



Phylogenetic status of some unique species representing *Blapstinina* Mulsant & Rey (Tenebrionidae: Blaptinae: Opatrini), and implications for continued study of the subtribe

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Abstract

Blapstinus Dejean is the most taxonomically challenging genus within *Blapstinina* Mulsant & Rey (Tenebrionidae: Opatrini). With over 120 species, it is widely distributed throughout the Americas, with representatives reaching Canada on the northern range edge, and Argentina, Chile, and Uruguay in the south. Traditionally, *Blapstinus* has been distinguished from other blapstinoid beetles via well-developed metathoracic wings and their lack of synapomorphies present in other genera; however, fused and tapering aedeagal parameres were recently introduced as a potential autapomorphy for the genus. This study used molecular data (nuclear ribosomal 28S, cytochrome oxidase subunit II (COII), arginine kinase (ArgK), carbonyl-phosphate synthetase domain of rudimentary (CAD), and *wingless* (*wg*)) to investigate the phylogenetic placement and taxonomic status of three *Blapstinus* species with distinct male genitalic morphology, i.e. *Blapstinus tibialis* Champion (USA), *B. grandis* Champion (Mexico, Nicaragua), and *B. punctulatus* Solier (Argentina, Bolivia, Brazil, Chile, Uruguay). Analyses highlight the phylogenetic informativeness of the aedeagal morphology within the subtribe, and support an urgent need for taxonomic studies of South American taxa. *Blapstinus tibialis* and *B. grandis* were recovered as a specific lineage within *Blapstinus* that can be easily distinguished from remaining congeners by having tridentate parameres. A lectotype for *B. grandis* is designated to fix the taxonomic status of this species. *Blapstinus punctulatus* was recovered outside of its current genus which, along with aedeagal morphology, supports a change of status of the species. As a result, the following synonymy and combinations are introduced: *Lodinus* Mulsant and Rey **stat. restit.** (= *Austrocaribius* Marcuzzi **syn. nov.**), *Lodinus araguae* (Marcuzzi) **comb. et stat. nov.**, *L. punctulatus* **comb. nov.**, *L. venezuelensis* (Marcuzzi) **comb. nov.** Lectotypes for *Lodinus nigroaeneus* Mulsant and Rey, *L. araguae*, and *L. punctulatus* are designated to fix the taxonomic status of these species.

Key words: darkling beetles, *Austrocaribius*, *Blapstinus*, *Lodinus*, parameres, Neotropics, South America

Introduction

Blapstinina Mulsant & Rey is a subtribe endemic to the Americas, containing over 200 species classified within the following genera (Hart & Ivie 2016a, Iwan & Kamiński 2016, Ivie & Hart 2016, Bousquet *et al.* 2018, Lumen *et al.* 2019, Kamiński *et al.* 2019a, b, 2021, Johnston *et al.* 2020, Bouchard *et al.* 2021): *Aconobius* Casey, *Ammodonus* Mulsant & Rey, *Austrocaribius* Marcuzzi, *Blapstinus* Sturm, *Cenophorus* Mulsant & Rey, *Conibiosoma* Casey, *Conibius* LeConte, *Cybotus* Casey, *Diastolinus* Mulsant & Rey, *Goajiria* Ivie & Hart, *Hummelinckia* Marcuzzi, *Nevisia* Marcuzzi, *Nocibiotes* Casey, *Notibius* LeConte, *Platylus* Mulsant & Rey, *Tonibius* Casey, *Tonibiastes* Casey, *Trichoton* Hope, *Ulus* Horn, *Xerolinus* Ivie & Hart. Morphologically, the subtribe is well defined within Opatrini Brullé; i.e. eyes completely divided by extending genae (Iwan & Kamiński 2016, Lumen *et al.* 2020, Kamiński *et al.* 2021).

Blapstinus, with over 120 species (present estimation), is the most speciose genus within *Blapstinina* (Casey

1890, Marcuzzi, 1951, Van Dyke 1953, Kaszab 1969, Davis 1970, Ardoin 1977, Doyen 1990, Aalbu & Triplehorn 1985, 1991, Schatz 1994, Steiner 2006, Ivie & Hart 2016, Bousquet *et al.* 2018). The genus is widely distributed throughout the Americas, with representatives ranging from Canada (e.g., *B. pratensis* LeConte and *B. substriatus* Champion) to Chile (*B. kulzeri* Kaszab) (Fairmaire 1883, Kaszab 1969, Bousquet *et al.* 2018). The current state of knowledge concerning the group disproportionately represents North America over South America (e.g., Davis 1970, Ardoin 1977, Marcuzzi 1982, Aalbu & Triplehorn 1985, Doyen 1990, Bousquet *et al.* 2018).

The majority of available morphological concepts for *Blapstinus* highlight the presence of metathoracic wings as the most reliable diagnostic feature for the genus (Davis 1970, 1976, 1980, Aalbu & Triplehorn 1985), while not providing any synapomorphies. Furthermore, in many direct comparisons *Blapstinus* has been defined by a lack of synapomorphies reported for other winged blapstinoid genera. For example, absence of lateral fimbrial setae extending off the pronotum and elytron, and unexpanded foretibia were used to distinguish it from *Ulus* (Davis 1976, Aalbu & Triplehorn 1985). Nevertheless, a recent molecular investigation of Blapstinina has supported the monophyly of *Blapstinus* including *Mecysmus* Horn—another previously recognized flighted genus in Blapstinina (Lumen *et al.* 2020). By comparing morphological (Davis 1970, Iwan 2001, 2004, Ivie & Hart 2016) and molecular data, Lumen *et al.* (2020) concluded that fused and tapering parameres could potentially be used as a reliable, diagnostic feature for *Blapstinus*.

The only known exceptions to this character were *Blapstinus tibialis* Champion and an unpublished species from Southern Texas introduced in Davis' (1970) dissertation, which both possess tridentate parameres. Recent dissections of Mexican and Central American *Blapstinus* revealed an additional species (*B. grandis* Champion) has similarly modified parameres (Fig. 1). Finally, *Blapstinus punctulatus* from South America was found to possess an aedeagus with a truncate apex of the tegmen (Fig. 1).

Given the importance of male aedeagal modifications in helping to define genera in Blapstinina (Marcuzzi 1954, Ivie & Hart 2016, Lumen *et al.* 2019), the aim of this investigation is to determine the phylogenetic placement of *B. grandis*, *B. tibialis*, and *B. punctulatus*. To this end, specimens were sequenced and included in the molecular dataset for Blapstinina from Lumen *et al.* (2020) to test whether these species with apomorphic aedeagi fall outside of *Blapstinus*. The implications for defining *Blapstinus* are then discussed in the context of the new phylogeny.

Material and methods

Molecular analysis

Molecular data for *Blapstinus grandis*, *B. tibialis*, and *B. punctulatus* were obtained from specimens collected into and stored in ethanol following methodologies presented in Lumen *et al.* (2020). The following loci were targeted: nuclear ribosomal 28S (1,087 bp), cytochrome oxidase subunit II (711 bp), arginine kinase (668 bp), carbamoyl-phosphate synthetase domain of *rudimentary* (906 bp), *wingless* (462 bp). All newly acquired sequences were submitted to GenBank and are available under the following accession numbers: (OL445118–OL445123 and OL438932–OL438933). Molecular voucher specimens are deposited in the Purdue Entomological Research Collection (PERC) at Purdue University in West Lafayette, Indiana.

Newly generated sequences were included with the dataset from Lumen *et al.* (2020) for phylogenetic analyses to examine the placement of the three newly investigated Blapstinina species (Kamiński 2021). Data partitions were determined by gene and codon position (for protein coding genes), and models of sequence evolution for Bayesian phylogenetic analyses were assessed in IQ-Tree v. 2.1.2 (Minh *et al.* 2020) implemented on the CIPRES Science Gateway (Miller *et al.*, 2010). Bayesian analyses were run through CIPRES using MrBayes v.3.2.6 (Ronquist *et al.* 2012). Two independent runs were performed, each with four chains. Analyses were run for 20 million generations and were sampled every 1,000 generations with a burn-in fraction of 25%. Branch support was displayed as posterior probabilities (PP). Maximum likelihood (ML) analysis was conducted in IQ-Tree on the CIPRES Science Gateway. The run was performed allowing partitions to have different speeds (--p). Branch support was estimated with 1,000 ultrafast bootstrap (UFB) replicates (Minh *et al.*, 2013). Models of sequence evolution for this analysis were assessed in IQ-Tree prior to phylogenetic analysis.

