/Tools/msa/mafft/; v. 7; Katoh et al. 2013) using the default settings.

A NJ tree (Saitou and Nei 1987) was constructed by using PAUP* (v. 4.0β10; Swofford 2003) using the p-distance setting. ML analyses were performed using Garli (v. 2.01; Zwickl 2006). For ML, the data were partitioned by codon position for COI.
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...We applied the most complex model available (GTR+I+G; Rodríguez et al. 1990) to each partition as per recommendations of Huelsenbeck and Rannala (2004) for likelihood-based analyses. Garli applies separate parameter estimates to each partition. A 20-replicate ML analysis was performed using default settings. Additionally, a ML bootstrap analysis (minimum 500 replicates) was conducted to assess nodal support (Garli, default settings). The COI data set analyzed herein is available from the senior author upon request.

Host use

Besides the notes included here additional data can be accessed at http://janzen.sas.upenn.edu (Janzen et al. 2009).

Species delimitation

The NJ tree and the tree of highest log-likelihood from 20 ML search reps in Fig. 1 and Fig. 2 were based solely on COI. These trees were constructed solely to assist in the delimitation of species. Molecular species concepts were initially based on the NJ tree and were compared to the best ML tree with COI data. The 2% genetic distance cut-off, which has been a conventional threshold for species delimitation using COI barcodes (Jones et al. 2011) and has been used in the Barcode Index Numbers (BINs) (http://www.barcodinglife.org/index.php/Public_BarcodeIndexNumber_Home), was used to cluster putative species (Smith et al. 2013). Morphological and host use data were then employed to make final decisions when genetic distances between putative molecular species were near the 2% threshold or below it, as is necessary for other groups of insects (e.g., Janzen et al. 2017).

Results and discussion

Species delimitation

The NJ tree and the highest log-likelihood ML tree with COI data both suggest twenty-eight molecular species, and twenty-eight putative species were clustered using the 2% genetic distance cut-off.

Before running the molecular analyses I.K. and M.S. independently sorted the specimens to morphospecies and had error rates of 62% and 54% respectively based on our final species delimitations. All possible types of errors were discovered, i.e., clumping, splitting, and both clumping and splitting (mixing the members of two or more species). In contrast the molecular species concepts matched with our final species delimitations at 96.6%. The implications for previous taxonomic
Figure 1. The NJ tree of the COI DNA barcode region for twenty-nine of the thirty-three *Lytopylus* species treated here. Triangles represent collapsed clades; their lengths (measured horizontally) represent the distance from the most basal node to the apex of the longest branch. The number of specimens in each triangle is given in parentheses following the species name. The node labeled with a red “A” is discussed in the text.

treatments of braconids (and other speciose small tropical insects) based solely on morphology are dire.

The sole incongruity between molecular species concepts and final species concepts concerned *L. sigifredomarini* and *L. guillermopereirai*. The genetic variation between these two species was 0.4%, and the ML tree grouped them together (Fig. 2, node A). We, however, delimited them as separate species because they are morphologically distinct in their strikingly different color patterns, and the NJ tree recovered these two species as monophylic sister taxa. (Fig. 1, node A). In addition, they attack different species of host caterpillars with different feeding niches.
Figure 2. Tree of highest log-likelihood from 20 ML search reps of the COI data set. Terminals with bold-faced type indicate species described herein. ML bootstrap values appear above the branches. Triangles represent collapsed clades; their lengths (measured horizontally) represent the distance from the most basal node to the apex of the longest branch. The number of specimens in each triangle is given in parentheses following the species name. The node labeled with a red “A” is discussed in the text.

The four species (L. alejandromasisi, L. ivanniasandovalae, L. josecortesi, L. mariamartachavarrae) for which genetic data were not available were delimited using morphological and host data.
Systematics

**Lytopylus Föster, 1862**


**Type species.** *Lytopylus azygos* Viereck, 1905, by monotypy, first included species.

**Diagnosis.** *Lytopylus* can be distinguished from all other agathidine genera with the following combination of characters: tarsal claws simple with a basal lobe; mesoscutum unsculptured and notauli absent; fore wing vein (RS+Ma) not complete; vein CUb of hind wing weak or absent and never tubular; hind coxal cavities open; median tergite 3 smooth.

**Distribution.** Restricted to the New World, from the northeastern USA south to Argentina, primarily Neotropical.

**Species diversity.** Including the thirty-two species described here, there are 39 described species of *Lytopylus*. Based on the diversity in the University of Kentucky Hymenoptera Institute Collection, there are hundreds more awaiting description.

**Key to the species of *Lytopylus* of Area de Conservación Guanacaste, Costa Rica**

1  A. Fore wing mostly or entirely infuscated ........................................2
–  B. Fore wing hyaline or with a slight yellow tinge .................................28
–  C. Fore wing with one apical black band .............................................31
–  D. Fore wing with two black bands....................................................33

2(1)  A. Median tergites mostly or entirely melanic (brown to black) ............3
–  B. Median tergites entirely pale (yellow to orange) or mostly pale with poste-
rior terga black.....................................................................................10
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3(2) A. Scutellar sulcus with at least one longitudinal carina.........................4
   – B. Scutellar sulcus lacking longitudinal carinae...............................6

4(3) A. Lateral tergites one and two entirely white...............................L. cesarmorai
   – B. Lateral tergites one and two mostly or entirely yellow....................5

5(4) A. Hind femur mostly pale (yellow to orange) or black and pale with a similar
      percentage of each color.............................................................L. motobasegawai ♂
   – B. Hind femur mostly black, pale apically.................................L. miguelviquezi ♂

6(3) A. Mesoscutum mostly or entirely melanic (brown to black) ....................L. guillermopereirai
   – B. Mesoscutum mostly or entirely pale (yellow to orange) .....................7
7(6)  A. Pronotum entirely pale (yellow to orange) ........................................... 8
– B. Pronotum bicolored .................................................................................... 9

8(7)  A. Anterior transverse carina of propodeum reaching the lateral margin........
.................................................................................................................. L. sarahmeierottoae
– B. Anterior transverse carina of propodeum not reaching the lateral margin or
absent ............................................................................................................... L. salvadorlopezi

9(7)  A. Mesopleuron bicolored................................................................. L. anamariamongeae
– B. Mesopleuron entirely pale (yellow to orange) ......................... L. luisgaritai
10(2)  A. Mesoscutum mostly or entirely melanic ........................................... 11
  – B. Mesoscutum mostly or entirely pale (yellow to orange) ..................... 18

