

Research article

urn:lsid:zoobank.org:pub:0C86F8BF-3B70-4822-9F89-9101F58949A8

**Comparative morphology of the genera with perpendicular parameres
in Anomalini (Coleoptera, Scarabaeidae, Rutelinae)
allows revalidation of the endemic Mexican
genus *Lamoana* Casey, 1915 stat. rev.**

Kevin MADRIGAL ¹, Santiago ZARAGOZA-CABALLERO ² &
Andrés RAMÍREZ-PONCE ^{3,*}

¹Licenciatura en Biología, Universidad Autónoma de Tlaxcala, Km 10.5 San Martín Texmelucan-Tlaxcala s/n, Ixtacuixtla de Mariano Matamoros, Tlaxcala 90120, Mexico.

²Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70–153, 04510, Mexico City, Mexico.

³Red de Biodiversidad y Sistemática, Instituto de Ecología, A.C. (INECOL), Carretera antigua a Coatepec 351, El Haya, 91073, Xalapa, Veracruz, Mexico.

*Corresponding author: andres.ramirez@inecol.mx

¹Email: kevinmad42@gmail.com

²Email: zaragoza@ib.unam.mx

¹urn:lsid:zoobank.org:author:E9CBAADF-5E5C-4FE1-B75E-593DA71B70CD

²urn:lsid:zoobank.org:author:505055A7-91E4-455C-905B-6E0E56C7BD98

³urn:lsid:zoobank.org:author:737C5C1F-1974-4EDF-BB32-4C5CA9173B00

Abstract. The endemic Mexican genus *Lamoana* Casey, 1915 stat. rev. is revalidated through a comparative morphological analysis of both male genitalia and somatic characters of all genera with perpendicular parameres. A comparative study and general description of the basic patterns in the morphology of the genitalia for the American genera are provided. A full redescription of the genus and a redescription of *L. villosella* (Blanchard, 1851) comb. rev. is provided herein, with the addition of generic and specific diagnostic characters and data about its geographical distribution. Further, possible relationships at generic level among American genera are provided. With this study, the number of Anomalini genera known for America and Mexico is now elevated to 17 and 14, respectively.

Keywords. Comparative morphology, endemic Mexican genus, nomenclatural changes, shining leaf chafers, taxonomic revalidation.

Madrigal K., Zaragoza-Caballero S. & Ramírez-Ponce A. 2023. Comparative morphology of the genera with perpendicular parameres in Anomalini (Coleoptera, Scarabaeidae, Rutelinae) allows revalidation of the endemic Mexican genus *Lamoana* Casey, 1915 stat. rev. *European Journal of Taxonomy* 910: 175–199.
<https://doi.org/10.5852/ejt.2023.910.2369>

Introduction

Anomalini Peringuey, 1902 is a largely diverse and widely distributed tribe of the subfamily Rutelinae MacLeay, 1819, usually known as shining leaf chafers. Anomalini is easy to recognize due to three

basic morphological characters: 1) antennae with 9 segments, 2) elytra with a membranous margin, and 3) a transverse labrum (Morón & Ramírez-Ponce 2012). It is a heterogeneous group formed by more than 2000 species in 71 genera (Ohaus 1918; Machatschke 1972–1974; Micó & Galante 2005; Morón & Ramírez-Ponce 2012; Ramírez-Ponce & Curoe 2014). Of these, only 13 have been cited for Mexico: *Balanogonia* Paucar-Cabrera, 2003, *Callistethus* Blanchard, 1851, *Callirhinus* Blanchard, 1851, *Dilophochila* Bates, 1888, *Epectinaspis* Blanchard, 1851, *Mazahuaertha* Morón & Nogueira, 1998, *Moroniella* Ramírez-Ponce, 2015, *Nayarita* Morón & Nogueira, 1998, *Paranomala* Casey, 1915, *Pachystethus* Blanchard, 1851, *Strigoderma* Burmeister, 1844, *Xochicotlia* Ramírez-Ponce & Morón, 2009, and *Yaaxkumukia* Morón & Nogueira, 1998 (Morón *et al.* 1997; Morón & Nogueira 1998; Paucar-Cabrera 2003; Ramírez-Ponce & Morón 2009; Ramírez-Ponce 2012, 2015).

Historically, some of the taxonomic works related to this tribe have been somewhat incongruent due to the use of different morphological criteria that have led to disagreements on supraspecific boundaries or have presented a geographical bias (Potts 1977; Morón *et al.* 1997; Morón & Nogueira 1998, 2002; Jameson *et al.* 2003; Micó & Galante 2005). Among these taxonomic imprecisions, in past studies, some taxa with doubtful generic positions or even others invalidated without any morphological criteria (Machatschke 1957), have been generating discussions about the internal classification of Anomalini that remain unresolved (Bates 1888; Ohaus 1934; Morón *et al.* 1997; Morón & Nogueira 1998; Jameson *et al.* 2003; Ramírez-Ponce & Morón 2009; Morón & Ramírez-Ponce 2012; Pardo-Lorcano *et al.* 2017). In general, character-based circumscriptions in supraspecific taxa are barely present, or lacking (Jameson *et al.* 2007), or authors offered definitions based on weak and subjective single characters (Uliana & Sabatinelli 2017), without an objective criterion of homology analysis.

The case of *Strigoderma villosella* (Blanchard, 1851) is quite interesting for many reasons (see Taxonomic history section). Firstly, its taxonomic history is full of generic changes (e.g., *Phyllopertha* Stephens, 1830, *Anomala* Samouelle, 1819, *Lamoana* Casey, 1915, *Paranomala* and *Strigoderma*), and one synonym (i.e., *Strigoderma hirsuta* Nonfried, 1983) (Blanchard 1851; Bates 1888; Casey 1915; Nonfried 1983; Ramírez-Ponce 2012). Secondly, the confusion due to its similarity with some species of *Strigoderma* (e.g., *Strigoderma presidii* Bates, 1888) (Bates 1888) that have mixed exemplars and geographical distributions.

Strigoderma villosella is a taxon whose stability has been compromised for quite a long time that resulted in the formulation and reformulation of different specific arrays. For that reason, in this study, our focus was to carry out a morphological revision of *S. villosella*, analyzing genital and somatic structures so we can establish congruent boundaries in both specific and supraspecific categories and contribute to the construction of a more stable tribal classification.

Taxonomic history of *Strigoderma villosella* (Blanchard, 1851)

Historical taxonomic records are fundamental and pivotal tools to any taxonomic work, as they form a link between past ideas and modern changes (Gravina *et al.* 2020). For that reason, it is important to take a brief look at the historic background of *S. villosella* so we can understand its present condition and justify our decisions.

Blanchard (1851) originally described *S. villosella* in the genus *Phyllopertha*. The information given by this author is somewhat simple and lacks certain important information such as the precise type locality and male genitalia. Bates (1888) made the first change to the genus *Anomala*, arguing that the legs were more robust than those of other species of *Phyllopertha*. In that study, Bates also described *Strigoderma presidii* but saw that its mesepimera did not rise near the elytral humeri, so he proposed that it might belong to *Anomala*. Nonfried (1893) made the revision of the genera *Epectinaspis* and *Strigoderma*, and described *S. hirsuta*. Casey (1915) established *Lamoana*, a monospecific genus created for *A. villosella*.

Casey's observations were quite complete, considering the standards of that time, but he did not make a morphological comparison of the male genitalia. It must be said that the specimens that Casey evaluated came from a different locality than those that Bates and Blanchard studied, so it is uncertain whether they belonged to the same species or not. Ohaus (1918) synonymized *S. hirsuta* with *A. villosella* and retained it in *Anomala*. This nomenclatural change was made without considering all the morphological criteria that Casey established for this taxon three years earlier. We must say that there is no explanation why Ohaus ignored Casey's decision.

In 1944, Blackwelder published a checklist of beetles of Mexico, Central America, South America, and the West Indies. In this study, he retained the synonymy between *A. villosella*–*S. hirsuta* and recognized *Lamoana* as a subgenus. Almost 50 years later, Bader (1992) redescribed *S. presidii* and made several notes about its position. He remarked on the similarity of *A. villosella* with *S. teapensis* Bates, 1888 and *S. presidii* in both general habitus and the shape of the male genitalia and noted that the latter presented an intermediate morphological condition between *Strigoderma* and *Anomala*, arguing that it must be placed in a new genus or be changed to *Anomala*. Ramírez-Ponce & Morón (2009) made a phylogenetic study to evaluate the relationships between the genera of Anomalini. They concluded that the principal difficulty in delimiting genera with precision within the tribe was that some of genera had been established on questionable criteria. They revalidated *Pachystethus*; demonstrated the paraphyly of *Callistethus*; validated the synonymy between *Anomalacra* Casey, 1915 and *Paranomala*; revalidated *Paranomala*, and thus *A. villosella* was transferred to *Paranomala*. Some years later, Ramírez-Ponce (2012), studied the supraspecific systematics of *Paranomala*, and found that *P. villosella* was near to the *Strigoderma*–*Epectinaspis* clade, so he decided to place it in *Strigoderma*. Notwithstanding his decision, he remarked on the similarity in terms of male genitalia to some species of *Epectinaspis* and *Balanogonia*, just as Paucar-Cabrera had in 2003.

In recent studies, the internal and external morphology have been carefully compared among the genera of Anomalini, which has allowed us to recognize patterns of variation and homologies at different levels, thus proposing taxonomic arrangements within the tribe, finding that the parameres in a perpendicular position with respect to the tectum presented in *Strigoderma villosella*, is shared with the genera *Balanogonia*, *Callirhinus*, *Dilophochila*, *Moroniella* and *Mazahuaapertha* (Morón & Ramírez-Ponce 2012; Ramírez-Ponce 2012, 2015). An overall comparative study of male genitalia within these genera has led us to recognize clear differences in *Strigoderma villosella* thus reinforcing the evidence for revalidating the genus *Lamoana*.

Material and methods

Specimens

For this study, we examined 73 specimens of *Strigoderma villosella* and several specimens of *Balanogonia*, *Callirhinus*, *Moroniella*, two specimens of *Mazahuaapertha*, as well as an undetermined number of species of almost all the other American genera in the tribe. For the comparison of the genus *Balanogonia* with the other genera with perpendicular parameres, *B. constricta* Paucar-Cabrera, 2003 was treated as the representative of the genus. The specimens were obtained from the following collections in Mexico and abroad:

- ARPC = Andrés Ramírez Ponce Collection, Mexico
- BMNH = The Natural History Museum, London, UK
- CEIFIT = Entomological collection of the Phytosanitary Institute, COLPOS, Mexico
- CNIN = National Insect Collection, UNAM, Mexico
- FESA = Scientific Collection of the Facultad de Estudios Superiores Zaragoza, UNAM, Mexico
- FESI = Scientific Collection of the Facultad de Estudios Superiores Iztacala, UNAM, Mexico

- IEXA = Entomological Collection of the Instituto de Ecología, A.C, Mexico
MGFT = Georg Frey Collection, Naturhistorisches Museum Basel, Switzerland
MNHN = Museum national d'histoire naturelle, Paris, France
MSPC = Matthias Seidel Collection, Vienna, Austria
MXAL = Miguel Ángel Morón Collection, Xalapa, Mexico
ZMHB = Museum für Naturkunde der Humboldt Universität, Berlin, Germany

Specimen processing

Specimen dissection and preparation procedure was done according to Ohaus (1934) with a ZEISS stemi 508 stereo microscope and a pair of fine entomological forceps. Pictures were taken with an AxioCam 506 placed on an AXIO-Zoom V ZEISS multifocal stereo microscope, and with the Zen pro software. Photographs were processed with Photoshop CS6.

The following measurements were taken in mm (except for *): total length, from the anterior border of clypeus to the apex of elytral suture. Maximum width at middle part of elytra. *Interocular width, expressed in transverse eye diameters. Antennae length includes scape, pedicel, funicle and club. Tarsus length, the first four tarsomeres and the fifth tarsomere were measured independently. Pronotum length is measured at the middle portion, pronotum width at the transverse middle portion. Elytral length, from the end of scutellum to the apex of elytral suture. Pygidium length at the middle portion and pygidium width at the transverse middle portion.