Morphological and distribution data

The descriptive style adopted here follows that of Lumen *et al.* (2019). Morphological terminology was adopted

after Ivie & Hart (2016), with additional specialized terms used for male and female genitalia (Iwan & Kamiński 2016). Taxa authors and publication years follow Bouchard *et al.* (2021). Images were taken using a Canon 1000D body with Canon Macro Lens EF 100. Photos of type specimens of *Blapstinus grandis* and *B. tibialis* were acquired from the Museum of Comparative Zoology, Harvard (MCZ) and Natural History Museum, London (BMNH) respectively. Pinned specimens of *Lodinus* for morphological examination were from the collections of Museum and Institute of Zoology of the Polish Academy of Sciences (MIZ PAS) and Muséum national d'Histoire naturelle, Paris (MNHN). Scanning electron microscopy images of *Lodinus araguae* parameres were acquired with a Hitachi S-3400 N in MIZ PAS.

A map illustrating the distribution of *Lodinus* was produced with Quantum GIS (QGIS) v. 2.4 and free GIS layers available at <https://www.naturalearthdata.com/>. Distributional data was acquired from labels of studied specimens and literature (Marcuzzi 1951, 1954, 1983, 1986, Peña 1966, Aballay *et al.* 2016). Records are represented by a centrally localized point(s) in cases of specimens with province-only data.

Results

The topology of Blapstinina recovered with IQ-Tree closely matches the ML tree presented by Lumen *et al.* (2020). Subtribe Blapstinina was again monophyletic and well-supported (UFB = 100, PP = 1.0) (Fig. 1). Each overall clade (*Ammodonus*, *Blapstinus*, *Conibius*+*Notibius*+*Nocibiotes*, *Trichoton*, and *Ulus*) remained intact as of this study, with high branch support (Fig. 1). However, relationships between some clades shifted in this analysis. The *Conibius*+*Notibius*+*Nocibiotes* clade, rather than being recovered sister to a clade made up of *Ulus* and *Xerolinus* (Lumen *et al.* 2020); was placed sister to a clade containing *Blapstinus*, *Ulus*, *Xerolinus*, and *B. punctulatus* (Fig. 1). Inconsistency between the ML topology of this study and Lumen *et al.* (2020) only concerns clades with negligible support in both studies.

The three focal taxa of this investigation were also recovered within Blapstinina (Fig. 1). Specifically, *Blapstinus grandis* and *B. tibialis* were recovered, in both Bayesian and maximum likelihood analyses, together within the *Blapstinus* clade and sister to *B. fortis* + *B. vestitus* with strong support (UFB = 100, PP = 1.0). Maximum likelihood analysis rendered *Blapstinus punctulatus* sister to *Ulus* with negligible support (UFB = 46), while Bayesian analyses placed it sister to a large clade containing the majority of included Blapstinina (all except *Ammodonus* and *Trichoton*). Statistical support for the clade grouping *Blapstinus*, *Conibius*, *Notibius*, *Nocibiotes*, *Ulus*, and *Xerolinus* was low (PP = 0.63). Divergences between maximum likelihood and Bayesian topologies only involved nodes that were poorly supported in both (Fig. 1).

Discussion

The results here challenge traditionally accepted diagnostic characters (i.e., presence of metathoracic wings, lack of externally distinct apomorphies) for *Blapstinus* (Davis 1970, Aalbu & Triplehorn 1985). Despite a high overall resemblance of all three examined species (Fig. 2), molecular data recovered them in different parts of the Blapstinina phylogenetic tree (Fig. 1). *Blapstinus tibialis* and *B. grandis* were placed among other *Blapstinus*, while *B. punctulatus* was recovered as a separate lineage far outside the genus (Fig. 1).

Status of *Blapstinus punctulatus*

Although molecular support for the placement of *B. punctulatus* is low, a review of available literature revealed that this species fell within the morphological concept of *Austrocaribius* (Marcuzzi 1982, 1986). Marcuzzi (1954) distinguished *Austrocaribius* from *Blapstinus* using the following characters: antennal segments eight-eleven transverse, segments six and seven more or less square, the remaining segments longer than wide; intercoxal process of prosternum developed posteriorly in an oval-lanceolate point, seen in profile prominent and abruptly truncate; penis widely projecting between the parameres, apical part of tegmen truncate, and contiguous. Upon examination of type material of *Austrocaribius* and comparison with representatives of *Blapstinus*, it is difficult to reliably separate *Austrocaribius* from *Blapstinus* using most of the characters Marcuzzi outlined (e.g., both *Blapstinus* and *Austrocaribius* have clavate antennae, resulting in the last 4 antennomeres becoming more-or-less transverse). The

aedeagal characters remain useful and, as of this study, can be used to consistently delineate the two genera (Fig. 1). However, the relationship uncovered by morphological comparison between *Blapstinus punctulatus* and previously known species of *Austrocaribius* necessitates the following nomenclatural acts: Namely, *Blapstinus punctulatus* is a synonym of *Lodinus nigroaeneus* Mulsant and Rey (see Bouchard *et al.* 2021), which is the type species of the monotypic genus *Lodinus* that was synonymised with *Blapstinus* by Gemminger in Gemminger and Harold (1870). Since the name *Lodinus* predates *Austrocaribius* by 95 years, the change in status of *Blapstinus punctulatus* therefore requires introduction of the following synonymy and combinations: *Lodinus* Mulsant and Rey **stat. restit.** (= *Austrocaribius* Marcuzzi **syn. nov.**), *Lodinus araguae* (Marcuzzi) **comb. et stat. nov.** [transferred from *Austrocaribius*], *L. punctulatus* **comb. nov.** (= *Lodinus nigroaeneus*), *L. venezuelensis* (Marcuzzi) **comb. nov.** [transferred from *Austrocaribius*].