11(10)  A. Anterior transverse carina of propodeum reaching the lateral margin.... 12
  – B. Anterior transverse carina of propodeum not reaching the lateral margin or absent ........................................................................................................... 15

12(11)  A. Hind coxa entirely black......................................................... *L. hermanbravoi*
  – B. Hind coxa mostly or entirely pale ................................................... 13

13(12)  A. Scutellar sulcus with at least one longitudinal carina......................... 14
  – B. Scutellar sulcus lacking longitudinal carinae ......................... *L. sigifredomarini*
14(13) A. Median syntergite 2+3 1.4× longer than wide. \( \textit{L. gabyunae} \)
- B. Median syntergite 2+3 as long as wide. \( \textit{L. sangyeoni} \)

15(11) A. Lateral longitudinal carinae of median tergite 1 well-defined. \( \textit{16} \)
- B. Lateral longitudinal carinae of median tergite 1 blunt. \( \textit{17} \)

16(15) A. Median areola of propodeum spindle-shaped; median areola length 6× its width; median areola closed posteriorly. \( \textit{L. josecortesi} \)
- B. Median areola of propodeum wide anteriorly narrow and not closed posteriorly; median areola length 11× its width. \( \textit{L. eliethcantillanoae} \)
17(15) A. Median areola of propodeum with well-defined margins. ... *L. rogerblancoi*
– B. Median areola of propodeum lacking well-defined margins

.............................................................................................................

*L. angelagonzalezae*

18(10) A. Anterior transverse carina of propodeum reaching the lateral margin. ... *19*
– B. Anterior transverse carina of propodeum not reaching the lateral margin or absent

.............................................................................................................

*21*

19(18) A. Pronotum entirely pale (yellow to orange) .................................................................. *20*
– B. Pronotum bicolored ..............................................................................................

*L. johanvalerioi*

20(19) A. Vertex of head entirely melanic; hind tibia black basally and distally, yellow at mid-length ............................................................................................................. *L. alejandromasisi*
– B. Vertex of head mostly or entirely yellow; hind tibia pale basally, black apically .............................................................................................................

*L. chrysokeras*
21(18)  A. Fore wing second submarginal cell weakly quadrate ........................................22  
– B. Fore wing second submarginal cell triangular .........................................................24

22(21)  A. Pronotum entirely pale (yellow to orange) ....................................................23  
– B. Pronotum bicolored .....................................................................................\textit{L. pablocobbi}

23(22)  A. Median areola length 4× its width; median areola of propodeum kite-shaped .............................................................................\textit{L. motobasegawai} ♀ 
– B. Median areola length 15× its width; median areola of propodeum spindle-shaped .............................................................................\textit{L. gisukae}
24(21) A. Apical flagellomeres usually bright yellow, always distinctly paler than sub-apical flagellomeres ................................................................. *L. chrysokeras*  
– B. Apical flagellomeres brown not distinctly paler than subapical flagellomeres ........................................................................... 25

25(24) A. Median areola of propodeum kite-shaped.................... *L. miguelviquezi* ♀  
– B. Median areola of propodeum spindle-shaped ........................................ 26

26(25) A. Vertex of head entirely melanic................................................................. 27  
– B. Vertex of head mostly or entirely yellow ........................................*L. gustavoindunii*

27(26) A. Median syntergite 2+3 1.1 times longer than wide ..... *L. alfredomainieri*  
– B. Median syntergite 2+3 1.5 times longer than wide ..................... *L. okchunae*
28(1)  
1. Median tergites mostly or entirely melanic (brown to black) ...(L. cesarmorai)
2. Median tergites entirely pale (yellow to orange) or mostly pale with posterior terga black...

29(28)

A. Anterior transverse carinae of propodeum reaching the lateral margin; median areola of propodeum kite-shaped...(L. ivanniasandovalae)

30(29)

A. Fore wing RS+Ma tubular on more than half its length...(L. sergiobermudezi)

31(1)

A. Vertex of head mostly or entirely melanic...(L. youngcheae)

B. Vertex of head mostly or entirely yellow...(L. mariamartachavarriae)
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32(31)  A. Mid tibia mostly black, yellow basally .......................... *L. eddysanchezi*
     – B. Mid tibia with a sub-basal black patch and black apically, yellow at mid-length and basally .......................... *L. bartmanguidoi*

33(1)  A. Pronotum entirely melanic ................................................. 34
     – B. Pronotum bicolored ............................................... *L. ericchapmani*

34(33)  A. Lateral longitudinal carinae of median tergite 1 well-defined.. *L. bokwoni*
     – B. Lateral longitudinal carinae of median tergite 1 blunt.. *L. robertofernandez*

Species descriptions

*Lytopylus alejandromasisi* Kang, sp. n.
http://zoobank.org/C27B1AC1-2924-4700-AB21-134B9882E3F2
Fig. 3

**Diagnosis.** Fore wing mostly infuscated; hind tibia black basally and distally, yellow at mid-length; pronotum entirely yellow; mesoscutum entirely pale; anterior transverse carina of propodeum reaching the lateral margin; median tergites entirely pale.

**Description.** Holotype: male. Body length 5.6 mm. Fore wing length 5.4 mm. Fore wing mostly infuscated. Scutellar sulcus with five longitudinal carinae. Median
Figure 3. *Lytopylus alejandromasisi* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.

areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide.

**Female.** Unknown.

**Etymology.** *Lytopylus alejandromasisi* is named in honor of Alejandro Masis in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared one time from Gelechiidae “same as 93-SRNP-3345.1” feeding on very new leaves of *Bursera tomentosa* (Burseraceae) in ACG dry forest at 280 m elevation.

**Type material.** Holotype ♂: Costa Rica, Guanacaste, Sector Santa Rosa, Quebrada Duende, Area de Conservación Guanacaste 10.83663N -85.61144W 280m., guasaneros coll., host plant: Burseraceae *Bursera tomentosa*, host caterpillar: Gelechiidae, same as 93-SRNP-3345.1, coll. date: 7/7/1993, parasitoid eclosion date: 7/25/1993, DHJPAR0015416.

*Lytopylus alfredomainieri* Kang, sp. n.
http://zoobank.org/ED76E996-F310-4605-BB8D-F1EC579B21D9
Fig. 4

**Diagnosis.** Apical flagellomeres brown not distinctly paler than subapical flagellomeres; vertex of head entirely melanic; fore wing mostly infuscated; pronotum entirely pale
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**Figure 4.** Lytopylus alfredomainieri holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E wings.