Taxonomic and evolutionary criteria

The comparative morphology analysis follows the criteria of Bates (1888) and Bader (1992). The general description of the genitalia follows the criteria of D'Hotman & Scholtz (1990a) with some modifications for Rutelinae, because for this subfamily, they characterized it with 11 species of Adoretini Burmeister, 1844, Anomalini, Anoplognathini MacLeay, 1819 and Rutelini MacLeay, 1819, although only in Anomalini there is more variation than described for the subfamily. For Anomalini they reviewed a few species of the genera *Anomala*, *Leptohoplia* Saylor, 1935, *Phyllopertha* Stephens, 1830 and *Popillia* Serville, 1825.

We use the phylogenetic species concept as defined by Wheeler & Platnick (2000): “A species is the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states”.

Results

The genital capsule in Anomalini

The aedeagus (Fig. 1a–b) in the American species of Anomalini (without considering the internal sac) is characterized by the following configuration of its parts:

TEGMEN. Subcylindrical and robust in shape, with a moderately to broadly convex lateral profile; the parameres almost always shorter than the basal piece. The relative position between the parameres and the tectum with various degrees of angulation, from aligned in most genera (Fig. 1a, c, e, g, i, k), to perpendicular (Fig. 3).

BASAL PIECE. Moderately sclerotized and symmetrical, with wide variation in length (Fig. 1c, g). The dorsum and laterals are moderately to highly sclerotized and the ventral side closed by the median lobe with different degrees of sclerotization, from a partially translucent thin surface (*Leptohoplia* in Fig. 2) to a highly sclerotized plaque (*Dilophochila* in Fig. 2).

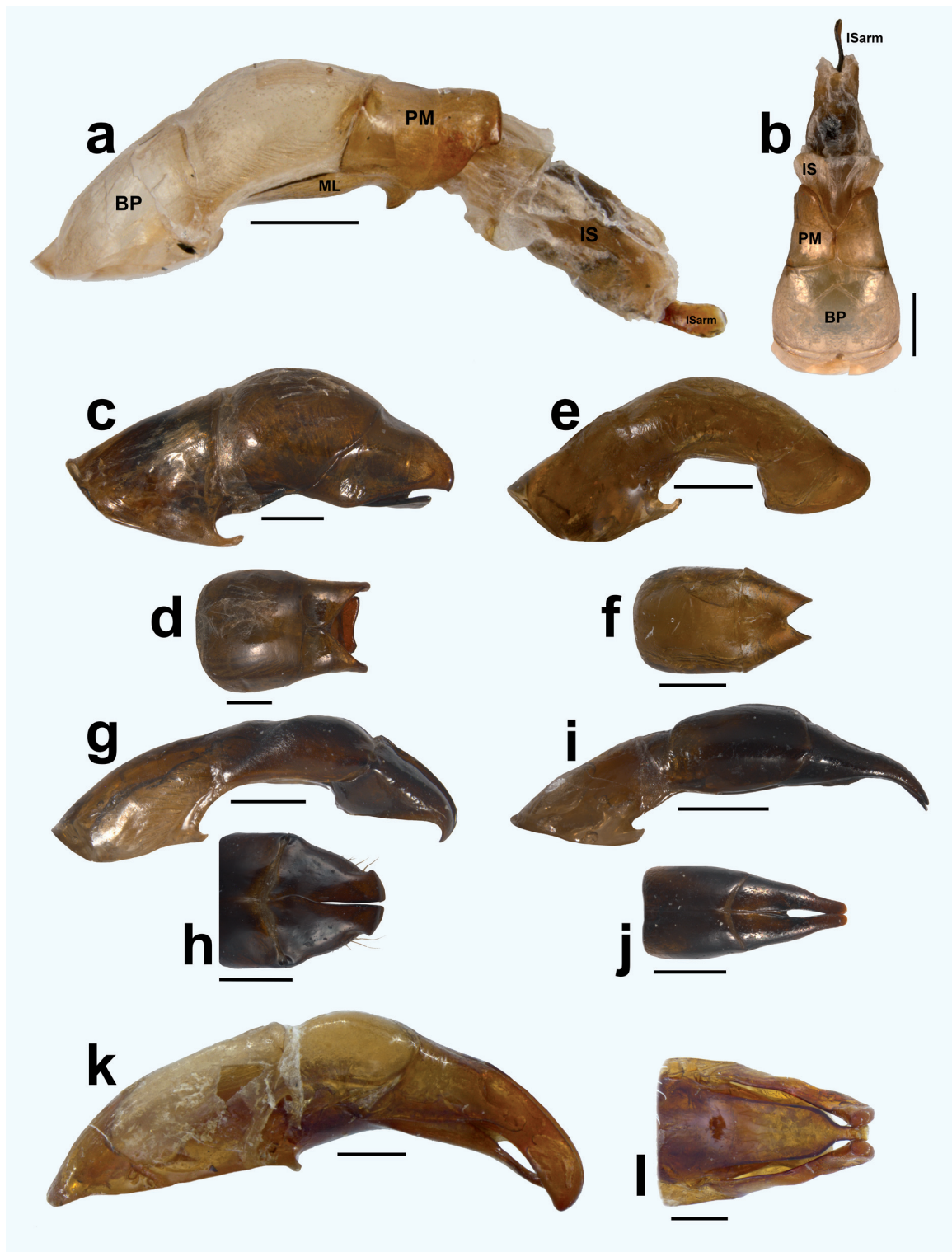


Fig. 1. Aedeagus and its parts. **a–b.** *Paranomala corcovada* Ramírez-Ponce *et al.*, 2014. **a.** Lateral view. **b.** Dorsal view. **c–l.** Tegmen in dorsal and lateral view. **c–d.** *Paranomala inbio* Ramírez-Ponce *et al.*, 2014. **e–f.** *Paranomala strigodermoides* (Filippini *et al.*, 2015). **g–h.** *Epectinaspis moreletiana* (Blanchard, 1851). **i–j.** *Strigoderma ngabe* Ramírez-Ponce & Curoe 2014. **k–l.** *Paranomala* Casey, 1915. Scale bar = 0.5 mm. Abbreviations: BP = basal piece; IS = internal sac; ISarm = internal sac armature; ML = median lobe; PM = parameres.

PARAMERES. Consist of a pair of structures with the greatest morphological variation, but with interspecific consistency (Fig. 1b, d, f, h, j, l). They are articulately attached to the phallobase and are symmetrical in the vast majority of American species, as well as with notable simplification in the development and complexity, with certain exceptions, where they can be very complex and long. [e.g., *Paranomala doryphorina* (Bates, 1888) (Fig. 1k–l), etc.]. Dorsally they may be separate (Fig. 1j), contiguous, or basally (Fig. 1d, h) or completely overlapping (Figs 1f, 4e), while ventrally they are independent and completely separated (Fig. 1l, and as *Strigoderma*, *Lamoana* and *Dilophochila* in Fig. 2), nearby (as in *Epectinaspis* and *Yaaxkumukia* in Fig. 2), or even fused with the median lobe forming a ring (as in *Callistethus* and *Pachystethus* in Fig. 2).

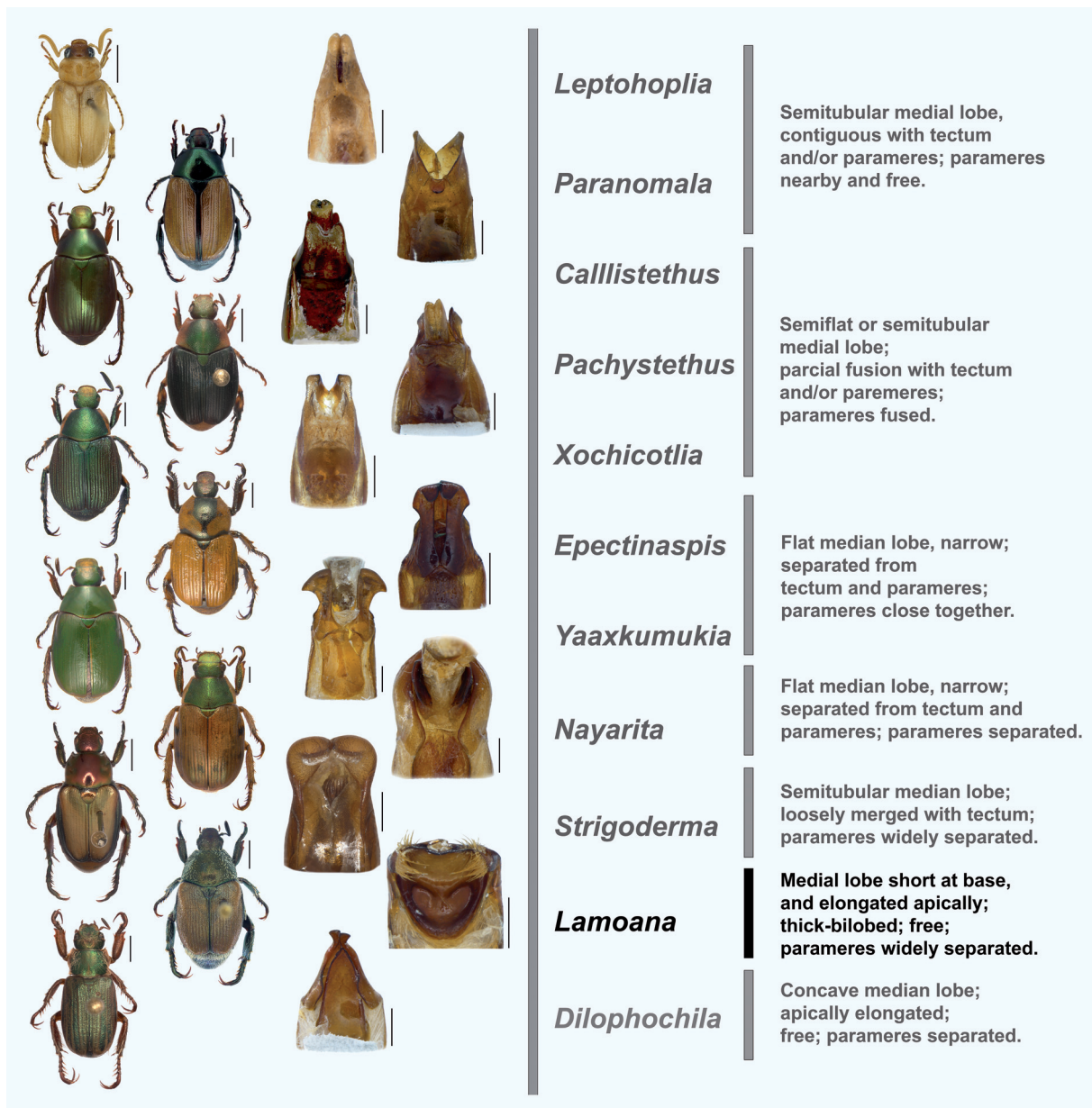


Fig. 2. Dorsal habitus of American genera of Anomalini Peringuey, 1902 with their corresponding tegmen in ventral view. Scale bars: specimen = 2 mm; tegmen = 0.5 mm.

MEDIAN LOBE. A plate that covers the ventral face. It presents various degrees of sclerotization, from a translucent membranous plate without apical development (as in *Leptohoplia* (Fig. 2) and some species of *Paranomala*), up to a strong plate with great apical development that projects to the apex of the parameres (Figs 1k–l, 3, 4a, c, g–h) (as in *Lamoana* and *Dilophochila* in Fig. 2). In most genera, the apical end is absent, converging with the ventral base of the parameres with little variation (as *Paranomala* in Fig. 2), but in a few cases it can also present great diverse morphological expressions, such as asymmetrical extensions (Fig. 1c–d), or a complex tubular or subtriangular elongated shape (Figs 1l, 3c).

In general terms, it is possible to recognize a configuration pattern of the tegmen at the genera level, whose own modifications of the basal piece, parameres and median lobe are congruent and constant, as outlined below.