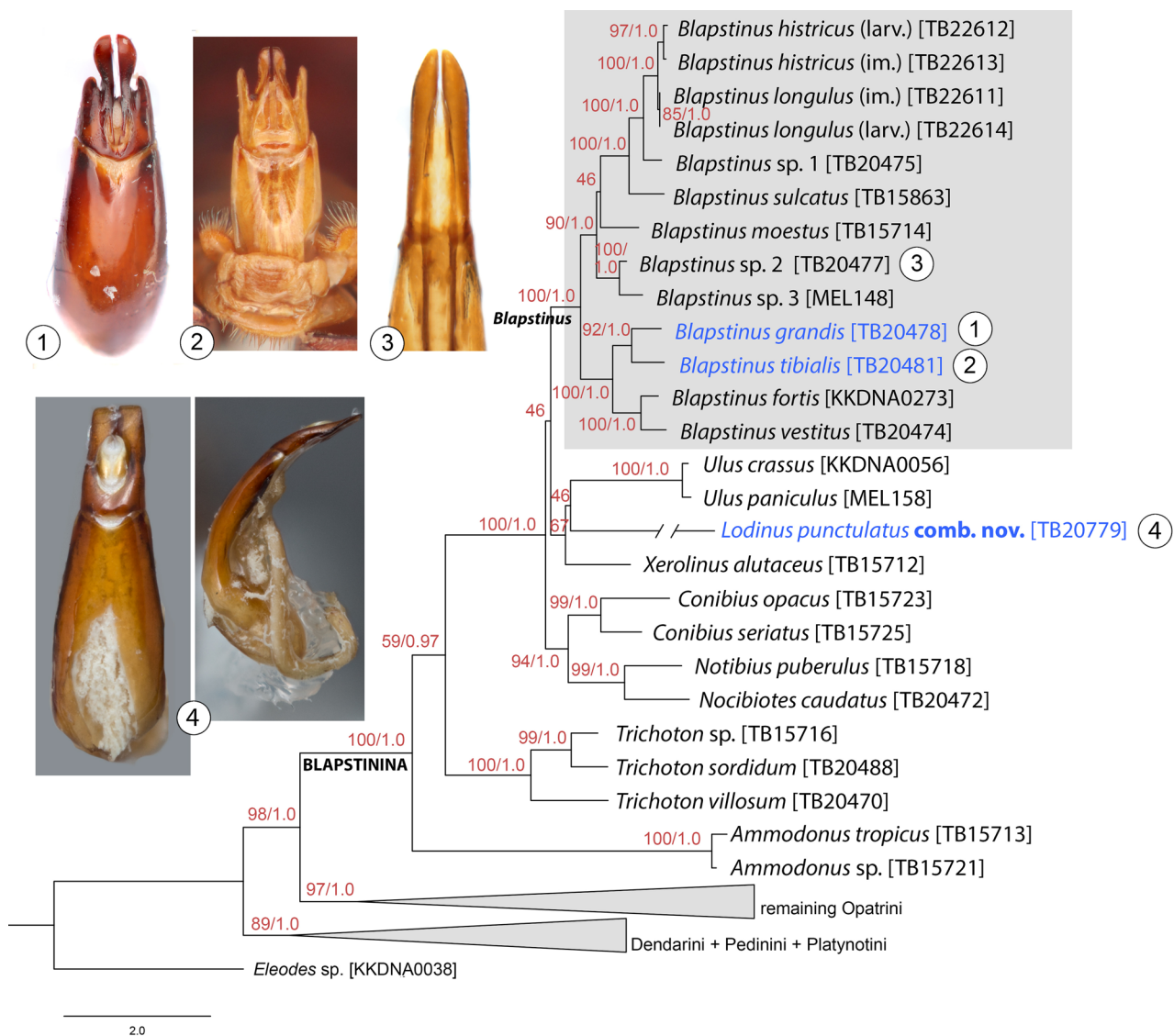


FIGURE 1. Phylogeny of subtribe Blapstinina. Figured topology was recovered in maximum likelihood analysis using IQ-Tree. Ultrafast bootstrap values (1,000 replicates) (integers) and posterior probabilities (20 million generations) acquired in Bayesian analysis (decimals) are displayed in red. The three investigated Blapstinina species are displayed in blue. Male genitalia (1–4) of selected species (dorsal views) are illustrated on the left. Topologies of collapsed clades ('remaining Opatrini' & 'Dendarini + Pedinini + Platynotini') are fully consistent with those presented in Lumen *et al.* (2020).

The unexpected phylogenetic position of *L. punctulatus* highlights an urgent need for additional morphological investigation of South American Blapstinina, especially those superficially resembling *Blapstinus*. Taxonomic acts in this paper greatly extend the range and change the status of a previously geographically restricted genus *Lodinus*. Furthermore, there are 75 species and subspecies of *Blapstinus* recorded North of Mexico (Bousquet *et al.* 2018), and

no official records available for Argentina (Fairmaire 1883, present paper, Gustavo Flores pers. comm.). Additionally, as a result of investigating taxon records for this study, it was revealed to the authors that the holotype of *Blapstinus metallescens* Fairmaire does not represent Tenebrionidae (Cabrera *et al.* 2010, Gustavo Flores pers. comm.).

Status of *Blapstinus tibialis* and *B. grandis*

Despite unique morphology of male genitalia (Fig. 1), *B. tibialis* and *B. grandis* were both recovered within *Blapstinus*—sister to *B. fortis* + *B. vestitus*, which both possess fused and tapering parameres. While this result potentially disrupts the clarity of diagnostic features proposed for *Blapstinus* by Lumen *et al.* (2020), recovery of a well-characterised *B. tibialis*-*B. grandis* species group may serve as a reference point in future revisionary work on the genus.

Taxonomy

Genus *Lodinus* Mulsant and Rey stat. restit. *Lodinus* Mulsant and Rey, 1859: 195.

Type species: *Lodinus nigroaeneus* Mulsant and Rey, 1859 (= *Blapstinus punctulatus* Solier, 1851), by monotypy.
= *Austrocaribius* Marcuzzi, 1954: 18 **syn. nov.** Type species: *Austrocaribius venezuelensis* Marcuzzi, 1954, by monotypy.

Composition (3 species, Fig. 4). *Lodinus araguae* **stat. et comb. nov.** (Marcuzzi) (Venezuela), *L. punctulatus* **comb. nov.** (Argentina, Bolivia, Chile, Uruguay), *L. venezuelensis* **comb. nov.** (Marcuzzi) (Colombia, Venezuela).

Diagnosis. While many Blapstinina possess overlapping characteristics, *Lodinus* can be distinguished from other genera through the combination of the following characters: unfused elytra, well-developed metathoracic wings, parameres with truncate apex (Fig. 1), and median lobe widely projecting between the parameres with the part visible from above oval-elongate and the apex acuminate.

Future studies should concentrate on investigating female terminalia within *Lodinus* as the current study revealed a presence of a hook-like baculus of the 4th coxite in the case of *L. punctulatus* (Fig. 3B). Ovipositors of *L. araguae* and *L. venezuelensis* were not possible to investigate here due to a lack of specimens.

More specific features separating *Lodinus* from other Blapstinina genera are listed below:

Aconobius (Southwestern US): Densely setose dorsally and laterally fimbriate (Aalbu & Triplehorn 1985). *Lodinus* lacks dense setae (Fig. 2A, E, F). Parameres of *Aconobius* evenly tapering towards apex (Iwan 2004), truncate in *Lodinus* (Fig. 1, 3D).

Ammodonus (North America, Central America, South America, and Caribbean Islands): Covered in flattened, scale-like setae (feature missing in *Lodinus*). Mentum with visible median keel and exposed lateral wings. All other Blapstinina, including *Lodinus*, characterized by flat mentum (Lumen *et al.* 2020).

Blapstinus (North America, Central America, South America, and Caribbean Islands): Only reliably distinguishable by differences in male genitalia morphology: median lobe within *Blapstinus* not widely projecting between parameres which are often fused together, and are not apically truncated (contrary to *Lodinus* with widely projecting median lobe and apically truncated parameres) (Fig. 1). Parameres usually tapering in *Blapstinus* (tridentate in *B. grandis*-*B. tibialis* species-group).

Cenophorus (Monotypic; Hispaniola): Fused elytra (flightless). Basal margin of pronotum interrupted in mesal 1/3 (basal margin complete in *Lodinus*), while hind margin of pronotum is medially depressed below plane of scutellar shield (Ivie & Hart 2016). Apex of parameres not truncated (Ivie & Hart 2016).

Diastolinus (Caribbean Islands): Clearly separated via rounded (not truncated) apex of parameres and fully fused elytra. See Hart & Ivie (2016a), Ivie & Hart (2016) for more details.

Conibiosoma (Monotypic; Southwest US): Lacks developed flight wings. Dense setal fimbriae on lateral margin of pronotum. With small tubercles on elytral intervals. Further separated from *Lodinus* through curvature in aedeagus in lateral view; sinuate in *Conibiosoma* (Aalbu & Triplehorn 1985, Iwan 2004), arcuate in *Lodinus* (Fig. 1).

Notibius (Southwest US and Mexico): Lacks developed flight wings. Dense setal fimbriae on lateral margin of pronotum. Foretibiae expanded and slightly curved (narrow and straight in *Lodinus*). Aedeagus curvature sinuate in lateral view (Iwan 2004).

Conibius (North and South America): Most plesiomorphic genus among flightless Blapstinina, and traditionally defined by lack of apomorphies reported for other genera (Aalbu & Triplehorn 1985). Male genitalia variable among species currently included in *Conibius* (Iwan 2004). Reliably separable from *Lodinus* via flightlessness regardless of current monophyly.