(yellow to orange); fore tibia entirely pale (yellow to orange); mesoscutum entirely pale; anterior transverse carina of propodeum not reaching the lateral margin; median tergites entirely pale (yellow to orange); median syntergite 2+3 1.1 times longer than wide.

**Description.** Holotype: female. Body length 4.4 mm. Fore wing length 5.1 mm. Fore wing mostly infuscated. Pronotum entirely pale (yellow to orange). Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor about same length as body.

**Males.** Similar to holotype except for face. Face usually paler than holotype.

**Etymology.** Lytopylus alfredomainieri is named in honor of Alfredo Mainieri in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared five times from two species of Olethreutes (Olethreutinae, Tortricidae) leaf-tiers feeding on mature leaves of Meliosma glabrata (Sabiaceae) in ACG cloud forest edge at 1220 to 1276 m elevation.

**Type material.** Holotype ♀: Costa Rica, Guanacaste, Sector Cacao, Sendero Derrumbe, Área de Conservación Guanacaste 10.92918N -85.46426W 1220m., Manuel Pereira coll., food plant: Sabiaceae Meliosma glabrata, host caterpillar: Tortricidae, Olethreutinae, Olethreutes Janzen188, coll. date: 2/2/2009, parasitoid eclosion date: 3/19/2009, DHJPAR0035525. Paratypes: [the following have the same data as the holotype except as indicated] ♂, DHJPAR0035519. ♀, DHJPAR0035513. ♂, Sector

_Lytopylus anamariamongeae_ Kang, sp. n.
[http://zoobank.org/14F4C7B3-3857-4584-8CCA-3781096E338C](http://zoobank.org/14F4C7B3-3857-4584-8CCA-3781096E338C)
Fig. 5

**Diagnosis.** Fore wing mostly infuscated; pronotum mostly pale, anteriorly black; mesoscutum entirely pale (yellow to orange); mesopleuron mostly pale, posteroventrally black; scutellar sulcus lacking longitudinal carina; median tergites entirely melanic.

**Description.** Holotype: female. Body length 6.2 mm. Fore wing length 5.5 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.5 times longer than wide. Ovipositor about same length as body.

**Male.** Unknown.

**Etymology.** _Lytopylus anamariamongeae_ is named in honor of Ana Maria Monge in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared one time from *Antaeocerconota* Janzen433 (Depressariidae) a leaf-tier feeding on mature leaves of *Inga punctata* (Fabaceae) in ACG dry forest – rain forest ecotone at 540 m elevation.


_Lytopylus angelagonzalezae_ Kang, sp. n.
Fig. 6

**Diagnosis.** Fore wing mostly infuscated; mesoscutum entirely melanic; median areola of propodeum lacking well-defined margins; anterior transverse carina of propodeum absent; median tergites entirely reddish orange; lateral longitudinal carinae of median tergite 1 blunt.

**Description.** Holotype: female. Body length 5.8 mm. Fore wing length 5.6 mm. Fore wing mostly infuscated. Scutellar sulcus with three longitudinal carinae. Me-
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**Figure 5.** *Lytopylus anamariamongae* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.

dian areola of propodeum lacking well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 blunt. Median syntergite 2+3 as long as wide. Ovipositor length longer than metasoma, but shorter than body.

**Figure 6.** *Lytopylus angelagonzalezae* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.
Male. Unknown.

Etymology. *Lytopylus angelagonzalezae* is named in honor of Angela González Grau in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Anacampsis Janzen353* (Anacampsinæ, Gelechiidae) feeding on two species of Rutaceae in ACG dry forest – rain forest ecotone at 280 to 825 m elevation.


*Lytopylus cesarmorai* Kang, sp. n.

http://zoobank.org/5D2E689D-6076-4242-938B-73C772324EE1

Fig. 7

Diagnosis. Fore wing mostly infuscated; scutellar sulcus with one median longitudinal carina; median tergites entirely melanic; lateral tergites one and two entirely white.

Description. Holotype: female. Body length 5.7 mm. Fore wing length 5.4 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.5 times longer than wide. Ovipositor slightly longer than body.

Male. Fore wing with a slight yellow tinge. Body color pattern similar to holotype, but slightly lighter.

Etymology. *Lytopylus cesarmorai* is named in honor of Cesar Mora in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Stenoma BioLep82* (Depressariidae) feeding on mature leaves of *Apeiba membranacea* (Malvaceae) in ACG rain forest at 527 m elevation.

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*Figure 7. Lytopylus cesarmorai* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

*Figure 7. Lytopylus cesarmorai* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

**Lytopylus chrysokeras** (Sharkey)

Fig. 8

*Austroearinus chrysokeras* (Sharkey), (Sharkey 2006).
*Lytopylus chrysokeras* Sharkey, (Sharkey et al. 2016).

**Diagnosis.** Apical flagellomeres usually bright yellow, always distinctly paler than subapical flagellomeres; fore wing mostly infuscated; hind tibia black apically; mesoscutum entirely pale; median tergites entirely pale (yellow to orange).

**Biology.** Reared 48 times from seven species of dichomeridine Gelechiidae feeding on seven species of mature leaves of Malvaceae, Violaceae, Rubiaceae, Asteraceae, and Fabaceae growing in ACG rain forest at 240 to 645 m elevation.


**Figure 8.** *Lytopylus chrysokeras*:

A lateral habitus

B anterior head

C propodeum

D dorsal habitus

E fore wing

F hind wing.
Revision of the species of Lytopylus from Area de Conservación Guanacaste...

**Lytopylus eddysanchezi** Kang, sp. n.
http://zoobank.org/7BD05EB2-A120-4442-AABA-0D70E4AE0FB6
Fig. 9

**Diagnosis.** Vertex of head entirely yellow; fore wing with one black band; mid tibia mostly melanic, yellow basally.

**Description.** Holotype: female. Body length 6.0 mm. Fore wing length 5.5 mm. Fore wing with one black band. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.2 times longer than wide. Ovipositor about same length as body.

**Males.** Similar to holotype except for fore legs color. Fore legs usually less melanic.

**Etymology.** *Lytopylus eddysanchezi* is named in honor of Eddy Sánchez in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared 11 times from one species leaf-tier in the Depressariidae, feeding on mature leaves of *Meliosma glabrata* (Sabiaceae) in ACG rain forest at 540 to 645 m elevation.