The free parameres, in vertical position, generally simple apices and aligned with the tectum, in close contact with the median lobe, both on the apex and on the lateral faces are typical of the genera *Leptohoplia* and *Paranomala* (Fig. 2); however, it is important to note that *Paranomala* is a polyphyletic taxon (Ramírez-Ponce & Morón 2009), so the numerous exceptions may be due to species related to other lineages.

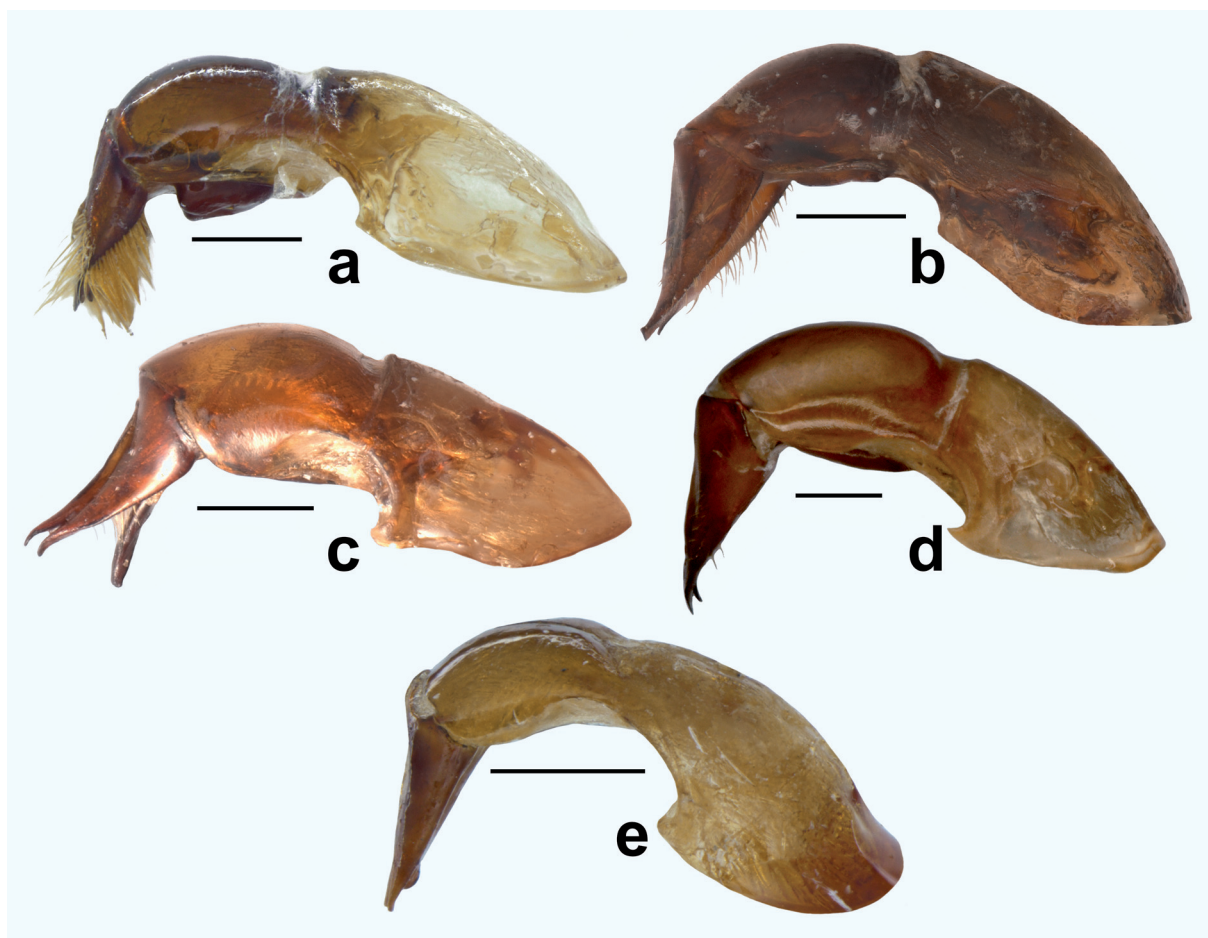


Fig. 3. Tegmen with the parameres in perpendicular position. **a.** *Strigoderma villosella* (Blanchard, 1851). **b.** *Moroniella* Ramírez-Ponce, 2015. **c.** *Balanogonia* Paucar-Cabrera, 2003. **d.** *Callirhinus* Blanchard, 1851. **e.** *Mazahuapertha* Morón & Nogueira, 1998. Scale bars = 0.5 mm.

The parameres in vertical position, fused partially or totally with the median lobe forming a ring, and the later partially fused with the basal piece are characteristic of the genera *Callistethus*, *Pachystethus* and *Xochicotlia* (Fig. 2). The genus *Callistethus* presents problems in its morphological delimitation and sometimes species of other genera are included, but have a different genital morphology (e.g., see Filippini *et al.* 2015). Additionally, it is a Pantropical genus, with a huge taxonomic problem in tropical Asia.

The parameres with the distal portion arranged dorsoventrally, contiguous ventrally and with the median lobe, and clearly separated from the basal piece, with the median lobe short, only developed to the base of the parameres, characterizes the genera *Epectinaspis* and *Yaaxkumukia*. Both genera have taxonomic treatments (Paucar-Cabrera 2003; Micó *et al.* 2006).

The monotypic genus *Nayarita* presents subcylindrical parameres with forceps-like apex, and moderately separated from each other ventrally, with the median lobe free (Fig. 2). It is an unusual shape compared to the rest of all the tribe.

The genus *Strigoderma* presents generally simple parameres with the distal portion in a dorso-ventral arrangement in most species (Fig. 1i), and always separated ventrally (Figs 1j, 2, 7b–f). The median lobe is subcylindrical, moderately sclerotized, and separated from the parameres and ventral plate (Fig. 7b–f). There is a revision of the genus (Bader 1992), although the morphological limits remained ambiguous both in the characterization of somatic and genital morphology. Some species with perpendicular parameres have frequently been classified in this genus, although one species, *S. guatemalicus* Katbeh-Bader, 2000 has the parameres markedly angulate, but neither perpendicular nor dorsoventrally depressed (Katbeh-Bader 2000).

The parameres arranged dorsoventrally, with a perpendicular position with respect to the tectum (Fig. 3), are a morphological pattern that also constantly presents sub-laminar parameres, vestiture, and are widely separated in the ventral face, with a widely projected sub-triangular median lobe that reach the apex of the parameres (Fig. 4). This type of tegmen is presented by the genera *Balanogonia*, *Callirhinus*, *Mazahuapertha* and *Moroniella* (Figs 5–6), whose species also present anthophagous habits (for *Mazahuapertha*, its natural history is unknown). Diverse species with these genitalia have frequently been classified in *Strigoderma* (e.g., Bates 1888; Bader 1992), as in the case of *S. villosella*, although the somatic (Figs 5a, 6a) and sexual differences (i.e., the shape and position of the parameres, and the unique median lobe), do not justify such an affinity (Fig. 7a).

The genus *Dilophochila* is atypical in its morphology with respect to the entire tribe (Fig. 6e). The parameres are angled respect to the tectum, though not reaching a perpendicular position. Also, they are subcylindrical in the basal half and widely separated on their ventral side. The median lobe is remarkably long, subtriangular, and completely separated of both the parameres and the basal piece (Fig. 2). There is a revision of the genus (Morón & Howden 2001).

Anomalini genera with perpendicular parameres

Paucar-Cabrera (2003) described *Balanogonia* with two species. One of the diagnostic characters that defined it was the perpendicular position of parameres regarding the tectum. In the same publication, she noticed that there are other species that share this character like *E. pilosipennis* Ohaus, 1897, *S. guatemalicus* Katbeh-Bader, 2000 and *S. villosella* Blanchard, 1851 (analyzed herein). This condition does not appear to be a diagnostic character that defines just a genus but an entire group of genera endemic to America, i.e., *Moroniella*, *Callirhinus*, *Mazahuapertha*. A comparison of the genitalia of *Balanogonia* with the genera mentioned before, raises doubt about the placement of *B. freudei* (Frey, 1968) (see Paucar-Cabrera 2003). This species has the parameres slightly inclined and neither totally

perpendicular nor dorsoventrally depressed, the median lobe is not developed, and the distribution is very different between the two species (Fig. 9). It must be said that besides the similar male genitalia morphology, this small group of genera also share specialized anthophilous feeding and diurnal habits. However, despite the similar genital morphological plan, differences between these genera are evident in both genital (Figs 3–4) and somatic morphology (Figs 5–6; Table 1).

For example, *Moroniella* is distinguished by having the apex of the parameres directed externally with the median lobe having a needle-shaped apex (Fig. 4c), and a longitudinal keel on each side of the base of the median lobe (Fig. 4d); *Balanogonia* presents simple parameres, completely overlapping (Fig. 4e), with the median lobe broadly rounded at the apex (Fig. 4f); *Callirhinus* presents the apex of the parameres directed internally with the median lobe acute triangular (Fig. 4g), and with a uniform and slightly concave surface (Fig. 4h); *Mazahuapertha* presents the apex of the parameres rounded and curved towards outside with the median lobe subtriangular rounded (Fig. 4i), and with the base of the median lobe with uniform and slightly concave surface (Fig. 4j). *Strigoderma villosella* differs with respect to the others by being

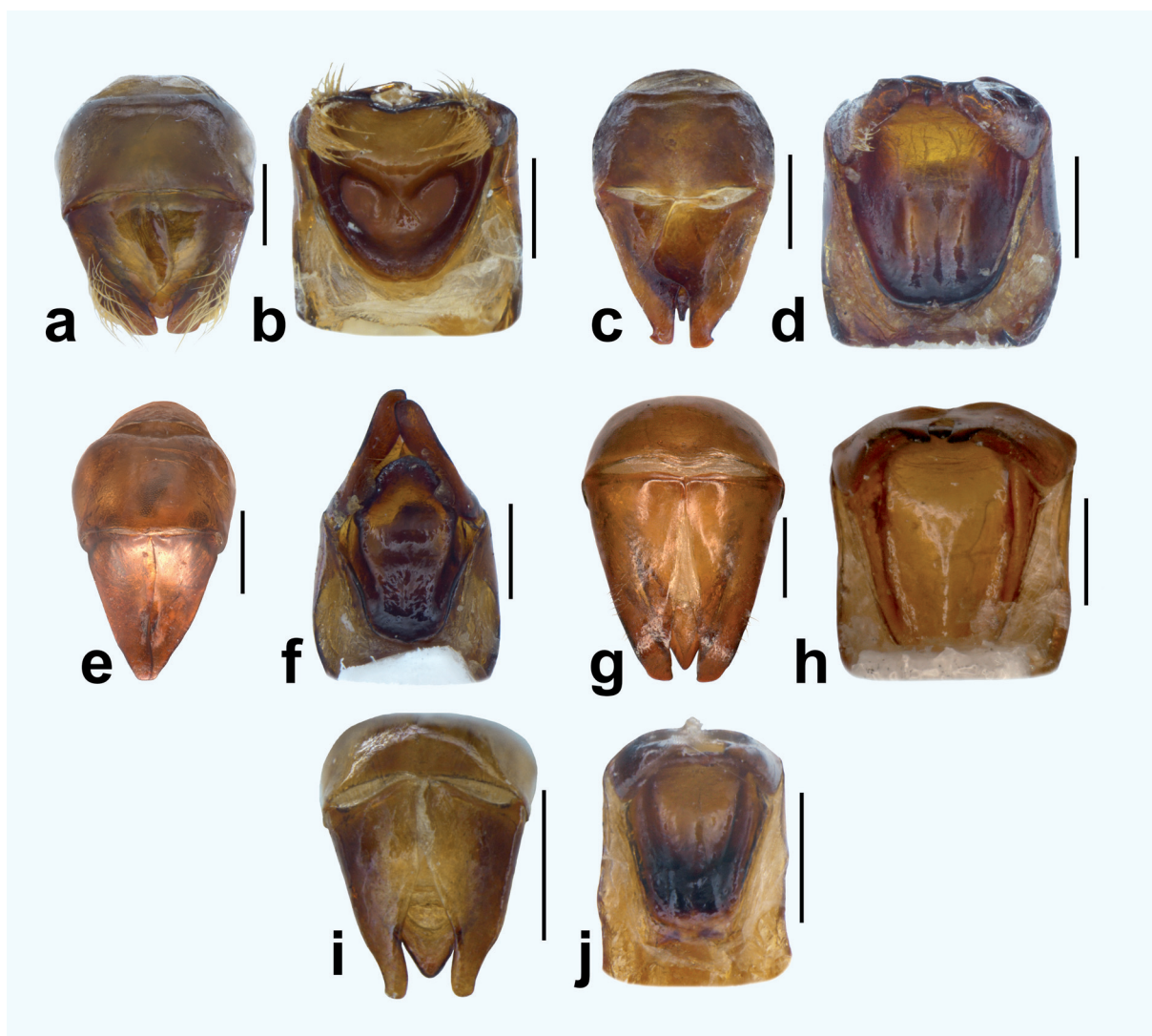


Fig. 4. Parameres (caudal view) and median lobe (ventral view). **a–b.** *Strigoderma villosella* (Blanchard, 1851). **c–d.** *Moroniella* Ramírez-Ponce, 2015. **e–f.** *Balanogonia* Paucar-Cabrera, 2003. **g–h.** *Callirhinus* Blanchard, 1851. **i–j.** *Mazahuapertha* Morón & Nogueira, 1998. Scale bars = 0.5 mm.