Cybotus (Monotypic; North and Central America): Flightless; with dense setal patches on metasternum (Aalbu & Triplehorn 1985, Morales-García & Lumen 2020). Aedeagal parameres evenly tapering towards apex (Iwan 2004).

Goajiria (Caribbean Islands and South America): Elytra fused. Similar to *Lodinus*, *Goajiria* possess truncate paramere apices. Median lobe of *Goajiria* does not widely project between parameres (Ivie & Hart 2016). Additionally, male mesofemur with patch of golden setae on underside of basal portion in *Goajiria* (absent in *Lodinus*).

Hummelinckia (Monotypic, Caribbean Islands): Lacks metathoracic wings (Marcuzzi 1954). Furthermore, according to Marcuzzi's description, unlike *Lodinus* (Fig. 2A, E, F), *Hummelinckia* with strongly reduced scutellar shield. Lastly, basal and apical portions of male genitalia (in lateral view) sinuate in *Hummelinckia* (similar to *Conibiosoma*, *Nocibiotes* & *Notibius*).

Nevisia (Monotypic, Caribbean Islands): Elytra fused. Parameres sinuate (in lateral view) and tapered apically (Ivie & Hart 2016).

Nocibiotes, Tonibiastes, and Tonibius (North America): Lack fully developed wings and possess costate/elevated elytral intervals (Aalbu & Triplehorn 1985).

Platylus (monotypic, Virgin Islands): Elytra fused (Ivie & Hart 2016). Compared to *Lodinus*, *Platylus* is well characterised by large body size (10.0–12.5 mm) and oval body shape. *Platylus* also possess two well-defined apophyseal indentations on pronotal disc (Ivie & Hart 2016), absent in *Lodinus*.

Trichoton: Characterised by curved/bent protibiae (Aalbu & Triplehorn 1985, Kamiński *et al.* 2019b). Densely covered with two types of setae, forming separated well-defined patches on pronotum and elytra (Aalbu & Triplehorn 1985, Kamiński *et al.* 2019b, Lumen *et al.* 2019).

Ulus: Pronotum and elytra covered with setae and bearing lateral fimbriae. Foretibia dilated, ending in a distal 'tooth' (Lumen *et al.* 2019). Appears to be only blapstinine with enlarged, membranous field on basal portion of aedeagal tegmen (Lumen *et al.* 2019).

Xerolinus (North America and Caribbean Islands): Recently erected genus differs from *Lodinus* as follows (Ivie & Hart 2016, Hart & Ivie 2016b): wings absent or reduced; seventh and eighth elytral striae fused anteriorly. Parameres rounded apically.

***Lodinus araguae* (Marcuzzi), comb. et stat. nov.**

Austrocaribius venezuelensis araguae Marcuzzi, 1983: 259

Notes. Taking into consideration new morphological data concerning *L. punctulatus* and coarse differences in male genitalia structure (Figs 46 and 46 in Marcuzzi 1983; Figs 1, 3D) between the two previously recognized subspecies of *L. venezuelensis* (i.e., *araguae* and *venezuelensis*), a decision is hereby made to elevate them to the species level.

While describing this species Marcuzzi (1983) did not designate a holotype, nor explicitly state the number of studied specimens. As a result a lectotype designation is needed to fix the taxonomic status of the species.

Studied material. LECTOTYPE (here designated), male (MIZ PAN): "Loma del Medio / San Sebastian / (Edo. Aragua)", "BORDON leg. \ 3-VI-1962" (Fig. 2E). **PARALECTOTYPES**, male (MIZ PAN): same data as lectotype; female (MIZ PAN): same data as lectotype with additional label: "Paratypus 1986 \ *Austrocaribius venezuelensis araguae* ssp. \ Marcuzzi" (Fig. 2F).

***Lodinus punctulatus* (Solier), comb. nov.**

Blapstinus punctulatus Solier, 1851: 233

=*Lodinus nigroaeneus* Mulsant and Rey, 1859: 131 (syn. by Gemminger in Gemminger and Harold, 1870)

=*Alphitobius punctatus* Curtis, 1845: 469 (syn. by Gebien 1938: 405).

Note: While proposing synonymy between *Alphitobius punctatus* Curtis, 1845 and *Blapstinus punctulatus* Solier,

1851, to avoid secondary homonymy with *Blapstinus punctatus* (Fabricius), Gebien (1938) rejected *Alphitobius punctatus* Curtis, 1845 and replaced it with its oldest available synonym—*Blapstinus punctulatus* Solier, 1851. According to the regulations of ICZN (1999), particularly art. 59.3, a junior secondary homonym replaced before 1961 is permanently invalid unless the substitute name is not in use and the relevant taxa are no longer considered congeneric. As a result the valid name of the below redescribed species is *Lodinus punctulatus* (Solier).

Descriptions of *B. punctulatus* and *L. nigroaeneus* do not include holotype designations. As a result, lectotype designations are needed to fix the taxonomic status of these names.

Studied material. Type material: *Blapstinus punctulatus*: **LECTOTYPE (here designated)**, male (MNHN): “Punc\tulatus” reverse side of the same label “Type\Solier”, “Lodinus\punctulatus\Chili *illegible*”, “Blapstinus\punctulatus\Chili\D. M-?”, „TYPE”. **PARALECTOTYPE**, male: same data as lectotype.

Lodinus nigroaeneus: **LECTOTYPE (here designated)**, male (MNHN): „nigro-aeneus” reverse side of the same label “Mulsant type”, “Lodinus/nigroaeneus/Chili *illegible*”, “TYPE”. **PARALECTOTYPES**, two females: same data as lectotype.

Additional material: male (PERC): “ARGENTINA: Cordoba: Reserva Chancani, 350m, 31.3755 S 65.4797 W, 7.iii.2011 DRM 11.007. D.R. Maddison”; 2 males and female (MIZ PAS): „Chile Santiago \ Baños Morales \ 19 Mayo 2001 \ leg. V. Manuel Diéguez”; 2 males and female (MIZ PAS): „Argentina Chubut \ Camino a cholila \ 580 MSNM \ 23/31 Enero 2000 \ Leg. V.M. Diéguez M.”; male and 2 females (MIZ PAS): „Chile Melipilla \ Pallocabe 300Mts. \ 9 Sept. 2001 \ leg. V. Manuel Diéguez”; male and female (MIZ PAS): “Santiago Thilippes”; 27 specimens (MIZ PAS): „Chile Philipp S”; female (MNHN): “Brasilien\Nova Teutania\2711’B—52 23t \Fritz Plaumann\300–800m\8-XI-1955”, “Museum Paris \Coll. P. Ardoin 1978”

Diagnosis. Newly examined material enables supplementation of available descriptions of this species (Curtis 1845, Solier 1851, Mulsant and Rey 1859, Aballay *et al.* 2016) with data on male and female terminalia. Therefore, a redescription is provided below and a new diagnosis is provided to accommodate this species with its new congeners.

The following features place this species within *Lodinus* (Marcuzzi 1954, 1982): median lobe of aedeagus widely projecting between parameres; parameres with truncate apex (Fig. 1).

Lodinus punctulatus can be easily distinguished from its congeners by differing pronotal structure (Marcuzzi 1954): anterior angles rounded, not prominent (pointed and prominent in remaining species); punctures sparsely distributed on disc (>1.0 diameters apart vs. <0.75 in remaining species). Furthermore, *L. punctulatus* is the only species within the genus which possesses subparallel parameres in their apical portion (slightly narrowing towards apex in *L. venezuelensis*—Figs 46 and 46 in Marcuzzi 1983; strongly indented in *L. araguae*—Fig. 3D). Lastly, as of this redescription, *L. punctulatus* is the only species of the genus known from south of the equator (Fig. 4).