**Type material.** Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Finca San Gabriel, Area de Conservación Guanacaste 10.87766N -85.39343W 645m., Gloria Sihezar coll., food plant: Sabiaceae *Meliosma glabrata*, host caterpillar: Depressariidae, subfamily unknown, elachJanzen01 Janzen900, coll. date: 1/7/2015, parasitoid eclosion date: 2/7/2015, DHJPAR0056978. Paratypes: [the following have the same data]

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*Figure 9. Lytopylus eddysanchezi* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.

**Lytopylus eliethcantillanoae** Kang, sp. n.

http://zoobank.org/747FAD7E-4637-4F8E-8E35-93BCFD8D5739

Fig. 10

**Diagnosis.** Fore wing mostly infuscated; mesoscutum entirely melanic; anterior transverse carina of propodeum absent; median areola of propodeum narrow and not closed posteriorly; median areola length 11x its width, lateral longitudinal carinae of median tergite 1 well-defined; median tergites entirely reddish orange.

**Description.** Holotype: male. Body length 5.2 mm. Fore wing length 5.3 mm. Fore wing mostly infuscated. Scutellar sulcus with three longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

**Female.** Unknown.

**Etymology.** *Lytopylus eliethcantillanoae* is named in honor of Elieth Cantillano in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared perhaps one time from elachJanzen01 Janzen873 (Depressariidae) feeding on *Malvaviscus arboreus* (Malvaceae) in ACG dry forest – rain forest ecotone at 840 m elevation.

Lytopylus ericchapmani Kang, sp. n.
http://zoobank.org/A2C8DCE5-4DA5-4F79-94A2-1D7750C5AFDA
Fig. 11

Diagnosis. Fore wing with two black bands; pronotum anteriorly black and posteriorly pale.


Male. Body color similar to holotype. Body length slightly shorter than holotype.

Etymology. Named in honor of Dr Eric G. Chapman, research analyst in the Department of Entomology at the University of Kentucky, for his kindly advice on molecular systematics and phylogenetics.

Biology. Reared five times but only from the leaf-tier Stenoma adytodes (Depressariidae) feeding on mature leaves of Pouteria juruana (Sapotaceae) at the intersection of the ACG dry forest and rain forest ecosystems at 722 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Jardin Estrada, Area de Conservación Guanacaste 10.86546N -85.39694W 722m., Carolina Cano coll., food plant: Sapotaceae Pouteria juruana, host caterpillar: Depressariidae, Stenomatinae, Stenoma adytodes, coll. date: 12/10/2013, parasitoid eclosion date: 1/12/2014, DHJPAR0054533. Paratypes: [the following have the same data as the hol-
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Lytopylus gahyunae Kang, sp. n.
http://zoobank.org/34C499A2-CEC2-4D38-8D16-342D152B15B8

Figure 11. *Lytopylus ericchapmani* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.

**Diagnosis.** Fore wing mostly infuscated; hind coxa entirely pale; mesoscutum entirely melanic; scutellar sulcus with one median longitudinal carina; anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly pale with posterior terga black; median syntergite 2+3 1.4 times longer than wide.

**Description.** Holotype: female. Body length 7.1 mm. Fore wing length 6.4 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.4 times longer than wide. Ovipositor slightly longer than body.

**Males.** Similar to holotype.

**Etymology.** *Lytopylus gahyunae* is named in honor of Gahyun Park, wife of the first author.
Biology. Reared 43 times from six species of *Antaeotricha* (40) and *Stenoma* (2) (Depressariidae) feeding on mature leaves of 3 species of *Guarea* and 1 of *Trichilia* (Meliaceae) in ACG rain forest at 380 to 620 m elevation.

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**Lytopylus gisukae** Kang, sp. n.
http://zoobank.org/40757AA3-B52C-4733-AEF2-334C861F561F

Fig. 13

**Diagnosis.** Vertex of head mostly pale; fore wing mostly infuscated with a quadrate second submarginal cell; mesoscutum entirely pale (yellow to orange); median areola of propodeum length 15x its width; anterior transverse carina of propodeum not reaching the lateral margin; median tergites entirely pale (yellow to orange).

**Description.** Holotype: female. Body length 5.0 mm. Fore wing length 5.0 mm. Fore wing mostly infuscated with a quadrate second submarginal cell. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum length 15x its width with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.2 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

**Male.** Unknown.

**Etymology.** *Lytopylus gisukae* is named in honor of Gisuk Lee, mother-in-law of the first author.

**Biology.** Reared one time from *Antaeotricha* Janzen405 (Stenomatinae, Depressariidae) feeding on mature leaves of *Astrocaryum alatum* (Arecaceae) in ACG rain forest at 420 m elevation.

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Figure 13. *Lytopylus gisukae* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E wings.

*Lytopylus guillermopereirai* Kang, sp. n.
http://zoobank.org/FAC851A7-13CC-4DB7-AFDE-562014FE4D02

**Fig. 14**

**Diagnosis.** Fore wing mostly infuscated; mesoscutum entirely melanic; scutellar sulcus lacking longitudinal carina; median tergites entirely melanic.

**Description.** Holotype: female. Body length 5.4 mm. Fore wing length 4.5 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.3 times longer than wide.

**Female.** Unknown.

**Etymology.** *Lytopylus guillermopereirai* is named in honor of Guillermo Pereira in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared one time from elachJanzen01 Janzen726 (Depressariidae) feeding on *Sloanea faginea* (Elaeocarpaceae) in ACG rain forest at 645 m elevation.

Figure 14. Lytopylus guillermopereirai holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.

Lytopylus gustavoindunii Kang, sp. n.
http://zoobank.org/9008E51A-5E03-4E95-BCF1-E427306B35F9
Fig. 15

Diagnosis. Apical flagellomeres brown not distinctly paler than subapical flagellomeres; vertex of head entirely pale; fore wing mostly infuscated with a triangular second submarginal cell; mesoscutum entirely pale (yellow to orange); median areola spindle-shaped; anterior transverse carina of propodeum absent; median tergites entirely pale (yellow to orange).


Male. Unknown.

Etymology. Lytopylus gustavoindunii is named in honor of Gustavo Induni in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared 12 times from two species of palm-feeding (Geonoma, Chamaedorea) Depressariidae (Stenoma Janzen142 and Stenoma Janzen284) in the understory of ACG rain forest from 645-742 m elevation.
Figure 15. *Lytopylus gustavoindunii* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.