Table 1. Morphological differential characters among the genera with perpendicular parameres.

Genera	<i>Lamoana</i> Casey, 1915	<i>Mazahuapertha</i> Morón & Nogueira, 1998	<i>Callirhinus</i> Blanchard, 1850	<i>Moroniella</i> Ramírez-Ponce, 2015	<i>Balanogonia</i> Paucar-Cabrera, 2003
Character/					
Dorsal vestiture	Abundant short setae on head, pronotum and elytra	Moderately abundant long setae in front and pronotum	Absent	Absent	Absent
Antennal club respect to scape, pedicel and funicle together	Slightly longer	Much longer	Subequal	Subequal	Slightly shorter
Clypeus	Semi-oval, slightly reflexed	Semicircular, reflexed	Subtriangular, reflexed	Subtrapezoidal, reflexed	Subtrapezoidal, slightly reflexed
Pronotum posterior margin	Incomplete	Complete	Complete	Absent	Complete
Apex of elytral suture	Spiniform	Rounded	Spiniform	Spiniform	Spiniform
Mesepimera	Slightly ascending	Not ascending	Ascending	Slightly ascending	Ascending
Intermesocoxal space	Very wide	Narrow	Wide	Wide	Wide
Protibia	Wide	Slender	Wide	Wide	
Protibial spur	Present	Absent	Present	Present	Present
Protibial internal claw	Highly cleft	Poorly cleft	Highly cleft	Highly cleft	Highly cleft
Protarsomeres 1–4	Wide, very short, subequal to each other and in length as the fifth	Thin, short, subequal to each other and longer than the fifth	Wide, subequal to each other and in length as the fifth	Wide, very short, subequal to each other and in length as the fifth	Thin, progressively shorter and longer than the fifth
Parameres vestiture	Abundant, dorsoventrally	Absent	Scarce, dorsoventrally	Sparse dorsally and abundant ventrally	Scarce, ventrally

the only one with the parameres with a pre-apical notch on the external border (Fig. 4a), abundant setae on both faces (Figs 3a, 4a–b), as well as a conspicuous lobe on each side of the median lobe (Figs 3a, 4b).

Taxonomic treatment

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Family Scarabaeidae Latreille, 1802
Subfamily Rutelinae MacLeay, 1819
Tribe Anomalini Peringuey, 1902

Genus *Lamoana* Casey, 1915 stat. rev.
Figs 2, 3a, 4a–b, 5a, 6a, 7a, 8–9

Lamoana Casey, 1915: 48. (Type species: *Phyllopertha villosella* Blanchard, 1851: 179, by original designation).

Lamoana – Blackwelder 1944: 245 (subgen.). — Machatschke 1957: 31 (syn.); 1972–1974: 85 (syn.).

Diagnosis

Body pubescent throughout, setae of short to moderate length and thickness (in *Mazahuapertha* present only on pronotum but long and thin, absent in *Balanogonia*, *Callirhinus* and *Moroniella*, in *Strigoderma* present only on the pronotum of a few species); pronotum posterior margin incomplete (complete in *Balanogonia*, *Mazahuapertha*, *Callirhinus* and *Strigoderma*, absent in *Moroniella*); apex of elytral suture spiniform (rounded in *Mazahuapertha*, spiniform in *Balanogonia*, *Callirhinus*, *Moroniella* and *Strigoderma*); intermesocoxal space very wide (apex of mesometasternal projection slightly greater than width of mesotrochanter) (narrow in *Mazahuapertha*, wide in *Balanogonia*, *Callirhinus* *Moroniella*, variable in *Strigoderma*); parameres with abundant setae both dorsal and ventral portion (glabrous in *Mazahuapertha*, lightly covered in *Balanogonia*, *Callirhinus*, *Moroniella*, and in some species of *Strigoderma*); medial lobe with one thick lobe on each side (absent in the others).

Etymology

Unknown.

Redescription of male

FORM. Oval body, slightly dorsoventrally flat.

SIZE. Total length 6.0–9.22 mm; maximum width 2.91–5.0 mm.

BODY. Bright coppery with or without metallic reflections and yellowish elytra; abundant vestiture, setae short on dorsum and moderately long ventrally (Fig. 5a).

HEAD. Clypeus subtrapezoidal to semioval, moderately reflexed; frons flat (Fig. 8d); antennal club generally longer than the previous antennomeres; ocular canthus wide, setose at apex; postgenal area setose.

PRONOTUM. Subtrapezoidal; surface with setaceous punctation, homogeneous; setae backwards decumbent; posterior margin incomplete; lateral borders angled; anterior and posterior angles rounded (Fig. 8b, d).

ELYTRA. Surface with 11 striae punctuate, deep or moderately marked; surface setose, setae short (Figs 5a, 6a, 8b); epipleura reaches 2nd visible sternite; apex of elytral suture spiniform.

MESEPIMERA. Projected further than the elytral humerus.

PREPYGIDIUM. Covered partially by elytral apex, widely setose in apical half (Figs 5a, 6a).

PYGIDIUM. Wider than long; uniformly setose; evenly concave.

MESOSTERNUM. Intercoxal space very wide.

MESOMETASTERNAL PROJECTION. Protuberant; generally, exceeds mesocoxae.

METASTERNUM. Surface abundantly setose, setae long.

ABDOMEN. Surface progressively setose towards sides, forming a patch laterad; visible sternites 2–4 generally similar in size; 5th sternite twice as long as posterior sternites (Fig. 8a, c).

LEGS. Protibia bidentate, wide, protibial spurs present (Fig. 8e); protarsus 1–4 short and thickened, subequal in length than apical tarsomere; fifth tarsomere with basal denticle reduced; inner claw notably cleft; interior ramus 4 times as wide as superior (Fig. 8f). Mesotibia wider in the middle; one subapical transverse carina with 4–6 long spiniform setae; apical crown of 7–8 spines. Metatibia wider in the middle; one subapical transverse carina with 9–12 short spiniform setae and one sub basal transverse carina with 8–10 short slender spiniform setae; apical crown with 11–15 short spines.

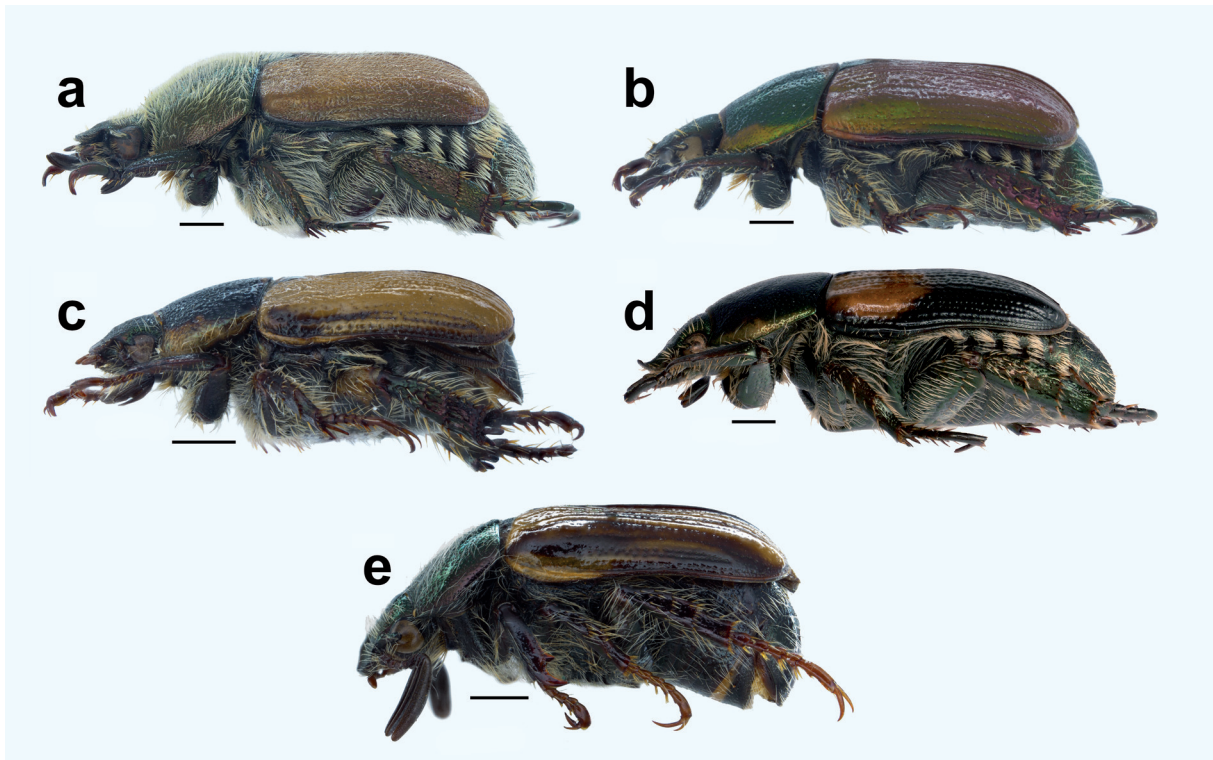


Fig. 5. Lateral view of the genera with perpendicular parameres. **a.** *Strigoderma villosella* (Blanchard, 1851). **b.** *Moroniella* Ramírez-Ponce, 2015. **c.** *Balanogonia* Paucar-Cabrera, 2003. **d.** *Callirhinus* Blanchard, 1851. **e.** *Mazahuapertha* Morón & Nogueira, 1998. Scale bars = 1 mm.

MALE GENITALIA. Parameres abundantly setose in ventral and dorsal sides, perpendicular to the tectum (lateral view) (Fig. 3a); dorsoventrally depressed; external borders with preapical notch; tips rounded or triangular (Fig. 4a); median lobe subtriangular with apex acute or rounded (caudal view) (Fig. 4a), separated from basal piece and parameres (ventral view) (Fig. 4b), one prominent lobe on each side near the base (ventral view) (Figs 3a, 4b).

Distribution

Lamoana is an endemic genus to Mexico, exhibiting a typical Neotropical distribution pattern, species being found mainly along the coasts in lowland tropical forest, having possibly dispersed from south to north (Halffter 1976; Halffter & Morrone 2017). It is present in the biogeographic provinces of the Balsas Basin and the Pacific Lowlands (Morrone 2015; Morrone *et al.* 2017), in ecosystems with tropical deciduous forest located between 0 and 1500 m a.s.l.

Taxonomic comments

Due to the morphological differences that distinguish this genus from the genera mentioned before, it is proposed, with the aims of stability and priority, to taxonomically revalidate *Lamoana* Casey, 1915, because it was first established to place the “aberrant” *A. villosella* (Casey 1915). Its special morphology caused it to be classified separately from the rest of the species (e.g., Blanchard 1851) or associated with species that now form different genera such as *Xochicotlia*, *Pachystethus* or *Moroniella* (Bates 1888). Considering both external and genital morphology, *Lamoana* most closely resembles the genus *Moroniella*; both share the robust and depressed body, the shortening and notable width of the protarsi in males, and are the only genera with ornamentation at the base of the median lobe, in the form of lobes in *Lamoana* (Fig. 4b) and keel-like in *Moroniella* (Fig. 4d) (Table 1).

