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.

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**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 chafer, taxonomic revalidation.

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**Introduction**

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

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 Strigiderma), 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 Strigiderma (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 Strigiderma, 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 *Mazahuapertha* (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 *Mazahuapertha*, 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
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.](image)

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 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

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

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<tbody>
<tr>
<td>Dorsal vestiture</td>
<td>Abundant short setae on head, pronotum and elytra</td>
<td>Moderately abundant long setae in front and pronotum</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Antennal club respect to scape, pedicel and funicle together</td>
<td>Slightly longer</td>
<td>Much longer</td>
<td>Subequal</td>
<td>Subequal</td>
<td>Slightly shorter</td>
</tr>
<tr>
<td>Clypeus</td>
<td>Semi-oval, slightly reflexed</td>
<td>Semicircular, reflexed</td>
<td>Subtriangular, reflexed</td>
<td>Subtrapezoidal, reflexed</td>
<td>Subtrapezoidal, slightly reflexed</td>
</tr>
<tr>
<td>Pronotum posterior margin</td>
<td>Incomplete</td>
<td>Complete</td>
<td>Complete</td>
<td>Absent</td>
<td>Complete</td>
</tr>
<tr>
<td>Apex of elytral suture</td>
<td>Spiniform</td>
<td>Rounded</td>
<td>Spiniform</td>
<td>Spiniform</td>
<td>Spiniform</td>
</tr>
<tr>
<td>Mesepimeras</td>
<td>Slightly ascending</td>
<td>Not ascending</td>
<td>Ascending</td>
<td>Slightly ascending</td>
<td>Ascending</td>
</tr>
<tr>
<td>Intermesocoxal space</td>
<td>Very wide</td>
<td>Narrow</td>
<td>Wide</td>
<td>Wide</td>
<td>Wide</td>
</tr>
<tr>
<td>Protibia</td>
<td>Wide</td>
<td>Slender</td>
<td>Wide</td>
<td>Wide</td>
<td>Wide</td>
</tr>
<tr>
<td>Protibial spur</td>
<td>Present</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td>Protibial internal claw</td>
<td>Highly cleft</td>
<td>Poorly cleft</td>
<td>Highly cleft</td>
<td>Highly cleft</td>
<td>Highly cleft</td>
</tr>
<tr>
<td>Protarsomeres 1–4</td>
<td>Wide, very short, subequal to each other and in length as the fifth</td>
<td>Thin, short, subequal to each other and longer than the fifth</td>
<td>Wide, subequal to each other and in length as the fifth</td>
<td>Wide, very short, subequal to each other and in length as the fifth</td>
<td>Thin, progressively shorter and longer than the fifth</td>
</tr>
<tr>
<td>Parameres vestiture</td>
<td>Abundant, dorsoventrally</td>
<td>Absent</td>
<td>Scarce, dorsoventrally</td>
<td>Sparse dorsally and abundant ventrally</td>
<td>Scarce, ventrally</td>
</tr>
</tbody>
</table>
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


**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 semi oval, 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.

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

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

MESOSTERNUM. Intercoccal 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.

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.


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 ♂;


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

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 semi-oval, anterior border moderately reflexed; hairy surface, setae of moderate thickness and length; rugose punctuated texture, homogeneous, broad, and deep punctuation; 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

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**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.

**Mesoroma.** 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 Ramirez-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 punctuation; 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 tropical coastline 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* (*Glaphyrocanthon*) *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).

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**References**


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