**Lytopylus hartmanguidoi** Kang, sp. n.
http://zoobank.org/42792E91-4825-4562-93BE-7B2BB40A40FA
Fig. 16

**Diagnosis.** Fore wing with one black band; mid tibia black basally and distally, yellow at mid-length.
Description. Holotype: female. Body length 4.3 mm. Fore wing length 4.3 mm. Fore wing with one black band. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.3 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Male. Unknown.

Etymology. Lytopylus hartmanguidoi is named in honor of Hartman Guido in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared five times from three species leaf-tiers in the Depressariidae, feeding on mature leaves of Hiraea reclinata (Malpighiaceae) at the intersection of the ACG dry forest and rain forest ecosystems at 540 m elevation.

*Lytopylus hermanbravoi* Kang, sp. n.  
http://zoobank.org/028AF18F-E671-4FC7-9447-6EAD6AA30616  
Fig. 17

**Diagnosis.** Fore wing mostly infuscated; hind coxa entirely black; mesoscutum entirely melanic; anterior transverse carina of propodeum reaching the lateral margin; median tergites entirely yellow.

**Description.** Holotype: male. Body length 6.0 mm. Fore wing length 6.7 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide.

**Female.** Unknown.

**Etymology.** *Lytopylus hermanbravoi* is named in honor of Hernan Bravo in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared one time from *Anadasmus* Janzen08 (Depressariidae), a stenomine leaf-tier feeding on mature foliage of *Ocotea austini* (Lauraceae) in ACG cloud forest at 1460 m elevation.


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**Figure 17.** *Lytopylus hermanbravoi* holotype: A lateral habitus B mid leg C hind leg D anterior head E propodeum F dorsal habitus G fore wing H hind wing.
**Lytopylus hokwoni** Kang, sp. n.
http://zoobank.org/21D4210B-AFC4-4FF0-9AE9-360D26C6C940

Fig. 18

**Diagnosis.** Fore wing with two black bands; pronotum entirely melanic; lateral longitudinal carinae of median tergite 1 well-defined.

**Description.** Holotype: female. Body length 8.0 mm. Fore wing length 4.6 mm. Fore wing with two black bands. Scutellar sulcus with one median longitudinal carina. Anterior transverse carina of propodeum reaching the lateral margin. Median areola of propodeum with well-defined margins. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.6 times longer than wide. Ovipositor slightly longer than body.

**Male.** Mesoscutum bicolored. Mesopleuron pale.

**Etymology.** Named in honor of Hokwon Kang, father of the first author.

**Biology.** Reared nine times from seven species of stenomatine Depressariidae feeding as leaf-tiers on six species of plants in seven plant families at the intersection of the ACG dry forest and rain forest ecosystems at 280-640 m elevation.

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Lytopylus ivanniasandovalae Kang, sp. n.
http://zoobank.org/11328F60-489F-41A1-B3FC-0F2EF21EAE40
Fig. 19

**Diagnosis.** Fore wing with a slight yellow tinge; anterior transverse carina of propodeum absent; median tergites entirely pale.

**Description.** Holotype: male. Body length 5.8 mm. Fore wing length 5.0 mm. Fore wing with a slight yellow tinge. Scutellar sulcus with four longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 as long as wide.

**Female.** Unknown.

**Etymology.** Lytopylus ivanniasandovalae is named in honor of Ivanna Sandoval in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared one time from Dichomerus Janzen703 (Dichomeridinae, Gelechiidae) tying and feeding on mature leaves of Neurolaena lobata (Asteraceae) in ACG rain forest at 660 m elevation.

Figure 18. Lytopylus hokwoni holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.
**Figure 19.** *Lytopylus ivanniasandovalae* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.


*Lytopylus johanvalerioi* Kang, sp. n.
http://zoobank.org/862254CE-7A11-4D65-B7A6-69A723E1392C
Fig. 20

**Diagnosis.** Fore wing mostly infuscated; pronotum mostly yellow; mesoscutum mostly pale (yellow to orange); anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly pale posterior tergum black.

**Description.** Holotype: female. Body length 4.9 mm. Fore wing length 4.6 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 0.9 times longer than wide. Ovipositor longer than metasoma, but shorter than body.
Males. Occiput usually more melanic. Median tergites usually mostly pale with posterior terga black.

Etymology. *Lytopylus johanvalerioi* is named in honor of Johan Valerio in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared six times from two species of *Cerconota* leaf-tiers in the Depressariidae, feeding on mature leaves of three species of *Inga* (Fabaceae) in ACG rain forest at 540-645 m elevation.


Figure 20. *Lytopylus johanvalerioi* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.
**Lytopylus josecortesi** Kang, sp. n.
http://zoobank.org/F15FE11D-1DE7-4A48-B4C5-0DCA61C97445
Fig. 21

**Diagnosis.** Fore wing mostly infuscated; mesoscutum entirely melanic; anterior transverse carina of propodeum absent; median areola of propodeum spindle-shape; lateral longitudinal carinae of median tergite 1 well-defined; median tergites entirely reddish orange.

**Description.** Holotype: female. Body length 5.2 mm. Fore wing length 5.3 mm. Fore wing mostly infuscated. Scutellar sulcus with three longitudinal carinae. Median areola of propodeum with well-defined margins. Median areola length 6x its width. Median areola closed posteriorly. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

**Male.** Similar to holotype.

**Etymology.** *Lytopylus josecortesi* is named in honor of José Cortés in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared two times from *Dichomeris Janzen703* (Dichomeridinae, Gel-echiidae) feeding on mature leaves of *Neurolaena lobata* (Asteraceae) in ACG dry forest – rain forest ecotone at 620 m elevation.

**Figure 21.** *Lytopylus josecortesi* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.
Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Del Oro, Bosque Aguirre, Area de Conservación Guanacaste 11.0006N -85.438W 620m., Elieth Cantillano coll., food plant: Asteraceae Neurolaena lobata, host caterpillar: Gelechiidae, Dichomeridinae, Dichomeris Janzen703, coll. date: 9/21/2004, parasitoid eclosion date: 10/3/2004, DHJPAR0015432. Paratype: [the following have the same data as the holotype except as indicated] ♂, parasitoid eclosion date: 10/13/2004, DHJPAR0015431.

Lytopylus luisgaritai Kang, sp. n.  
http://zoobank.org/EE7D1A31-9D2F-4B74-A6A6-C95012768953
Fig. 22

Diagnosis. Fore wing mostly infuscated; pronotum mostly pale, anteriorly melanic; mesoscutum entirely pale; mesopleuron entirely orange; scutellar sulcus lacking longitudinal carina; median tergites mostly melanic.