Biological information

The genus *Lamoana* is diurnal and anthophagous, distributed in central and south Mexico, with activity between May to November.

Lamoana villosella (Blanchard, 1851) comb. rev.
Figs 2, 3a, 4a–b, 5a, 6a, 7a, 8–9

Phyllopertha villosella Blanchard, 1851: 179.

Strigoderma hirsuta Nonfried, 1893: 291 (by Ohaus 1918: 110).

Phyllopertha villosella – Blanchard 1851: 179. — Bates 1888: 246. — Ohaus 1897: 399; 1902: 43; 1918: 110. — Casey 1915: 48. — Blackwelder 1944: 245. — Machatschke 1957: 79.

Etymology

Although it was not expressed by the author of the nominal taxon, the noun derives from ‘*villus*’ (plural ‘*villi*’) meaning ‘hair’, and refers the abundant vestiture that covers all the body, and that is now a generic character.

Material examined

Lectotype (here designated)

MEXICO • ♂; “Ohaus determ. *Spilota villosella* Blanchard”; [green label (Reverse)] “2, 44”; MNHN. (Designated herein by monotypy sensu Art. 73.1.2 of ICZN.)

Other material

MEXICO – Colima • 1 ♀; “Tonila, Colima. Höge.; H.W. Bates, Biol. Cent. Amer”; MNHN • 1 ♂; “Colima, Mex. Höge.; *Spilota villosella* Bl.; *Anomala villosella* Blanch. Museum f. Naturkunde Berlin

(MFNB)”; ZMHB • 1 ♂; “Colima, 12/VII. Mexico. 300 m.; *Anomala villosella* Blanch. Museum f. Naturkunde Berlin (MFNB)”; ZMHB • 1 ♂; “MEXICO: Colima, Colima; Ohaus determ. *Anomala villosella* Blanch.; ZMHB • 1 ♂; “Iguala, Guerrero. Höge.; ♂; *Phyllopertha villosella* Blanch; H.W. Bates, Biol. Cent. Amer”; MNHN. – **Durango** • 1 ♀; “Ventanas, Durango, Hoege; *Spilota villosella* Bl.; *Anomala villosella* Blanch.; *Anomala villosella* Blanch. Museum f. Naturkunde Berlin (MFNB)”; ZMHB. – **Guerrero** • 2 ♂♂; “Iguala, Guerrero. Höge; H.W. Bates, Biol, Cent, Amer”; MNHN • 1 ♂; “México: Guerrero 3 km sur de Mezcala 13/VI/2001 H. Brailovsky, E. Barrera; Colección del Instituto de Biología, UNAM. México, D.F.”; CNIN • 2 ♂♂; “STHMM0013 MÉXICO: GUERRERO. Los Amates, Iguala, SBC. 18°24'52.7" 99°30'0.1". 29-VIII-2009. 20:55 Graminea. G. Rodríguez col.”; FESA • 1 ♀; “México: Guerrero. Alpoeyca 26-V-2006. 17°35'15"N, 98°32'46.6"O. E. Barrera; Colección del Instituto de Biología, UNAM. México, D. F.”; CNIN • 1 ♂, 1 ♀; “MÉXICO: Guerrero, Ixtapa, zona hotelera. 04-Nov-2008. Recol. Ricardo Medina Ortiz; JPZ2015, LJ002259 & LJ002257”; FESI • 1 ♂, 2 ♀♀; “P. Marqués, Gro. 13-IX-81. Col. WLFC; IBUNAM: CNIN: CO45229 (barcode); 45229 (QR code); *Strigoderma presidii* Bates, 1889. Det. C.X. Pérez-Hernández, 2013”; CNIN • 2 ♀♀; same collection data as for preceding, except: IBUNAM: CNIN: CO45230 (barcode); 45230 (QR code), and IBUNAM: CNIN: CO45231 (barcode); 45231 (QR code); CNIN • 1 ♀; “MÉXICO: GUERRERO, IXTAPA ZIHUATANEJO. 26-27-XII-1993. H.Y.KA. BRAILOVSKY; IBUNAM: CNIN: CO45227 (barcode); 45227 (QR code); *Strigoderma presidii* Bates, 1889. Det. C.X. Pérez-Hernández, 2013”; CNIN • 1 ♀; “Mescal, Guerrero. H.H. Smith.; 86492; *Anomala villosella* Blanch. Museum f. Naturkunde Berlin (MFNB)”; ZMHB. – **Jalisco** • 1 ♂, 2 ♀♀; “MÉXICO: Jalisco, Pto. Vallarta, CUC. 11/07/2013. A. Bitar col.; Flores, colecta directa 3:00 pm”; ARPC • 1 ♂; “MÉXICO: Jalisco, Tenacatita, Los Angeles Locos. 70 m. 14-VI-94. Luz. G. Nogueira; *Strigoderma praesidii* Bates. M.A. Morón, det. 98”; ARPC • 2 ♂♂; “MÉX: Jal. La Huerta. 9/VII/81. Curoe col.”; MXAL • 1 ♂; “MÉXICO: Jalisco, Casimiro Castillo. 390 m. 17-VI-94. G. Nogueira col.”; MXAL • 1 ♀; “México: Jalisco, Estación Biológica de Chamela. 19.48928 N, 105.0376 O. 107 m. 10-17/V/2013. Trampa de intercepción 3. Col. S. Zaragoza-Caballero; Melolonthidae 212 Morfo 11”; CNIN • 1 ♀; “CHAMELA, JAL. X-74 H.B.B; IBUNAM: CNIN: CO45228 (barcode); 45228 (QR code); *Strigoderma presidii* Bates, 1889. Det. C.X. Pérez-Hernández, 2013”; CNIN. – **Morelos** • 1 ♂; “Xochitepec, Mor. 30 Juni 62. Blume. Col. J. Hendrichs S.; Ex-Colección Jorge Hendrichs S.H.”; CNIN • 4 ♂♂; “PALO BOLERO, Mor. 21 Mai 65. Flor del Zopilote. Col J. Hendrichs S.; Ex-Colección Jorge Hendrichs S.H.”; CNIN • 1 ♂; “ESTACAS, Mor. 5 Juni 55. FleiB Lieschen. J. Hendrichs; Ex-Colección Jorge Hendrichs S.H.”; CNIN • 1 ♀; “XOCHITEPEC, Mor. 7 Juni 64. Copa de Oro. Col J Hendrichs S; Ex-Colección Jorge Hendrichs S.H.”; CNIN • 1 ♀; “XOCHITEPEC, Mor. 5 Juni 66. Strauch. Col J Hendrichs S; Ex-Colección Jorge Hendrichs S.H.”; CNIN • 2 ♀♀; “XOCHITEPEC, Mor. 28-IX-75. Col J Hendrichs S; Ex-Colección Jorge Hendrichs S.H.”; CNIN • 1 ♂; “SAN RAFAEL, Mor. 2 Nov 53. Violette Hinde. J Hendrichs; Ex-Colección Jorge Hendrichs S.H.”; CNIN • 2 ♂♂; “México: Morelos, Huautla. 8/X/96. A Pérez; *Strigoderma villosela*; CNIN • 1 ♀; “CPO. EXP. Xalostoc, Mor. Sep. 24-62. E. Pacheco.; algodón; *Epectinaspis opacicollis* Bates, 1888. L.L. Delgado C. det. 1989”; CEIFIT • 1 ♂; “Cpo. Experim. TEPALCINGO, Mor. Sep.-3-1961. E Pacheco m.; algodón; *Anomala villosella* Blanch. Det. Cartw '62.”; CEIFIT • 1 ♂; “San Isidro, Yauteppec, Mor. 8/IX/1995. 1100 msnm. s/maleza. Victor R. Castrejón”; CEIFIT. • 1 ♀; “MEXICO: Morelos. 2.5 km N 4 km O. Huautla. Estación CEAMISH. Selva Baja Caducifolia. 4-8.X.1996. alt. 940 m. en vegetación. A. Pérez Col.; *Anomala villosella* Blanchard 1850. A. Pérez det. 1996”; CNIN • 1 ♂, 1 ♀; “MÉXICO: Morelos. 2.5 km N, 4 km O Huautla. Estación CEAMISH. 8-IX-1996. Alt. 940 m. 18°27'.671 N 99°02'.475 O. Col. M. A. Morales”; CNIN. • 13 ♂♂; “MÉXICO: Morelos. Loc. 2. 2.5 km O de Ajuchitlán. Selva baja caducifolia. 5-9.X.1996. Alt. 950 m. 18°28'.065 N, 96°59'.546 O. en vegetación. A. Pérez Col.”; CNIN • 1 ♂; “Yauteppec 25; México J. Flohr G.; 88531; *Anomala villosella* Blanch. Museum f. Naturkunde Berlin (MFNB)”; ZMHB. – **Oaxaca** • 1 ♂; “BALS03345 MÉXICO: OAXACA, cerro El Coralillo, SB. 17°53'44.7", 96°3'31.3" 1453 m. 23/VIII/2004, 22:00. M.A. Hollenbach, G. Hubbard, cols.”; FESA • 1 ♂; “E. Barrera col. MÉXICO. Huajuapán de León, Oaxaca. 17-IX-80.; Colección del Instituto de Biología, UNAM. México, DF.”; CNIN • 1 ♂, 1 ♀; “Oaxaca, Huatulco, Hotel Camino Real. 15.774303°, -96.091766°. En flores 12:30 pm.

Selva Baja Caducifolia. 10 msnm.”; ARPC. – **Puebla** • 1 ♂, 1 ♀; “Matamoros, Izucar, Puebla, Höge; H.W. Bates, Biol. Cent. Amer”; MNHN • 4 ♂♂; “Ant. Col. Mus. de Hist. Nat. Matamoros Puebla. 1171; *Epectinaspis opacicollis* Bates. M.A. Morón det. 97”; CNIN.

Redescription

Male

FORM. Body slightly convex and robust.

SIZE. Total length from 7.60–9.22 mm; maximum width from 2.91–5.0 mm.