Redescription. Length 4.9–6.2 mm, width 2.1–2.6 mm. **Body** (Fig. 2A): dull brown to black; dorsal and ventral surfaces matte; ovate-oblong; widest at 2/3 of elytral length; weakly convex in lateral view; evenly covered with fine setae dorsally. **Head:** Epistoma broadly convex; punctures equal to diameter of an ommatidium (distributed 1–2 diameters apart); setae equal in length to intervals between punctures. Fronto-epistomal suture slightly marked on sides. Epistoma weakly emarginate. **Prothorax:** Pronotum narrowing anteriorly, apical angles sharp. Lateral margin slightly rounded; marginated. Basal width slightly narrower than humeri; basal margin slightly bisinuate. Disc sparsely but noticeably covered with setae; finely punctate (punctures 1–3 diameters apart). Lateral sides marginated. Hypomeron dull and rugose; hypomeron impressed on sides. Intercostal process of prosternum not depressed in lateral view. **Scutellar shield:** Pentagonal, of equal width and length, finely punctate. **Pterothorax:** Elytral striae shallow and punctate (1–2 diameters apart). Striae not joining prior humeral angle. Intervals flat, punctate (0.5–1.0 diameters apart), with noticeable microsculpture. Epipleura finely punctate. Metathoracic wings well developed. Metaventricle long, sparsely punctate; sparse setae present. **Legs:** Protibia apically dilated with lateral projection at apex. Meso and meta tibia straight and dilated apically. Pro- and mesotarsomeres 2 and 3 dilated in males (Fig. 2B, C). Abdominal ventrites: Finely punctate, scattered with setae; intercoxal process narrowly rounded; ventrite 5 with posterior margin evenly rounded, not bordered. **Aedeagus** (Fig. 1): whole tegmen evenly curved in lateral view. Apical part of aedeagus truncate; median lobe opening circular. **Female terminalia** (Fig. 3A–C): Ovipositor with paraprocts slightly longer than coxites. Paraproct does not shield valvifer and other lobes (directed basally). Valvifer wide and short; second lobe elongate; third one semicircular (about 0.5 of height of third one); apical lobe rounded, situated apically, sclerotised at outer and inner edges, inner sclerotisation hook-like, gonostyli on dorsal side, directed inwards. Proctiger covering nearly whole ovipositor. Vagina without sclerites. Spermatheca with narrow duct. Spiculum ventrale short.

Distribution. ARGENTINA, BRASIL, BOLIVIA, CHILE, URUGUAY (Fig. 4).

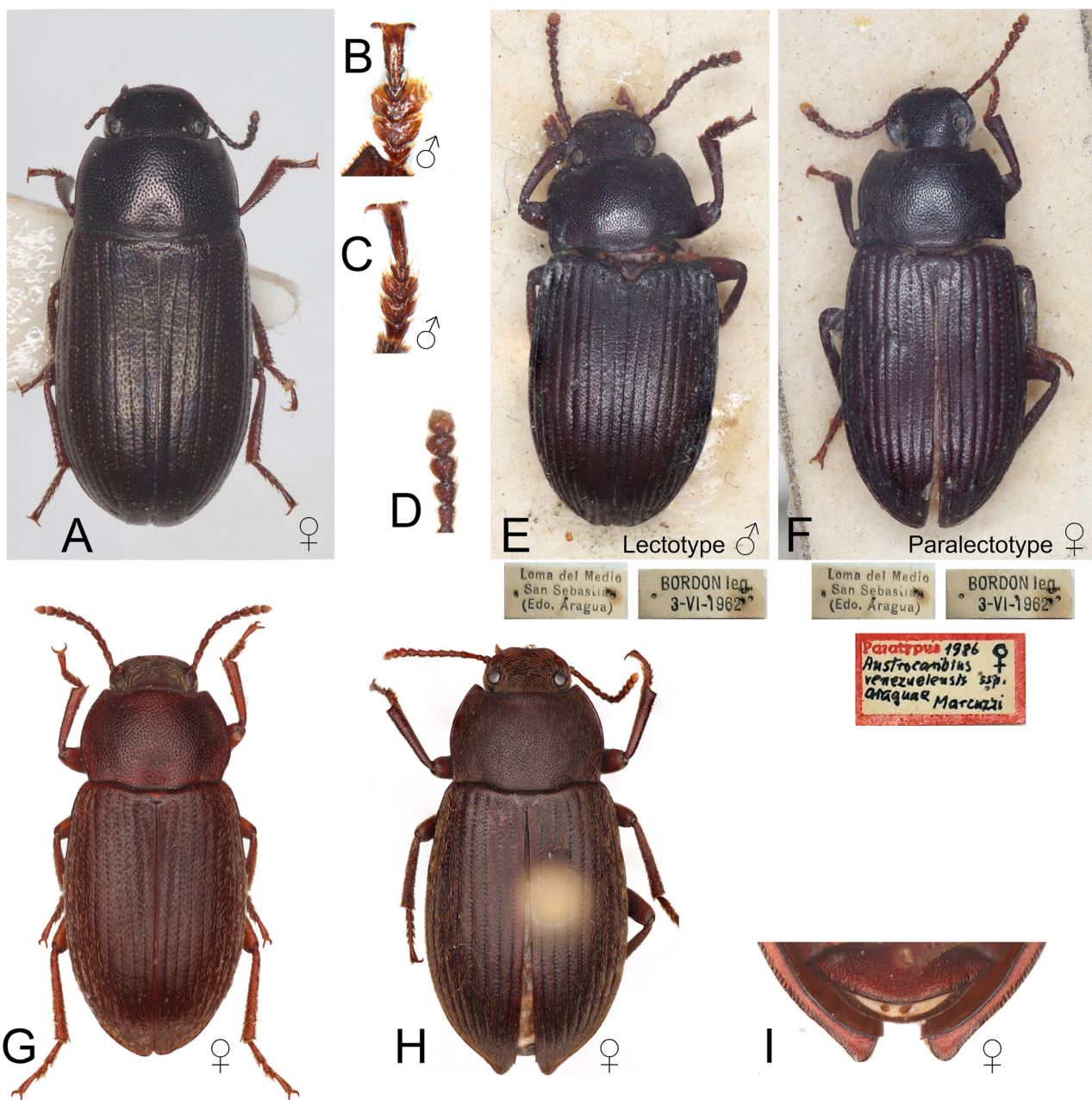


FIGURE 2. Morphology of studied Blapstinina species. Habitus photographs and diagnostic features. (A–C) *Lodinus punctulatus* comb. nov., (D–F) *Lodinus araguae* comb. nov., (G) *Blapstinus tibialis*, (H, I) *Blapstinus grandis*. (B) protarsus, (C) mesotarsus, (D) last 5 antennomeres, (I) apical tip of epipleura.

Genus *Blapstinus* Dejean, 1821

Blapstinus grandis Champion, 1885

Note. While describing this species Champion (1885) did not designate a holotype, nor state the exact number of the studied specimens. However, from the context it is clear that *B. grandis* was described based on at least two specimens (female and male). As a result a lectotype designation is needed to fix the taxonomic status of the species.

Studied material. **LECTOTYPE (here designated)**, female (MCZ): “Chontales / Nicaragua. / Janson.”, “Type / 7089”, “Ex / Godman / and / Salvin.”, “*Blapstinus / grandis*, Ch”, “*grandis / Champ.*”. **Additional material:** 29 specimens (PERC): “MEXICO: Chiapas / 12.4 km NE of Tonalá / 16.153, -93.6466, 435m / 12.Aug.2015, AD-

Smith”, “Fiesta de los Escarabajos / NAUF-CNIN-OSAC-ASUT, / ADSmith, GRodriguez-Miron, / RAGomez, and MAJohnston”.