Male. Unknown.

Figure 22. Lytopylus luisgaritai holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.
Variation. Paratype propodeum mostly pale.

Etymology. *Lytopylus luisgaritai* is named in honor of Luis Garita in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Oecophora* Janzen52 (Oecophorinae, Oecophoridae) feeding on mature leaves of *Clethra lanata* (Clethraceae) in ACG dry forest at 733–740 m elevation.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Mundo Nuevo, Camino Pozo Tres, Area de Conservación Guanacaste 10.77079N -85.37422W 733m., Jose Cortez coll., food plant: Clethraceae *Clethra lanata*, host caterpillar: Depressariidae, Oecophorinae, *Oecophora* Janzen52, coll. date: 1/22/2012, parasitoid eclosion date: 3/3/2012, DHJPAR0049053. Paratype: [the following have the same data as the holotype except as indicated] ♀, Cerro Gongora Pelado, 10.76307N -85.41332W 740m., coll. date: 1/18/2014, parasitoid eclosion date: 2/22/2014, DHJPAR0055239.

*Lytopylus mariamartachavarriae* Kang, sp. n.

http://zoobank.org/1691B66E-87CB-475D-AA54-0588AD1BCB13

Fig. 23

Diagnosis. Fore wing hyaline; fore wing RS+Ma tubular on less than one third its length; anterior transverse carina of propodeum reaching the lateral margin; median tergites entirely pale.

Description. Holotype: female. Body length 4.4 mm. Fore wing length 4.0 mm. Fore wing hyaline. Scutellar sulcus with three longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 0.9 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

Male. Similar to holotype, but median tergites mostly pale with three posterior terga melanic.

Etymology. *Lytopylus mariamartachavarriae* is named in honor of Marí­a Marta Chavarría in recognition of her participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared four times from *Dichomeris santarosensis* (Dichomeridinae, Gelechiidae) feeding on new leaves of *Quercus oleoides* (Fagaceae) in ACG dry forest at 305 m elevation.

Type material. Holotype ♀: Costa Rica, Guanacaste, Sector Santa Rosa, Arboles Via, Area de Conservación Guanacaste 10.86081N -85.60828W 305m., Daniel H. Janzen coll., food plant: Fagaceae *Quercus oleoides*, host caterpillar: Gelechiidae, Dichomeridinae, *Dichomeris santarosensis*, coll. date: 6/24/1982, eclosion date unknown, DHJPAR0015502. Paratypes: [the following have the same data as the holotype except as indicated] 2♀, 1♂, DHJPAR0015501, DHJPAR0015503, DHJPAR0015500.
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Figure 23. *Lytopylus mariamartachavarriae* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.

*Lytopylus miguelviquezi* Kang, sp. n.  
http://zoobank.org/1BE064F2-17DB-44CB-8B99-5A6F4224C7C1  
Fig. 24, 25

**Diagnosis.** Apical flagellomeres brown not distinctly paler than subapical flagellomeres; fore wing mostly infuscated with a triangular second submarginal cell; fore tibia mostly melanic, yellow basally; hind tibia black basally and distally, yellow at mid-length; pronotum entirely pale (yellow to orange); mesoscutum entirely pale (yellow to orange); median areola of propodeum kite-shaped; anterior transverse carina of propodeum not reaching the lateral margin; median tergites mostly pale with posterior terga black; median syntergite 2+3 1.1 times longer than wide.

**Description.** Holotype: female. Body length 5.1 mm. Fore wing length 4.9 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

**Males.** Body length usually shorter than holotype. Median tergites mostly melanic.

**Variation.** Female anterior head varies from mostly pale to mostly melanic.

**Etymology.** *Lytopylus miguelviquezi* is named in honor of Miguel Viquez in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.
**Biology.** Reared 58 times from the *Dichomeris designatella* complex (21), gel-Janzen01 Janzen179 (13), and gelJanzen01 Janzen485 (16), all leaf tying dichomeridine Gelechiidae feeding on mature leaves of two species of *Erythroxylum* (Erythroxylaceae) and two species of *Rinorea* (Violaceae) in ACG rain forest-dry forest ecotone, and rain forest at 109 to 540 m elevation.

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![Figure 25. *Lytopylus miguelviquezi* male: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.](image)


**Lytopylus motohasegawai** Kang, sp. n.
http://zoobank.org/2F55247B-D2C7-4931-982F-7105C023953C
Fig. 26, 27

**Diagnosis.** Vertex of head entirely yellow; fore wing mostly infuscated with a quadrate second submarginal cell; mesoscutum mostly or entirely pale (yellow to orange); median areola of propodeum kite-shaped; anterior transverse carina of propodeum not reaching the lateral margin; median tergites entirely pale (yellow to orange).

**Description.** Holotype: female. Body length 4.9 mm. Fore wing length 4.9 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 as long as wide. Ovipositor longer than metasoma, but shorter than body.

**Males.** Vertical of head and occiput usually mostly melanic. Body length usually shorter than holotype. Median tergites mostly melanic.

**Variation.** Female occiput varies from entirely pale to mostly pale. Male hind femur color varies from mostly pale to black and pale with a similar percentage of each color.

**Etymology.** *Lytopylus motohasegawai* is named in honor of Motohiro Hasegawa in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared 36 times from gelJanzen01 Janzen28, a leaf-tier in the Gelechiidae feeding on mature leaves of two species of *Roupala* (Proteaceae) in ACG rain forest at 415 to 740 m elevation.

Figure 26. *Lytopylus motohasegawai*, holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.

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**Figure 27.** *Lytopylus motohasegawai* male: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.


*B* *Lytopylus okchunae* Kang, sp. n.
Fig. 28

**Diagnosis.** Apical flagellomeres brown not distinctly paler than subapical flagellomeres; vertex of head entirely melanic; fore wing mostly infuscated; mesoscutum entirely orange; anterior transverse carina of propodeum absent; median tergites entirely orange; median syntergite 2+3 1.5 times longer than wide.

**Description.** Holotype: female. Body length 6.8 mm. Fore wing length 6.3 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.5 times longer than wide. Ovipositor about same length as body.
Figure 28. Lytopylus okchunae holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.

**Males.** Similar to holotype except for median tergite color. Median tergites usually mostly pale with posterior three terga melanic.