COLOR. Clypeus, frons, pronotum and scutellum shiny green or brown with violet sparkles; antennal club dark brown; pronotum with brown reddish tones in lateral borders; elytra and striae brown yellowish; elytral suture and epipleura dark brown; prepygidium dark brown; pygidium light brown in lateral basal

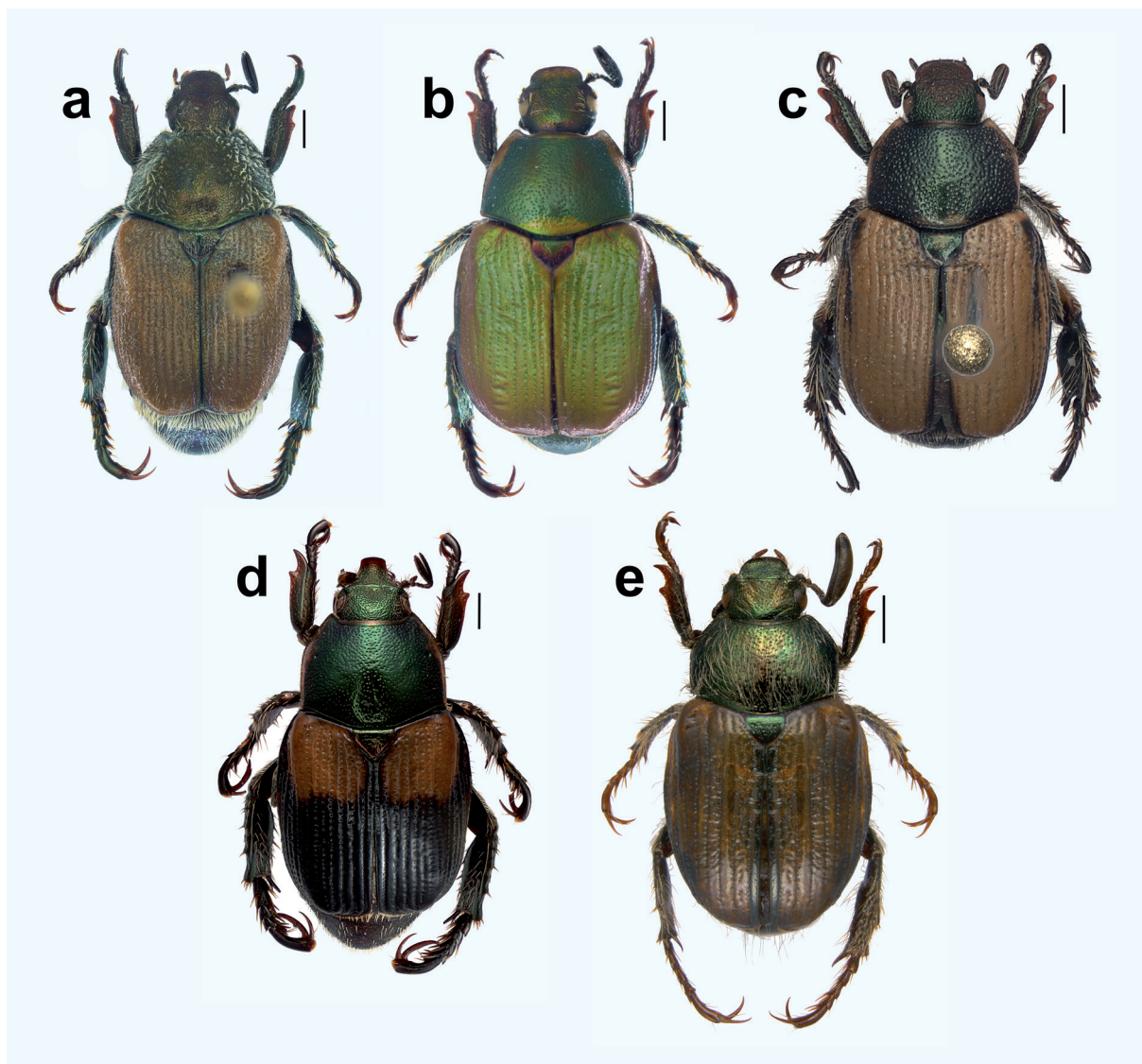


Fig. 6. Dorsal habitus of the genera with perpendicular parameres. **a.** *Strigoderma villosella* (Blanchard, 1851). **b.** *Moroniella* Ramírez-Ponce, 2015. **c.** *Balanogonia* Paucar-Cabrera, 2003. **d.** *Callirhinus* Blanchard, 1851. **e.** *Mazahuapertha* Morón & Nogueira, 1998. Scale bars = 1 mm.

portion and dark brown in center; abdomen dark brown in 1st and 2nd sternites, light brown in anal plate; pro-, meso-, and metasternum from dark brown to almost black with green or violet sparkles; legs dark brown with green sparkles.

HEAD. Clypeus semioval, anterior border moderately reflexed; hairy surface, setae of moderate thickness and length; rugose punctuated texture, homogeneous, broad, and deep punctation; frontoclypeal suture continuous and conspicuous, elevated; antennal escape highly covered by hairs, long and thick setae; pedicel and funicle poorly covered; antennal club (0.86–1.35 mm) similar or slightly bigger than escape (0.19–0.39 mm), pedicel (0.09–0.12 mm) and funicle (0.21–0.48 mm) together; interocular width between 3.81–4.57 transverse eye diameters.

PRONOTUM. Subtrapezoidal, wider (2.69–3.46 mm) than long (1.73–2.71 mm); lateral borders rounded; lateral margins straight in posterior portion; anterior cuticular projection complete; punctuated and

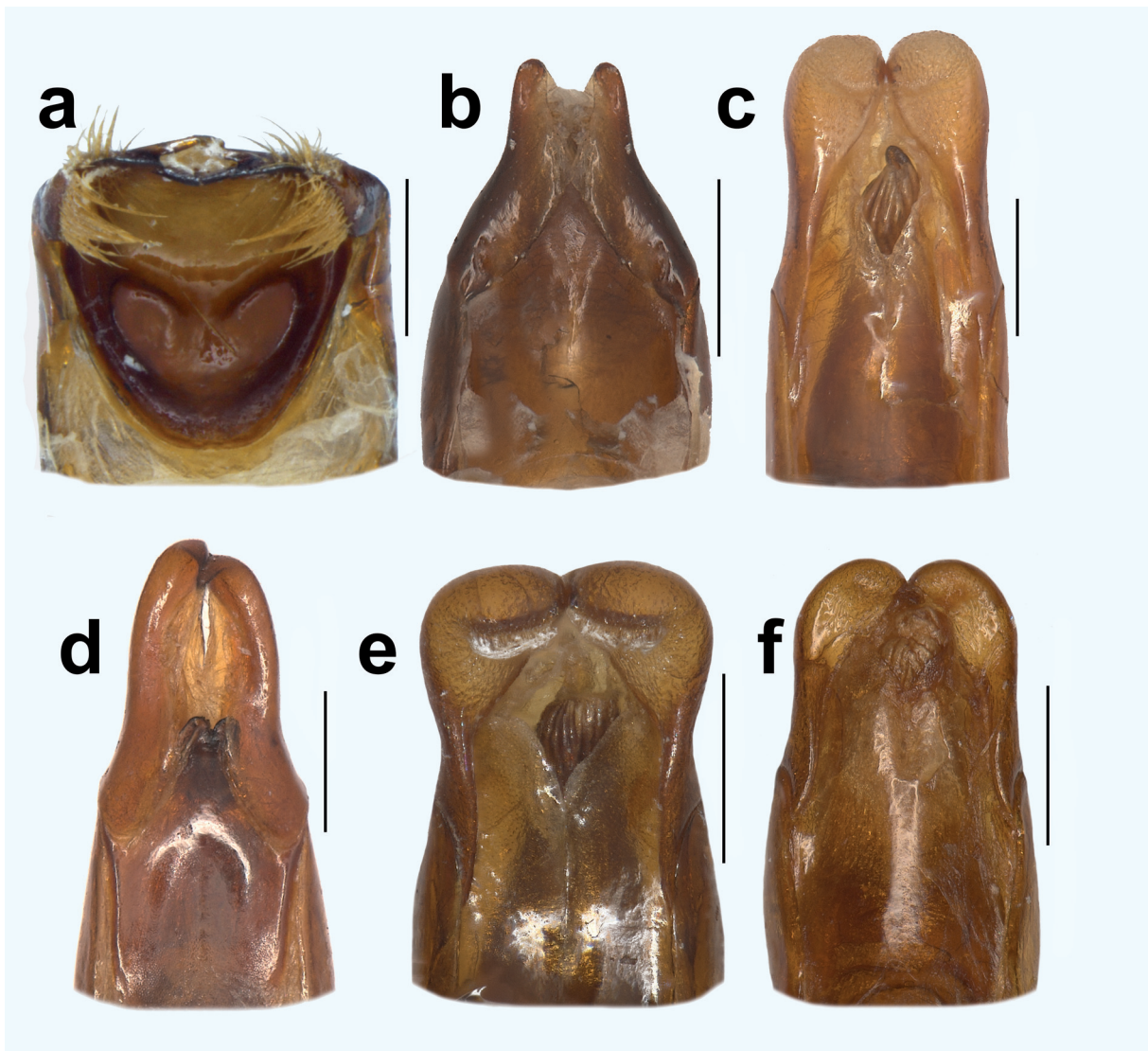


Fig. 7. Parameres and median lobe in ventral view. **a.** *Strigoderma villosella* (Blanchard, 1851). **b–f.** *Strigoderma* spp. Scale bars = 0.5 mm.

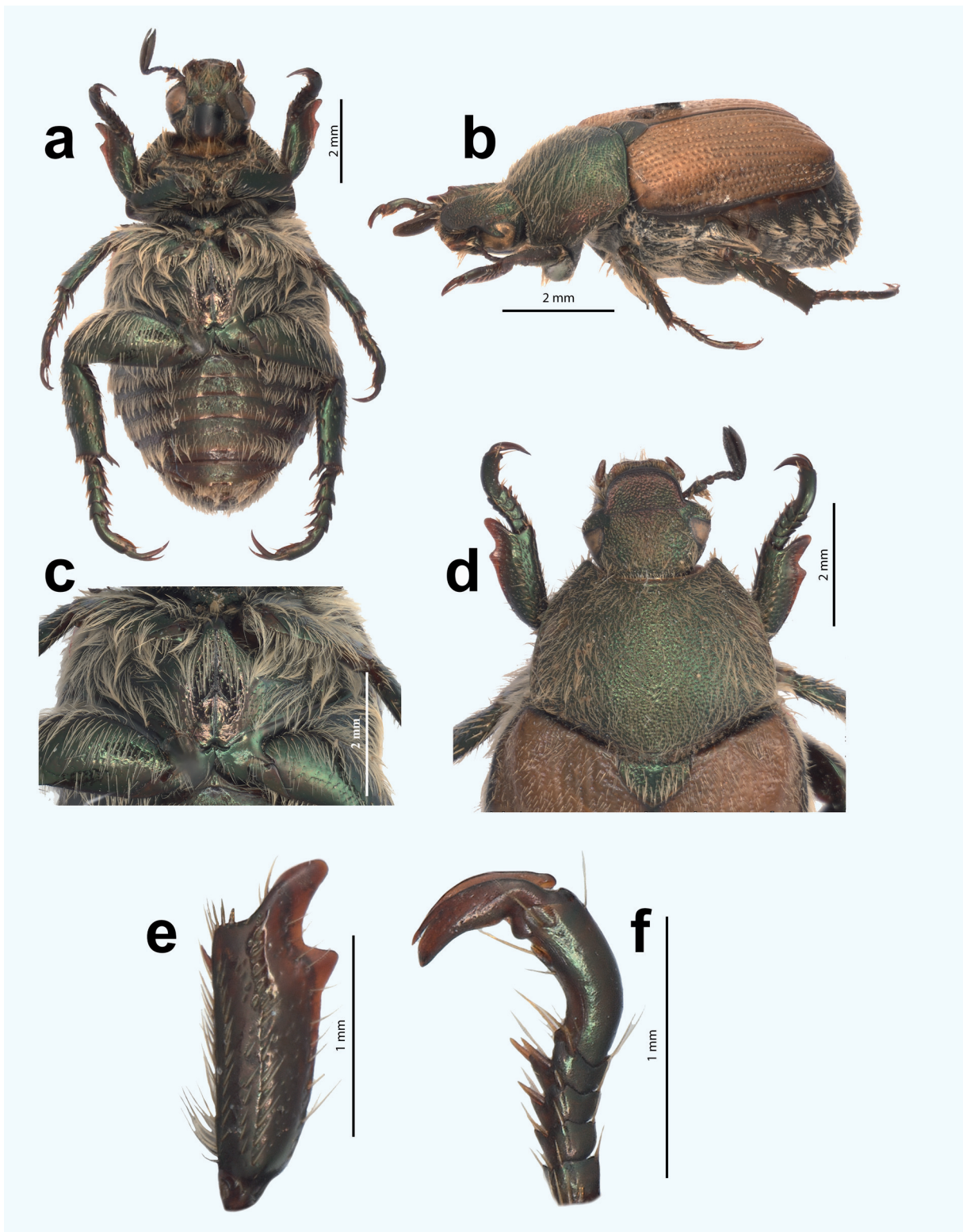


Fig. 8. Morphological characters in *Lamoana villosella* (Blanchard, 1851). **a.** Ventral view of habitus. **b.** Oblique view of habitus. **c.** Metasternum. **d.** Dorsal view of head and pronotum. **e.** Protibia. **f.** Protarsus.

setose surface, fine and shallow punctures; setae of moderate length, backwards decumbent, base as wide as elytral base.

SCUTELLUM. Subtriangular; basally setose, setae like those of pronotum; punctuated surface.