Redescription. Length 9.5–11.0 mm, width 4.5–5.0 mm. **Body** (Fig. 2H): black, reddish or brown, legs and antennomeres brown; dorsal and ventral surfaces matte; ovate-oblong; widest at 2/3 of elytral length; weakly convex in lateral view; evenly covered with fine setae dorsally. **Head:** Epistoma broadly convex; punctures equal to diameter of an ommatidium (distributed less than single diameter apart); setae 2x length of internals between punctures. Fronto-epistomal suture visible on sides. Epistoma weakly emarginate. **Prothorax:** Widest at middle; apical margin evenly, broadly emarginate; apical angles sharp. Lateral margin evenly rounded or slightly sinuate. Basal width slightly narrower than humeri; basal margin bisinuate; dorsal surface broadly, evenly convex; all margins narrowly beaded, except obsolete at middle of anterior margin; disc finely punctate (punctures 1–3 diameters apart). Hypomeron glabrous near margin, then rugulose; whole hypomeron in single plane. Intercostal process of prosternum tongue-like, densely punctate, depressed in lateral view. **Scutellar shield:** Subtriangular, of equal width and length, finely punctate. **Pterothorax:** Elytral striae impressed; striae punctures shallow (single diameter apart); intervals flat, finely punctate (3–5 diameters apart), punctures setose. Striae not joining prior humeral angle. Epipleura evenly and slightly narrowing towards apex in males; in females tip of epipleura circularly expanded (Fig. 2I). Metathoracic wings well developed. Metaventricle long, punctate; sparse setae present. **Legs:** Inner surfaces of tibiae densely setose and finely punctate in males; sparsely setose in female. Male protibia narrow, with a shallow, longitudinal cavity on inner side; female protibia lacking this feature. Male and female protarsi with tarsomeres 1–3 slightly expanded, ventrally with golden, densely setose pads. Male foretibia slightly bent. Remaining leg parts not modified in both sexes. **Abdominal ventrites:** Finely punctate, scattered with setae; intercostal process narrowly rounded; ventrite 5, in males, medially slightly concave, posterior margin evenly rounded. **Aedeagus** (Fig. 1): Basal piece slightly curved basally (lateral view); parameres straight, appearing as tridentate, length of lateral outgrowths equal to 0.6 of total parameres length. **Female terminalia:** Ovipositor with paraprocts slightly longer than coxites. Paraproct does not shield valvifer and other lobes (directed basally). Valvifer wide and short; second lobe elongate; third one triangular (about 0.5 of height of third one); apical lobe rounded, situated dorsally, bearing reduced gonostylus on dorsal side. Proctiger covering nearly whole ovipositor. Vagina without sclerites; bursa largely widened and curved. Spermatheca with narrow duct. Spiculum ventrale short.

Distribution. CARIBBEAN, MEXICO (Jalisco, Sinaloa), NICARAGUA (Bousquet *et al.* 2018); MEXICO (Chiapas) (present paper).

Blapstinus tibialis Champion, 1885

Studied material. **SYNTYPE**, male (BMNH): “Zapote / Guatemala, / C. Champion”, “Sp. figured”, „Godman-Salyin / Coll. Biol / Centr.-Amer.”, [circular label with red outline] “Type”, “Blapstinus / tibialis , Ch.”. **Additional material:** 3 males and 3 females (Kojun Kanda private collection): “USA: Texas: Hidalgo Co., Bentsen / Rio Grande Valley SP, off ground at / night, 40m, 26.1789°N 98.38366°W, / 16–17.vi.2014, KK14_075 K. / Kanda, K. T. Eldredge, J. M. Pflug”.

Redescription. Length 5.5–7.0 mm, width 3.0–3.5 mm. **Body** (Fig. 2G): black, reddish or brown, legs and antennomeres brown; dorsal and ventral surfaces shiny; ovate-oblong; widest at 2/3 of elytral length; weakly convex in lateral view; evenly covered with fine setae dorsally. **Head:** Epistoma broadly convex; punctures equal to diameter of an ommatidium (distributed less than single diameter apart); setae 2x length of intervals between punctures. Fronto-epistomal suture nearly invisible. Epistoma weakly emarginate. Antennae weakly clavate, with third antennomere twice longer than preceding one. Dorsal and ventral portions of eye roughly equal in size and shape. **Prothorax:** Widest at middle; apical margin evenly, broadly emarginate; apical angles rounded; lateral margin evenly rounded; basal width slightly narrower than humeri; basal margin bisinuate; dorsal surface broadly, evenly convex; all margins narrowly beaded, except obsolete at middle of anterior margin; disc finely punctate (punctures single diameter apart). Hypomeron glabrous near margin, strongly rugulose medially. Intercostal process of prosternum tongue-like, sparsely punctate, depressed in lateral view. **Scutellar shield:** Subtriangular, of equal width and length, finely punctate. **Pterothorax:** Elytra widest in 2/3 of its length; striae impressed; striae punctures shallow (2 diameters apart), punctures setose; intervals flat, finely punctate (3–4 diameters apart). Striae not joining prior humeral angle. Epipleura evenly and slightly narrowing towards apex. Metathoracic wings well developed.

Metaventricle long, punctate; sparse setae present. **Legs:** Surfaces sparsely setose and finely punctate. Male protibia narrow, with a shallow, longitudinal cavity on inner side; female protibia lacking this feature. Male protarsus with tarsomeres 1–3 expanded, ventrally with golden, densely setose pads; female with subsequent segments of nearly equal width. Remaining leg parts not modified in both sexes. **Abdominal ventrites:** Finely punctate, scattered with setae; intercoxal process narrowly rounded; ventrite 5, in males, medially slightly concave, posterior margin evenly rounded. **Aedeagus** (Fig. 1): Basal piece curved (lateral view); parameres straight basally, appearing as tridentate, length of lateral outgrowns nearly equal to total parameres length. **Female terminalia** (Fig. 3E, F): Ovipositor with paraprocts slightly longer than coxites. Paraproct does not shield valvifer and other lobes (directed basally). Valvifer wide and short; second lobe elongate; third one triangular (about 0.5 of length of third one); apical lobe rounded, situated dorsally, bearing reduced gonostylus on dorsal side. Proctiger covering nearly whole ovipositor. Vagina and bursa copulatrix without sclerites; bursa largely widened and curved. Spermatheca with narrow duct. Spiculum ventrale short.