**Etymology.** Lytopylus okchunae is named in honor of Okchun Kim, grandmother of the first author.

**Biology.** Reared 18 times from three species of *Antaeotricha* (Depressariidae) leaf-webbers feeding on mature leaves of five species of broad-leaved monocots (Hylaeanthina, Renealmia, Hedychium, Pleiostachya, Calathea) in the Marantaceae and Zingiberaceae in ACG rain forest 96-575 m elevation.


*Lytopylus pablocobbi* Kang, sp. n. 
http://zoobank.org/388474DC-9ED2-4C53-A0EA-46C8AA3EAFB4

Fig. 29

**Diagnosis.** Vertex of head entirely melanic; fore wing mostly infuscated; pronotum mostly orange, anteriorly black; mesoscutum entirely orange; anterior transverse carina of propodeum absent; median tergites entirely pale (yellow to orange); median syntergite 2+3 1.1 times longer than wide.

**Description.** Holotype: female. Body length 4.8 mm. Fore wing length 5.0 mm. Fore wing mostly infuscated. Pronotum bicolored. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide. Ovipositor longer than metasoma, but shorter than body.

**Male.** Unknown.

**Etymology.** *Lytopylus pablocobbi* is named in honor of Pablo Cobb in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.
**Biology.** Reared one time from elachJanzen01 Janzen640 (Depressariidae), a stenomine leaf-tier feeding on mature foliage of *Bunchosia odorata* (Malpighiaceae) in ACG dry forest – rain forest ecotone at 722 m elevation.


**Lytopylus robertofernandezi** Kang, sp. n.
http://zoobank.org/E4012DEC-AAA8-4964-A1D2-F714C99EC057
Fig. 30

**Diagnosis.** Fore wing with two black bands; pronotum entirely black; lateral longitudinal carinae of median tergite 1 blunt.

**Description.** Holotype: male. Body length 7.6 mm. Fore wing length 6.7 mm. Fore wing with two black bands. Scutellar sulcus with two longitudinal carinae. Anterior transverse carina of propodeum absent. Median areola of propodeum lacking well-defined margins. Lateral longitudinal carinae of median tergite 1 blunt. Median syntergite 2+3 1.6 times longer than wide.

**Female.** Unknown.

**Etymology.** *Lytopylus robertofernandezi* is named in honor of Roberto Fernández in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.
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Figure 30. *Lytopylus robertofernandezi* holotype: **A** lateral habitus **B** anterior head **C** propodeum **D** dorsal habitus **E** fore wing **F** hind wing.

**Biology.** Reared only one time and from the leaf-tier *Stenoma* Janzen687 (Depressariidae) feeding on mature leaves of *Pouteria exfoliata* (Sapotaceae) at the intersection of the ACG dry forest and rain forest ecosystems at 540 m elevation.


*Lytopylus rogerblancoi* Kang, sp. n.

http://zoobank.org/DE0D5410-134C-43BF-8A55-51B006AE8C76

Fig. 31

**Diagnosis.** Fore wing mostly infuscated; mesoscutum entirely black; median areola of propodeum with well-defined margins; anterior transverse carina of propodeum absent; median tergites entirely orange; lateral longitudinal carinae of median tergite 1 blunt.

**Description.** Holotype: female. Body length 6.0 mm. Fore wing length 6.4 mm. Fore wing mostly infuscated. Scutellar sulcus with three longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum absent. Lateral longitudinal carinae of median tergite 1 blunt. Ovipositor longer than metasoma, but shorter than body. Median syntergite 2+3 0.9 times longer than wide.

**Male.** Similar to holotype.
**Etymology.** *Lytopylus rogerblancoi* is named in honor of Roger Blanco in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared eight times, one time from a waif pupa and seven times from gel-Janzen01 Janzen356 (Dichomeridinae, Gelechiidae) feeding on mature leaves of *Hampea* and *Mortoniodendron* (Malvaceae) in ACG rainforest at 600 to 1180 m elevation.

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Lytopylus salvadorlopezi Kang, sp. n.
http://zoobank.org/6E529BF2-79C8-4B9C-9C3C-DC555133BCCD
Fig. 32

Diagnosis. Scutellar sulcus lacking longitudinal carina; fore wing mostly infuscated; anterior transverse carina of propodeum not reaching the lateral margin; median tergites mostly black.

Description. Holotype: female. Body length 7.5 mm. Fore wing length 7.3 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum not reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.2 times longer than wide. Ovipositor length about same length as body.

Male. Unknown.

Etymology. Lytopylus salvadorlopezi is named in honor of Salvador López in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared five times from two species of leaf-tying Stenoma (Depressariidae) feeding on Persea schiedeana (Lauraceae) in ACG in the rain forest rain forest at 700 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Quebrada Cementerio, Area de Conservación Guanacaste 10.87124N -85.38749W 700m., Osvaldo Espinoza coll., food plant: Lauraceae Persea schiedeana, host caterpillar: Depressariidae, Stenomatinae, Stenoma Janzen06, coll. date: 7/6/2009, parasitoid eclosion date: 8/6/2009, DHJPAR0036355. Paratypes: [the following have the same data
Figure 33. *Lytopylus sangyeoni* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.


*Lytopylus sangyeoni* Kang, sp. n.
http://zoobank.org/571E1D60-DF10-4EB9-B070-8291838382F7
Fig. 33

**Diagnosis.** Fore wing mostly infuscated; hind coxa entirely pale; mesoscutum entirely black; scutellar sulcus with one median longitudinal carina; anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly pale with posterior terga black; median syntergite 2+3 as long as wide.

**Description.** Holotype: female. Body length 5.5 mm. Fore wing length 5.3 mm. Fore wing mostly infuscated. Scutellar sulcus with one median longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 as long as wide. Ovipositor longer than metasoma, but shorter than body.

**Male.** Unknown.

**Etymology.** Named in honor of Sangyeon Park, father-in-law of the first author.

**Biology.** Reared one time from elachJanzen01 Janzen847 (Depressariidae) as a leaf-tier feeding on mature leaves of *Senegalia tenuifolia* (Fabaceae) in ACG rain forest at 527 m elevation.

Lytopylus sarahmeierottoae Kang, sp. n.
http://zoobank.org/8A0864DC-0480-4A42-9052-2E32B869093B
Fig. 34

Diagnosis. Fore wing mostly infuscated; pronotum entirely pale; mesoscutum entirely pale; scutellar sulcus lacking longitudinal carina; anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly melanic, anteriorly white.