ELYTRA. Slightly wider (3.58–5.00 mm) than long (3.83–4.50 mm); humeral calli elongated and constrained until half of elytra; elytral suture apex spiniform with oblique tips; striae marked by punctures irregularly separated from one another; surface uniformly setose, setae length like those of pronotum; epipleura thick and developed until de 2nd visible sternite; subtly thickened; notable apical calli.

MESEPIMERA. Visible over the elytral base.

PREPYGIDIUM. Surface punctuated in anterolateral and posterior portions; highly hairy in posterior part, setae long and decumbent.

PYGIDIUM. Subtriangular, convex, slightly wider (2.269–2.564 mm) than long (1.692–2.115 mm); setose surface except in a middle longitudinal line, thick and long setae like those of prepygidium, highly dense.



Fig. 9. Distribution map of the genera with perpendicular parameres (the only genus not endemic to Mexico is *Moroniella* Ramírez-Ponce, 2015, which extends into Central America).

MESOMETASTERNAL PROJECTION. Slightly protuberant at mesocoxal level; barely appreciated in lateral view.

METASTERNUM. Lustrous; slightly punctuated; strongly setose; middle portion glabrous and excavated.

ABDOMEN. 1.46 times as wide as long; sternites from 2–5, hairy along a transverse line, setae of medium thickness and length, denser like locks in pleural borders, scarce in center; very shallow punctation; sternites from 2–4 with the same width, 5th sternite two times as wide as the previous; 6th sternite border clearly sinuated.

LEGS. Protibia gradually widened; tarsomeres from 1–4 notably thickened and reduced, of similar length; 5th tarsomere with a small inner, basal and blunt denticle, and slightly longer than (0.49–0.58 mm) or equal to the previous tarsomeres together (0.39–0.47 mm); inner claw highly cleft, very narrowed; superior ramus acute and short; inferior ramus thickened, highly oblique almost spiniform, three or four times as wide as superior ramus. Mesotibia very wide at center; carina oblique with 5–8 thick spiniform setae; apical crown with 7–8 spines; spurs acute and curved at apex; inner spur longer than the 2nd tarsomere. Metatibia short, widened at center; carina at the inferior third with 10–12 spiniform setae; apical crown with 12–15 spines; surface notably punctuated; 5th tarsomere slightly smaller (0.74–0.86 mm) than the previous tarsomeres together (0.86–1.03 mm); tarsomeres from 1–4 highly widened, progressively short, similar in length; apical spur very thick, curved at apex, inner spur little longer than the 1st tarsomere.

MALE GENITALIA. Parameres dorsoventrally depressed, in perpendicular position; setose in dorsal and ventral sides, setae long and denser in ventral side; external borders curved, with preapical notch; medial lobe triangular, shorter than parameres, not fused with basal piece or parameres; one prominent lobe on each side ventrally.

Taxonomic comments

This species was described by Blanchard (1851) in the genus *Phyllopertha* and was transferred between the genera *Anomala* and *Strigoderma* throughout its history. Casey (1915) established it as the type species of his new genus *Lamoana*; this decision is herein supported and thus we revalidate *Lamoana* for this species.

Variation

Some specimens present the clypeus with a subrectangular to oval form, with the anterior border poorly reflexed or almost flat. The frontoclypeal suture without any apparent elevation, discontinuous or barely noticeable. The antennal club is very variable, it can be as long or even longer than the previous antennomeres. The lateral borders of pronotum can be rounded to slightly angulated in the front third. The protarsomeres vary slightly in length and thickness, and the metatibia vary in length, width, and in the density of pubescence.

Sexual dimorphism

Females have a shorter antennal club (similar to the length of the pedicel and funicle together), the epipleuron wider, the protibia and protarsomeres thinner, the 1st protarsomere longer than 2nd, 3rd and 4th protarsomere, the protarsal claw with ramus similar in thickness and the abdomen less depressed.

Distribution

Lamoana villosella has a wide distribution range, mainly in the north central part of Mexico in the states Colima, Guerrero, Jalisco, Morelos, Oaxaca, and Puebla, extending north to the state of Durango. Its geographical distribution corresponds to the Balsas Basin and the Pacific Lowlands provinces (in the

Nayarit-Guerrero district) (Morrone 2019), in ecosystems with dry and tropical forest (Dinerstein *et al.* 1995) located between 0 and 1500 m a.s.l.

Phenology

This species is from May to November.

Biological data

This is a species apparently with anthophilous habits, some records show that the specimens have been collected in grasses, cotton and flowers in deciduous forest ecosystems. The life cycle and immature states are still unknown.

Discussion

Historically, *Lamoana villosella* has been a controversial taxon due to the imprecise criteria that defined some Anomalini genera at the time, and its morphologically transitional character configuration. Since Bates (1888) commented about its incorrect classification in *Phyllopertha*, a debate was opened about its validity, true position, and nature of its relationships with other tribe members.

Regarding the geographical distribution, *Lamoana* has a typical Neotropical pattern in the Mexican territory (Halffter 1976; Halffter & Morrone 2017), that extends north through the Pacific lowlands, near the occidental coasts and is limited in the center by the Balsas Basin province. Taxa with this biogeographical pattern show a paleotropical affinity (Ramírez-Ponce 2015) with ancestors of possible Gondwanan origin (Halffter 1976), that dispersed from the South once the Central American nucleus linked both Americas through the Panamanian land bridge, as part of the neotropical taxa modern migration, and that penetrated to the north by the occidental and oriental coast limited by the barriers of the Sierras Madres, the Mexican Plateau and the Transmexican Volcanic Belt (Halffter 2017; Halffter & Morrone 2017). There are cases where a species could penetrate deeper into the Mexican territory reaching the Sierra Madre Occidental region (e.g., *Canthon indigaceus* LeConte, 1866) or even the Mexican Plateau (e.g., *Canthon (Glaphyrocanton) viridis* species group) (Halffter 1962; Rivera-Cervantes & Halffter 1999), so it is not surprising at all to find *L. villosella* in the Sierra Madre Occidental, and it might be possible to find it even further.

Considering that *Lamoana*, with a distribution in central and southern Mexico, has the greatest morphological similarity with *Moroniella*, an eminently Central American genus with presence in the south of Mexico, both would form a lineage that adjusts to the Typical Neotropical Distribution Pattern of medium penetration into Mexico, restricted by ecological conditions in lowland tropical forests (Halffter & Morrone 2017). Other Mesoamerican genera with anthophagous habits such as *Pachystethus*, *Epectinaspis*, and *Callirhinus* also conform to this pattern, with possible Pantropical affinity (Ramírez-Ponce & Morón 2012; Ramírez-Ponce 2015).

The only two classical works that gave clear reasons to make nomenclatural changes in the taxon were those of Bates (1888) and Casey (1915). Bates thought that the tibiae and tarsus were too broad for *L. villosella* to be placed in *Phyllopertha*, and the latter made his decision based on a more detailed series of characters like body form, cover and punctuation, striae configuration, pygidium and protarsal claws to propose the genus *Lamoana*. In the most recent work, Ramírez-Ponce (2012) considered this species as a *Strigoderma* due to characters such as the thickened and reduced protarsus, and the reduction of both the intercoxal space and the elytra. However, with morphological revision and genitalia comparison of the Mexican species of *Strigoderma*, it has been possible to establish morphological correspondences and homologies in genital configuration, so the special condition of the perpendicular and dorsoventrally depressed parameres and other external characters are not present in species of *Strigoderma*, nor in *Epectinaspis* nor *Balanogonia*, as already indicated by Paucar-Cabrera (2003).

Analysis of the structure of the genitalia was fundamental to this revision. It allowed us to reconsider the validity of *Lamoana* as an independent entity at generic level, and to separate the unusual species *L. villosella* from the genera in which it was previously placed. The position of the parameres relative to the tectum is very similar to that presented by *Moroniella*, *Callirhinus* and *Mazahuapertha*. On the other hand, observations of the general habitus (Table 1) demonstrated clear differences of sufficient constancy to revalidate the genus with new morphological criteria based on never previously described characters of the median lobe.

The utility of a comparative analysis of the male genitalia for the characterization of supraspecific taxa has been demonstrated in various works (Matthews 1974; Morón 1986; Nguyen-Phung & Cambefort 1987; López-Guerrero 2005). It is also important in phylogenetic studies (Zunino & Halffter 1988; D'Hotman & Scholtz 1990b; Montreuil 1998; Tarasov & Solodovnikov 2011). However, there is a marked tradition in the study of comparative genital morphology in Scarabaeinae, but much less analysis in phytophagous groups, which highlights the relevance of the current contribution.

The similarity and complexity in the morphological expression of the genitalia, not only in the perpendicular arrangement of the parameres, but also in their constant general configuration characterized by subtriangular and dorsoventrally compressed parameres, an apically exposed, highly sclerotized, triangular median lobe, reinforce its homologous condition (*sensu* De Pinna 1991); the topology of each element present, special similarity and function provide independent evidence of their common inheritance (Remane 1952; Agnarsson & Coddington 2008).

Acknowledgments

This work was supported by UNAM-PAPIIT (Universidad Nacional Autónoma de México-Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica) <IN208121>. We want to acknowledge all the institutions and the owners of private collections that lend us key material so we could develop our study. ARP thanks Olivier Montreuil, Antoine Mantilleri (Muséum national d'histoire naturelle, Paris), Johannes Frisch and Bernd Jaeger (Museum für Naturkunde, Berlin), Gloria Morón (MXAL, Mexico), and Cristina Mayorga (CNIN, Mexico) for their hospitality, technical support in academic stays, and the loan of specimens. The support of Roberto Arce (INECOL) is gratefully acknowledged for the processing of museum samples.

References

- Agnarsson I. & Coddington J. 2008. Quantitative tests of primary homology. *Cladistics* 24: 51–61. <https://doi.org/10.1111/j.1096-0031.2007.00168.x>
- Bader A. 1992. A review of the North and Central American *Strigoderma* (Coleoptera: Scarabaeidae). *Transactions of the American Entomological Society* 118 (2): 269–335.
- Bates H.W. 1888. Pectinicornia and Lamellicornia, family Rutelidae. *In*: Godman F.D. & Salvin O. (eds) *Biologia Centrali-Americana. Insecta Coleoptera, Vol. II, Part 2*: 216–413. Taylor and Francis, London. <https://doi.org/10.5962/bhl.title.730>
- Blackwelder R. 1944. *Checklist of the Coleopterous Insects of Mexico, Central America, The West Indies, and South America, Part 2*. Smithsonian University, United States National Museum. <https://doi.org/10.5479/si.03629236.185.2>
- Blanchard É. 1851. *Catalogue de la Collection Entomologique du Muséum d'Histoire naturelle de Paris. Classe des Insectes. Ordre des Coléoptères. Tome 2*. Gide et Baudry, Paris.
- Casey T.L. 1915. A review of the American species of Rutelinae, Dynastinae and Cetoniinae. *Memoirs on the Coleoptera* 6: 1460. <https://doi.org/10.5962/bhl.title.15993>