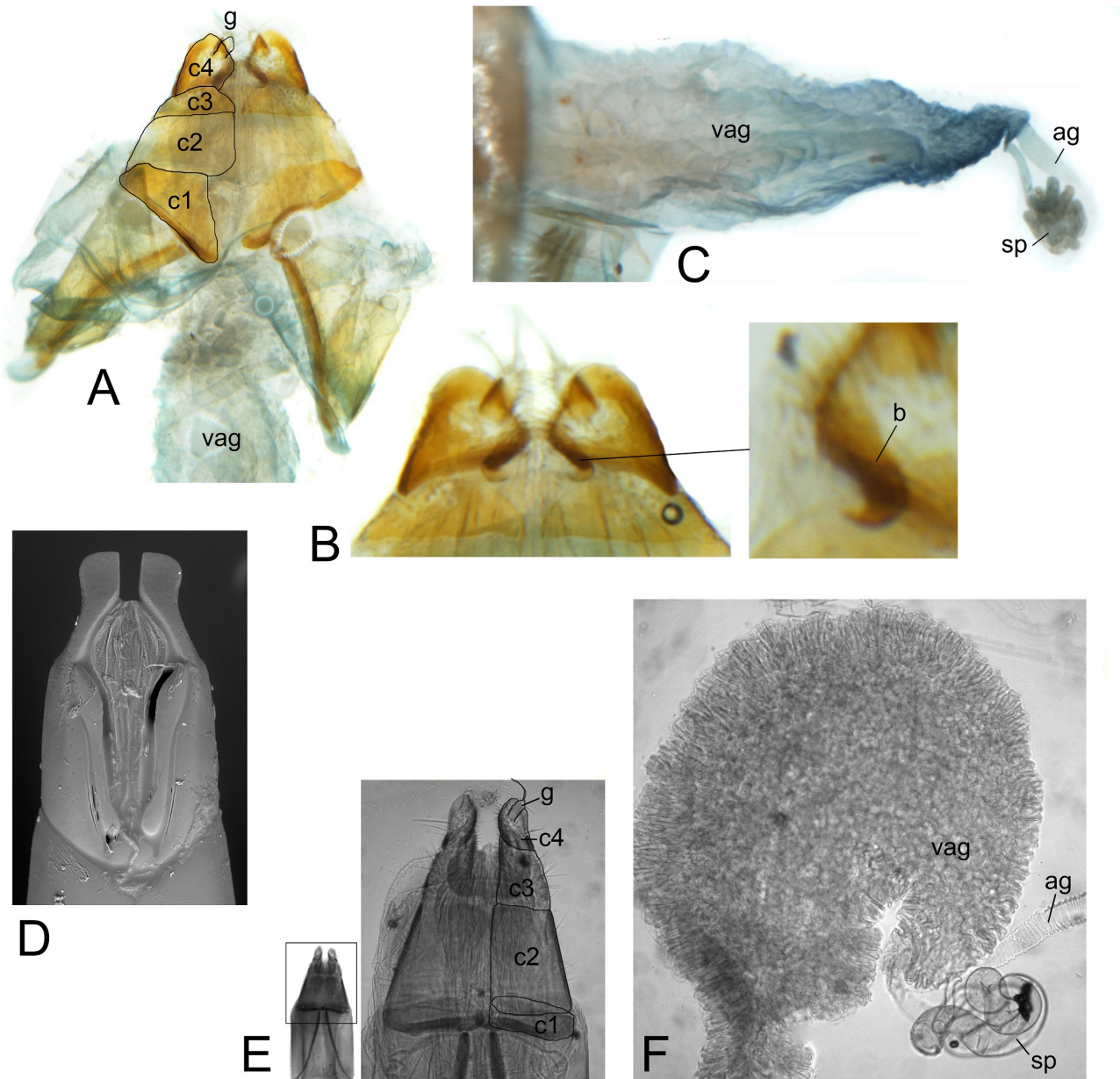


FIGURE 3. Morphology of female and male terminalia of selected Blapstinina species. (A–C) *Lodinus punctulatus* **comb. nov.**, (D) *Lodinus araguae* **comb. nov.**, (E, F) *Blapstinus tibialis*. (A, B, E) ovipositor, (C, F) genital tubes, (D) parameres. *Abbreviations:* ag—accessory gland, b—hooked baculus of c4, c1–c4—subsequent lobes of coxites, g—gonostylus, sp—spermatheca, vag—vagina.



FIGURE 4. Distribution of *Lodinus*.

Note. In his unpublished PhD dissertation, Davis (1970) recognized a new species, “*Blapstinus lobatus*”, from Southern Texas. However, this species was never formally described and the name remains unavailable. This taxon also possesses tridentate parameres. Davis did not directly compare “*B. lobatus*” to types of *B. tibialis*, but instead based his diagnoses on a series of specimens that matched Champion’s description of *B. tibialis*. The authors of the present paper did not have access to specimens identified by Davis as “*B. lobatus*”, but were able to compare specimens from Southern Texas with tridentate parameters (see Additional Materials above) to images of syntypes of *B. tibialis*. No characters distinguishing these entities were found. Whether Davis’s species represents a sympatric species to *B. tibialis* in Southern Texas, or falls within morphological variation in *B. tibialis* requires further study and is outside the scope of this study. In any case, *B. tibialis* should be included in the fauna of the USA. A lectotype is not designated here in deference to a separate manuscript in preparation treating the concerned taxa.

Distribution. GUATEMALA, MEXICO, NICARAGUA (Champion 1885); CARIBBEAN (Bousquet *et al.* 2018); USA (TX) (present paper).

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References

- Aalbu, R.L. & Triplehorn, C.A. (1985) Redefinition of the opatrine tribes in North America with notes on some apterous genera (Coleoptera: Tenebrionidae: Tenebrioninae). *The Coleopterists Bulletin*, 39, 272–280.
- Aalbu, R.L. & Triplehorn, C.A. (1991) *Pedonoeces* G.R. Waterhouse = *Blapstinus* Sturm, relevant name changes for California and Galapagos Island species and new insular species from Mexico (Coleoptera: Tenebrionidae). *The Coleopterists Bulletin*, 45, 169–175.
- Aballay, F.H., Flores, G.E., Silvestro, V.A., Zanetti, N.I. & Centeno, N.D. (2016) An illustrated key to, and diagnoses of the species of Tenebrionidae (Coleoptera) associated with decaying carcasses in Argentina. *Annales Zoologici*, 66, 703–726. <https://doi.org/10.3161/00034541ANZ2016.66.4.021>
- Ardoin, P. (1977) Tenebrionidae (Coleoptera) récoltés par la deuxième Expédition biospéologique cubano-roumaine à Cuba (1973). In: Orghidan, T., Núñez Jiménez, A., Decou, V., Negrea, S. & Viña Bayés, N. (Eds.), *Résultats des expéditions biospéologiques cubano-roumaines à Cuba*. Academiei Republicii Socialiste România, Bucuresti, pp. 387–392.
- Bouchard, P., Bousquet, Y., Aalbu, R.L., Alonso-Zarazaga, M.A., Merkl, O. & Davies, A.E. (2021) Review of genus group names in the family Tenebrionidae (Insecta, Coleoptera). *ZooKeys*, 1050, 1–633. <https://doi.org/10.3897/zookeys.1050.64217>
- Bousquet, Y., Thomas, D.B., Bouchard, P., Smith, A.D., Aalbu, R.L., Johnston, M.A. & Steiner, W. (2018) Catalogue of Tenebrionidae (Coleoptera) of North America. *Zookeys*, 728, 1–455. <https://doi.org/10.3897/zookeys.728.20602>
- Cabrera, N., Fernandez, L.A., Flores, G.E. & Lattari, M. (2010) Catalog of the types of Tenebrionidae and Perirnylopidae (Insecta, Coleoptera) deposited at Museo de La Plata (Argentina). *Transactions of the American Entomological Society*, 136, 107–123.
- Casey, T.L. (1890) Coleopterological notices. II. *Annals of the New York Academy of Sciences*, 5, 307–504. [1889–91] <https://doi.org/10.3157/061.136.0202>
- Champion, G.C. (1885) Insecta. Coleoptera. Vol. IV. Part 1. Heteromera (part). In: Godman, F.D. & Salvin, O. (Eds.), *Biologia*

- Centrali-Americana*. Taylor & Francis, London, pp. 89–136.
- Curtis, J. (1845) Descriptions, &c. of the insects collected by Captain P.P. King in the survey of the Straits of Magellan. *Transactions of the Linnean Society of London*, 19, 441–476.
<https://doi.org/10.1111/j.1096-3642.1842.tb00371.x>
- Davis, J.C. (1970) *Revision of the genus Blapstinus Sturm of America North of Mexico with notes on extralimital species (Coleoptera: Tenebrionidae)*. Ph.D. Thesis, Ohio State University, Columbus, Ohio, 459 pp.
- Davis, J.C. (1976) A review of the genus *Blapstinus* (Coleoptera: Tenebrionidae). *Transactions of the Kentucky Academy of Science*, 37, 35–40.
- Davis, J.C. (1980) Morphology of the genus *Blapstinus* (Coleoptera: Tenebrionidae) with emphasis on characters of taxonomic significance. *Transactions of the Kentucky Academy of Science*, 41, 89–98.
- Doyen, J.T. (1990) Tenebrionidae and Zopheridae of the Chamela Biological Station and vicinity, Jalisco, Mexico (Coleoptera). *Folia Entomologica Mexicana*, 77, 211–276.
- Fairmaire, L. (1883) Descriptions de Coléoptères de la République-Argentine. *Annales de la Société entomologique de France*, 6, 507–516.
- Gebien, H. (1938) Katalog der Tenebrioniden. Teil II. *Mitteilungen der Münchener Entomologischen Gesellschaft*, 28, 283–314. [kat. 402–433]
- Gemminger, M. & Harold, E. von (1870) a.n. In: *Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. VII. Tenebrionidae, Nilionidae, Pythidae, Melandryidae, Lagriidae, Pedilidae, Anthicidae, Pyrochroidae, Mordellidae, Rhipidophoridae, Cantharidae, Oedemeridae*. E. H. Gummi, Monachium [München], pp. 1801–2179.
- Hart, C.J. & Ivie, M.A. (2016a) A revision of the genus *Diastolinus* Mulsant and Rey (Coleoptera: Tenebrionidae). *The Coleopterists Bulletin*, 70, 485–540.
<https://doi.org/10.1649/0010-065X-70.3.485>
- Hart, C.J. & Ivie, M.A. (2016b) Two new species of *Xerolinus* Ivie and Hart (Coleoptera: Tenebrionidae: Opatrini) from Jamaica and the Virgin Islands. *The Coleopterists Bulletin*, 70, 885–891.
<https://doi.org/10.1649/0010-065X-70.4.885>
- Ivie M.A. & Hart, C.J. (2016) Redefinition of *Diastolinus* Mulsant and Rey, with a review of west indian blapstinoid genera (Coleoptera: Tenebrionidae: Opatrini). *The Coleopterists Bulletin*, 70 (3), 447–481.
<https://doi.org/10.1649/0010-065X-70.3.447>
- Iwan, D. (2001) Comparative study of male genitalia in Opatrinae sensu Medvedev (1968) (Coleoptera: Tenebrionidae), with notes on the tribal classification. Part I. *Annales Zoologici*, 51, 351–390.
- Iwan, D. (2004) A comparative study of male genitalia in Opatrinae sensu Medvedev (1968) (Coleoptera: Tenebrionidae), with notes on the reinterpreted tribal classification. Part II. *Annales Zoologici*, 54, 735–765.
<https://doi.org/10.3161/0003454043651780>
- Iwan, D. & Kamiński, M.J. (2016) Toward a natural classification of opatrine darkling beetles: comparative study of female terminalia. *Zoomorphology*, 135 (4), 453–485.
<https://doi.org/10.1007/s00435-016-0328-5>
- Johnston, M.A., Smith, A.D., Matsumoto, K. & Kamiński, M.J. (2020) On the taxonomic placement of *Penichrus* Champion, 1885 and a synopsis of North American Opatrini (Coleoptera: Tenebrionidae: Blaptinae). *Annales Zoologici*, 70, 765–774.
<https://doi.org/10.3161/00034541ANZ2020.70.4.017>
- Kamiński, M.J. (2021) Molecular matrix used in the publication entitled: „Phylogenetic status of some unique Blapstinina Mulsant & Rey species (Tenebrionidae: Blaptinae: Opatrini), and implications for the continued study of the subtribe”. Harvard Dataverse, V1. Available from: <https://doi.org/10.7910/DVN/UTX8AU> (accessed 14 January 2022)
- Kamiński, M.J., Kanda, K., Lumen, R., Smith, A.D. & Iwan, D. (2019a) Molecular phylogeny of Pedinini (Coleoptera: Tenebrionidae) and its implications for higher-level classification. *Zoological Journal of the Linnean Society*, 185, 77–97.
<https://doi.org/10.1093/zoolinnean/zly033>
- Kamiński, M.J., Lumen, R., Kubicz, M., Kanda, K. & Iwan, D. (2019b) Immature stages of beetles representing the ‘Opatrinoid’ clade (Coleoptera: Tenebrionidae): an overview of current knowledge of the larval morphology. *Zoomorphology*, 38, 349–370.
<https://doi.org/10.1007/s00435-019-00443-7>
- Kamiński, M.J., Lumen, R., Kanda, K., Iwan, D., Johnston, M.A., Kergoat, G., Bouchard, P., Bai, X.-L., Li, X.-M., Ren, G.-D. & Smith, A.D. (2021) Reevaluation of Blapimorpha and Opatrinae: addressing a major phylogeny-classification gap in darkling beetles (Coleoptera: Tenebrionidae: Blaptinae). *Systematic Entomology*, 46, 140–156.
<https://doi.org/10.1111/syen.12453>
- Kaszab, Z. (1969) The scientific results of the Hungarian Soil Zoological Expeditions to South America. 17. Tenebrioniden aus Chile (Coleoptera). *Opuscula Zoologica, Budapest*, 9, 291–337.
- Lumen, R., Kanda, K., Iwan, D., Smith, A.D. & Kamiński, M. (2020) Molecular insights into the phylogeny of Blapstinina (Coleoptera: Tenebrionidae: Opatrini). *Systematic Entomology*, 45, 337–348.
<https://doi.org/10.1111/syen.12398>
- Lumen, R., Kamiński, M.J., Crowley, J. & Smith, A.D. (2019) Revision of the genus *Ulus* Horn, 1870 (Coleoptera: Tenebrionidae: Opatrini: Blapstinina). *Annales Zoologici*, 69, 827–856.

<https://doi.org/10.3161/00034541ANZ2019.69.4.014>

- Marcuzzi, G. (1951) Contributi alla conoscenza dei Tenebrionidi venezuelani (Coleoptera). Specie inedite del genere *Blapstinus*, ed osservazioni su varie specie note. *Atti del Museo Civico di Storia Naturale di Trieste*, 18, 61–80.
- Marcuzzi, G. (1954) Studies on the fauna of Curaçao and other Caribbean Islands: no. 22. Tenebrionid beetles of Curaçao, Aruba, Bonaire, and the Venezuelan Islands. *Natuurwetenschappelijke Studiekring voor Suriname*, 10, 1–36.
- Marcuzzi, G. (1983) Description of the external male genitalia of some neotropical tenebrionidae coleoptera heteromera. *Folia Entomologica Hungarica*, 44 (2), 239–269.
- Marcuzzi, G. (1986) Descrizione di nuovi taxa di Tenebrionidi Neotropicali (Coleoptera, Tenebrionidae). *Annales Historico-Naturales Musei Nationalis Hungarici*, 78, 177–186.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14 November 2010, 1–8.
<https://doi.org/10.1109/GCE.2010.5676129>
- Minh, B.Q., Nguyen, M.A. & von Haeseler, A. (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30 (5), 1188–1195.
<https://doi.org/10.1093/molbev/mst024>
- Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. & Lanfear, R. (2020) IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. *Molecular Biology and Evolution*, 37, 1530–1534.
<https://doi.org/10.1093/molbev/msaa015>
- Morales-García, J. & Lumen, R. (2020) First record of *Cybotus estriatus* (LeConte 1878) (Coleoptera: Tenebrionidae) in Costa Rica. *Boletín de la Sociedad Entomológica Aragonesa*, 67, 431–432.
- Mulsant, E. & Rey, C. (1859) Essai d'une division des derniers Mélasomes. *Opuscules Entomologiques*, 9, 65–157.
<https://doi.org/10.5962/bhl.title.2682>
- Peña, L.E. (1966) Catálogo de los Tenebrionidae (Coleoptera) de Chile. *Entomologische Arbeiten aus dem Museum Georg Frey*, 17, 397–453.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
<https://doi.org/10.1093/sysbio/sys029>
- Schatz, I. (1994) *Blapstinus desenderi* sp. nov. from the Galapagos Islands (Ecuador) (Coleoptera, Tenebrionidae). *Entomofauna*, 15, 417–424.
- Solier, A.J. (1851) Insectos. Coleopteros. In: *Historia física y política de Chile según documentos adquiridos en esta república durante doce años de residencia en ella y publicada bajo los auspicios del supremo gobierno por Claudio Gay*. *Zoología. Tomo Quinto*. Museo de Historia Natural de Santiago, Paris, pp. 5–285.
- Steiner, W.E. Jr. (2006) New species of darkling beetles (Coleoptera: Tenebrionidae) from San Salvador Island, Bahamas. *Zootaxa*, 1158 (1), 1–38.
<https://doi.org/10.11646/zootaxa.1158.1.1>
- Van Dyke, E.C. (1953) The Coleoptera of the Galapagos Islands. *Occasional Papers of the California Academy of Sciences*, 22, 1–181.