Male. Unknown.

Etymology. Named in honor of Sarah Meierotto, graduate student in the Department of Entomology at the University of Kentucky, for her assistance.

Biology. Reared four times from Cerconota Janzen82 (Stenomatinae, Depressariidae) feeding on mature leaves of Inga micheliana (Fabaceae) in ACG rain forest at 730 m elevation.

Type material. Holotype ♀: Costa Rica, Alajuela, Sector San Cristobal, Sendero Vivero, Area de Conservación Guanacaste 10.86739N -85.38744W 730m., Elda Araya coll., food plant: Fabaceae Inga micheliana, host caterpillar: Depressariidae, Stenomatinae, Cerconota Janzen82, coll. date: 12/20/2014, parasitoid eclosion date: 1/13/2015, DHJPAR0056993. Paratypes: [the following have the same data as the holotype except as indicated] 2♀, parasitoid eclosion date: 1/10/2015, DHJPAR0056984, DHJPAR0056991. ♀, parasitoid eclosion date: 1/17/2015, DHJPAR0056992.

Lytopylus sergiobermudezi Kang, sp. n.
http://zoobank.org/93CB5271-223B-4600-8D35-75486F6BA0C5
Fig. 35

Diagnosis. Fore wing hyaline; fore wing RS+Ma tubular on more than half its length; anterior transverse carina of propodeum reaching the lateral margin; median tergites mostly pale with posterior terga black.

Description. Holotype: male. Body length 3.9 mm. Fore wing length 3.6 mm. Fore wing hyaline. Fore wing RS+Ma more complete. Scutellar sulcus with four
Figure 34. *Lytopylus sarahmeierottoae* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E wings.

Figure 35. *Lytopylus sergiobermudezi* holotype: A lateral habitus, B. anterior head C propodeum D dorsal habitus E fore wing F hind wing.

longitudinal carinae. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.1 times longer than wide.
Female. Unknown.

Variation. Male mesoscutum varies from less melanic to mostly pale. Male propodeum varies bicolored to entirely pale.

Etymology. *Lytopylus sergiobermudezi* is named in honor of Sergio Bermúdez in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

Biology. Reared two times from *Dichomerus santarosensis* (Dichomeridinae, Gelechiidae) leaf-tier feeding on new foliage of *Quercus oleioides* (Fagaceae) in ACG dry forest at 420 m elevation.

Type material. Holotype ♂: Costa Rica, Guanacaste, Sector Mundo Nuevo, Punta Plancha, Area de Conservación Guanacaste 10.7416N -85.42734W 420m., Mariano Pereira coll., food plant: Fagaceae *Quercus oleioides*, host caterpillar: Gelechiidae, Dichomeridinae, *Dichomeris santarosensis*, coll. date: 1/5/2009, parasitoid eclosion date: 1/19/2009, DHJPAR0034286. Paratype: [the following has the same data as the holotype except as indicated] DHJPAR0030601.

*Lytopylus sigifredomarini* Kang, sp. n.

http://zoobank.org/5E10353D-E093-4A12-886F-C92596DEE86E

Fig. 36

**Diagnosis.** Fore wing mostly infuscated; hind coxa entirely pale; mesoscutum entirely black; scutellar sulcus lacking longitudinal carina; anterior transverse carina of propodeum reaching the lateral margin.

**Description.** Holotype: male. Body length 5.2 mm. Fore wing length 4.8 mm. Fore wing mostly infuscated. Scutellar sulcus lacking longitudinal carina. Median areola of propodeum with well-defined margins. Anterior transverse carina of propodeum reaching the lateral margin. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.2 times longer than wide.

Female. Unknown.

**Etymology.** *Lytopylus sigifredomarini* is named in honor of Sigifredo Marín in recognition of his participation in the collaborative development of the ICE-ACG geothermal project of Pailas II, northwestern Costa Rica.

**Biology.** Reared three times from *Antaeotricha Janzen224* (Stenomatinae, Depressariidae) feeding on mature leaves of *Hirtella media* (Chrysobalanaceae) in ACG rain forest at 410 to 620 m elevation.

**Type material.** Holotype ♂: Costa Rica, Guanacaste, Sector Del Oro, Tangelo, Area de Conservación Guanacaste 11.01823N -85.45024W 410m., Elieth Cantillano coll., food plant: Chrysobalanaceae *Hirtella triandra*, host caterpillar: Depressariidae, Stenomatinae, *Antaeotricha Janzen224*, coll. date: 1/6/2011, parasitoid eclosion date: 1/31/2011, DHJPAR0042545. Paratypes: [the following have the same data as the holotype except as indicated] ♂, Bosque Aguirre, 11.0006N -85.438W 620m., Roster Moraga coll., coll. date: 5/7/2010, parasitoid eclosion date: 5/31/2010, DHJ-
Figure 36. *Lytopylus sigfredomarini* holotype: A lateral habitus B anterior head C propodeum D dorsal habitus E fore wing F hind wing.


*Lytopylus youngcheae* Kang, sp. n.
http://zoobank.org/6890246F-A78D-4AA9-AE26-F4322390B5DE

Fig. 37

**Diagnosis.** Fore wing with one black band; vertex of head entirely melanic.

**Description.** Holotype: female. Body length 8.9 mm. Fore wing length 8.1 mm. Fore wing with one black band. Scutellar sulcus with one median longitudinal carina. Anterior transverse carina of propodeum not reaching the lateral margin. Median areola of propodeum with well-defined margins. Lateral longitudinal carinae of median tergite 1 well-defined. Median syntergite 2+3 1.5 times longer than wide. Ovipositor slightly longer than body.

**Males.** Body length usually shorter than holotype. Hind femur varies from mostly pale to mostly melanic.

**Etymology.** Named in honor of Youngche Choi, mother of the first author.

**Biology.** Reared five times from two species of stenomatine Depressariidae leaf-tiers feeding on mature leaves of *Calophyllum brasiliense* (Calophyllaceae) in ACG rain forest at 540 to 740 m elevation.
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References


Supplementary material 1

Interactive key, DELTA data matrix, and images for the revision of the species of *Lytopylus* from Area de Conservación Guanacaste, northwestern Costa Rica (Hymenoptera, Braconidae, Agathidinae)
Authors: Ilgoo Kang, Eric G. Chapman, Daniel H. Janzen, Winnie Hallwachs, Tanya Dapkey, Smith M. Alex, Michael J. Sharkey
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