- De Pinna M. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7 (4): 367–394. <https://doi.org/10.1111/j.1096-0031.1991.tb00045.x>
- D’Hotman D. & Scholtz C.H. 1990a. Phylogenetic significance of the structure of the external male genitalia in Scarabaeoidea. *Entomology Memoirs* 77: 1–51.
- D’Hotman D. & Scholtz C.H. 1990b. Comparative morphology of the male genitalia of derived groups of Scarabaeoidea (Coleoptera). *Elytron* 4: 3–39.
- Dinerstein E., Olson D.M., Graham D.J., Webster A.L., Primm S.A., Bookbinder M.P. & Ledec G. (eds). 1995. *A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean*. The World Bank. <https://doi.org/10.1596/0-8213-3295-3>
- Filippini V., Galante E. & Micó E. 2015. The genus *Callistethus* (Coleoptera: Scarabaeidae: Rutelinae) in the Neotropics: new data and new species from Costa Rica. *Arthropod Systematics & Phylogeny* 73 (2): 199–238. <https://doi.org/10.3897/asp.73.e31796>
- Gravina M.F., Bonifazi A., Del Pasqua M., Giampaolletti J., Lezzi M., Ventura D. & Giangrande A. 2020. Perception of changes in marine benthic habitats: the relevance of taxonomic and ecology memory. *Diversity* 12 (12): 480. <https://doi.org/10.3390/d12120480>
- Halffter G. 1962. Explicación preliminar de la distribución geográfica de los Scarabaeidae mexicanos. *Acta zoológica mexicana* 5 (4): 1–17.
- Halffter G. 1976. Distribución de los insectos en la Zona de Transición Mexicana: relaciones con la fauna de Norteamérica. *Folia entomológica mexicana* 35: 1–64.
- Halffter G. 2017. La zona de transición mexicana y la megadiversidad de México: del marco histórico a la riqueza actual. *Dugesiana* 24 (2): 77–89. <https://doi.org/10.32870/dugesiana.v24i2.6572>
- Halffter G. & Morrone J.J. 2017. An analytical review of Halffter’s Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. *Zootaxa* 4226 (1): 1–46. <https://doi.org/10.11646/zootaxa.4226.1.1>
- Jameson M.L., Paucar-Cabrera A. & Solís A. 2003. Synopsis of the New World genera of Anomalini (Coleoptera: Scarabaeidae: Rutelinae) and description of a new genus from Costa Rica and Nicaragua. *Annals of the Entomological Society of America* 96 (4): 415–432. [https://doi.org/10.1603/0013-8746\(2003\)096\[0415:SOTNWG\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2003)096[0415:SOTNWG]2.0.CO;2)
- Jameson M.L., Micó E. & Galante E. 2007. Evolution and phylogeny of the scarab subtribe Anisopliina (Coleoptera: Scarabaeidae: Rutelinae: Anomalini). *Systematic Entomology* 32 (3): 429–449. <https://doi.org/10.1111/j.1365-3113.2006.00380.x>
- Katbeh-Bader A. 2000. Description of two new species of *Strigoderma* from Central America (Coleoptera, Rutelidae). *Fragmenta Entomologica* 32 (2): 293–296.
- López-Guerrero I. 2005. Los *Dichotomius* de la fauna de México. *Boletín de la Sociedad Entomológica Aragonesa* 36: 195–209.
- Machatschke J. 1957. Coleoptera Lamellicornia, Fam. Scarabaeidae Subfam. Rutelinae, Tribus Anomalini, Pars 2. *Genera Insectorum* Fasc. 199B: 1–219.
- Machatschke J. 1972–1974. Scarabaeoidea: Melolonthidae, Rutelinae. *Coleopterorum Catalogus Supplementa* 66: 363–429.
- Matthews E.G. 1974. A revision of the Scarabaeine dung beetles of Australia II. Tribe Scarabaeini. *Australian Journal of Zoology* 24: 1–211. <https://doi.org/10.1071/AJZS024>

- Micó E. & Galante E. 2005. Larva morphology and biology of some European Anomalini (Coleoptera: Scarabaeoidea: Rutelinae: Anomalinae). A phyogenetical approach. *Insect Systematics & Evolution* 36 (2): 183–198. <https://doi.org/10.1163/187631205788838519>
- Micó E., Gómez B. & Galante E. 2006. The Mesoamerican genus *Yaaxkumukia*: biogeography and descriptions of new species (Coleoptera: Rutelidae). *Annals of the Entomological Society of America* 99 (1): 1–6. [https://doi.org/10.1603/0013-8746\(2006\)099\[0001:TMGYBA\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2006)099[0001:TMGYBA]2.0.CO;2)
- Montreuil O. 1998. Analyse phylogénétique et paraphylie des Coprini et di Dichotomiini (Coleoptera: Scarabaeidae). Scénario biogéographique. *Annales de la Société entomologique de France (N.S.)* 34 (2): 135–148. <https://doi.org/10.1080/21686351.1998.12277767>
- Morón M.A. 1986. *El Género Phyllophaga en México. Morfología, Distribución y Sistemática Supraespecífica (Insecta: Coleoptera)*. Publ. 20, Instituto de Ecología, A.C., México.
- Morón M.A. & Howden H.F. 2001. New species in the genus *Dilophochila* Bates (Coleoptera: Melolonthidae: Rutelinae: Anomalini). *The Coleopterists Bulletin* 55: 51–64. [https://doi.org/10.1649/0010-065X\(2001\)055\[0051:NSITGD\]2.0.CO;2](https://doi.org/10.1649/0010-065X(2001)055[0051:NSITGD]2.0.CO;2)
- Morón M.A. & Nogueira G. 1998. Adiciones y actualizaciones en los Anomalini (Coleoptera: Melolonthidae: Rutelinae) de la zona de transición mexicana (I). *Folia entomológica mexicana* 103: 14–54.
- Morón M.A. & Nogueira G. 2002. Adiciones y actualizaciones en los Anomalini (Coleoptera: Melolonthidae: Rutelinae) de la zona de transición mexicana (II). *Folia entomológica mexicana* 41 (1): 31–56.
- Morón M.A. & Ramírez-Ponce A. 2012. Mesoamerican genera of Anomalini (Coleoptera: Melolonthidae: Rutelinae): a brief review. *Trends in Entomology* 8: 97–114.
- Morón M.A., Ratcliffe B.C. & Deloya C. 1997. Atlas de los escarabajos de México. Coleoptera: Lamellicornia. Vol. I Familia Melolonthidae. *The Coleopterists Bulletin* 55 (1): 51–64.
- Morrone J.J. 2015. Biogeographical regionalization of the Andean region. *Zootaxa* 3936 (2): 207–236. <https://doi.org/10.11646/zootaxa.3936.2.3>
- Morrone J.J. 2019. Regionalización biogeográfica y evolución biótica de México: encrucijada de la biodiversidad del Nuevo Mundo. *Revista mexicana de Biodiversidad* 90: 1–86. <https://doi.org/10.22201/ib.20078706e.2019.90.2980>
- Morrone J.J., Escalante T. & Rodríguez-Tapia G. 2017. Mexican biogeographic provinces: map and shapefiles. *Zootaxa* 4277 (2): 277–279. <https://doi.org/10.11646/zootaxa.4277.2.8>
- Nguyen-Phung T. & Cambefort Y. 1987. Révision des espèces afrotropicales du genre *Copris* Müller, 1764. II. Le groupe *jacchus* (Fabricius) (Coleoptera Scarabaeidae s. str.). *Annales de la Société entomologique de France* 23 (1): 67–75. <https://doi.org/10.1080/21686351.1987.12278809>
- Nonfried A.F. 1893. Monographische Beiträge zur Käferfauna von Central-Amerika. I. Rutelidae: *Epectinaspis* und *Strigoderma*. *Berliner entomologische Zeitschrift* 38: 279–297. <https://doi.org/10.1002/mmnd.18940380304>
- Ohaus F. 1897. Beiträge zur Kenntniss der Ruteliden. I. Die Gattung *Popillia* Serv. und ihre nächsten Verwandten. *Entomologische Zeitung* 58: 341–440. Available from <https://www.biodiversitylibrary.org/page/9009146> [accessed 28 Nov. 2023].
- Ohaus F. 1902. Beiträge zur Kenntnis der Ruteliden. *Entomologische Zeitung* 63: 3–57. Available from <https://www.biodiversitylibrary.org/page/33379663> [accessed 28 Nov. 2023].

- Ohaus F. 1918. Scarabaeidae: Euchirinae, Phaenomerinae, Rutelinae. *In*: Junk W. & Schenkling S. (eds) *Coleopterorum Catalogus* 66: 1–241.
Available from <https://www.biodiversitylibrary.org/page/10439622> [accessed 23 Oct. 2023].
- Ohaus F. 1934. Coleoptera Lamellicornia, Familia Scarabaeidae, Subfamilia Rutelinae. *In*: Wytzman P. (ed.) *Genera Insectorum* 199A: 1–172.
Available from <https://www.biodiversitylibrary.org/page/53209785> [accessed 23 Oct. 2023].
- Pardo-Lorcano L.C., Yepes F. & Posada-Flórez F.J. 2017. Morfología larval e importancia agronómica de tres especies de Anomalini colombianos (Coleoptera: Scarabaeoidea), con una clave para larvas de especies americanas. *Boletín del Museo de Entomología de la Universidad del Valle* 17 (2): 1–15.
- Paucar-Cabrera A. 2003. Systematics and phylogeny of the genus *Epectinaspis* Blanchard (Coleoptera: Scarabaeidae: Rutelinae) and description of a new genus of Anomalini of Mexico. *Coleopterists Society Monograph* 2: 3–60. [https://doi.org/10.1649/0010-065X\(2003\)57\[3:SAPOTG\]2.0.CO;2](https://doi.org/10.1649/0010-065X(2003)57[3:SAPOTG]2.0.CO;2)
- Potts W. 1977. Revision of the Scarabaeidae: Anomalinae 2. An annotated checklist of *Anomala* for the United States and Canada. *The Pan-Pacific Entomologist* 53: 34–42.
- Ramírez-Ponce A. 2012. *Sistemática Supraespecífica del Género Paranomala Casey en el Norte y Centroamérica (Coleoptera: Melolonthidae: Rutelinae: Anomalini)*. PhD thesis, Universidad Nacional Autónoma de México, D.F.
- Ramírez-Ponce A. 2015. *Moroniella*, un nuevo género americano de Anomalini (Coleoptera: Melolonthidae). *Dugesiana* 22 (2): 261–266. <https://doi.org/10.32870/dugesiana.v22i2.4742>
- Ramírez-Ponce A. & Curoe D. 2014. Description of two new species in the genera *Epectinaspis* Blanchard and *Strigoderma* Burmeister (Coleoptera: Scarabaeidae: Rutelinae: Anomalini). *Zootaxa* 3287 (1): 87–94. <https://doi.org/10.11646/zootaxa.3287.1.8>
- Ramírez-Ponce A. & Morón M.A. 2009. Relaciones filogenéticas del género *Anomala* (Coleoptera: Melolonthidae: Rutelinae). *Revista mexicana de Biodiversidad* 80: 357–394.
<https://doi.org/10.22201/ib.20078706e.2009.002.610>
- Ramírez-Ponce A. & Morón M.A. 2012. Revision of the genus *Pachystethus* Blanchard with description of three new species from Mexico (Coleoptera: Scarabaeidae: Rutelinae: Anomalini). *Zootaxa* 3394 (1): 1–24. <https://doi.org/10.11646/zootaxa.3394.1.1>
- Remane A. 1952. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Geest und Portig, Leipzig.
- Rivera-Cervantes L.E.R. & Halffter G. 1999. Monografía de las especies mexicanas de *Canthon* del subgénero *Glaphyrocantón* (Coleoptera: Scarabaeidae: Scarabaeinae). *Acta zoológica mexicana* 77: 23–150. <https://doi.org/10.21829/azm.1999.77771693>
- Tarasov S.I. & Solodovnikov A.Y. 2011. Phylogenetic analyses reveal reliable morphological markers to classify mega-diversity in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Cladistics* 27: 1–39. <https://doi.org/10.1111/j.1096-0031.2011.00351.x>
- Uliana M. & Sabatinelli G. 2017. *Araboplia lorisi* new genus and species of Rutelinae from Saudi Arabia (Coleoptera, Scarabaeidae), with comments on the subtribe Popilliina. *European Journal of Taxonomy* 373: 1–12. <https://doi.org/10.5852/ejt.2017.373>
- Wheeler Q.D. & Platnick N.I. 2000. The phylogenetic species concept (sensu Wheeler and Platnick). *In*: Wheeler Q.D. & Meier R. (eds) *Species Concepts and Phylogenetic Theory: A Debate*: 55–69. Columbia University Press, New York, NY.

Zunino M. & Halffter G. 1988. Análisis taxonómico, ecológico y biogeográfico de un grupo americano de *Onthophagus*. *Museo Regionale di Scienze Naturale Torino. Monografia* 9: 1–211.

Manuscript received: 24 January 2023

Manuscript accepted: 6 July 2023

Published on: 13 December 2023

Topic editor: Tony Robillard

Section editor: Max Barclay

Desk editor: Pepe Fernández

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic.