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A review of New World *Malaxa* (Hemiptera: Fulgoroidea: Delphacidae)

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Abstract

The New World species attributed to the genus *Malaxa* Melichar (Hemiptera: Fulgoroidea: Delphacidae) are reviewed with special reference to the type species *Malaxa acutipennis* from the Philippines. We provide an amended diagnosis for *Malaxa acutipennis* contrasted with the genus delineation presented for Chinese *Malaxa*, most recently by Hou *et al.* (2013). We find *Malaxa* to be an Old World genus and segregate New World species into two new genera, *Lamaxa* and *Xalama*, diagnosed most readily by proportions of the antennae and features of the terminalia. Both *Lamaxa* and *Xalama* are uncommonly encountered. *Lamaxa* is distributed widely through the Neotropics, whereas *Xalama* is heretofore known only from Bolivia and Peru.

Key words: Delphacidae, Auchenorrhyncha, Tropidocephalini, planthopper, new genus

Introduction

The genus *Malaxa* Melichar, 1914 (Hemiptera: Auchenorrhyncha: Fulgoroidea: Delphacidae), as currently composed, includes 3 Neotropical species and 9 Paleotropical (Indomalayan) species. The history, nomenclature, and composition of the genus have been recently reviewed, including keys and descriptions for the species of China (Chen *et al.* 2006, Hou *et al.* 2013). These works provide guidance to the species within China, but apparently did not consider species outside that region (beyond annotating known distribution and plant associations, reported previously by, e.g., Metcalf 1943). The type species of *Malaxa—M. acutipennis* Melichar, 1914—is from the Philippines and was not explicitly considered in the context of the amended genus-descriptions for Chinese *Malaxa*, and therefore the amended descriptions may not reliably represent the features of the type species.

Malaxa falls within the tribe Tropidocephalini in the subfamily Delphacinae. The Tropidocephalini consists of approximately 35 genera and 179 species widely distributed throughout the Palaearctic, Afrotropical, Indomalayan, Australian, Neotropical, and Pacific Regions, but is most diverse in the Indomalayan Region (Chen & Tsai 2009, Ren *et al.* 2014, Huang *et al.* 2017, Bourgoin 2017). New World Tropidocephalini was reviewed by Bartlett (2009) including a key to genus and a review of reported plant associations. New World Tropidocephalini consist of 5 genera and 20 species, all reported from the South American Neotropics. Bartlett (2009) asserted that the apparent paucity of species diversity in New World Tropidocephalini (compared to that of the Old World) may result from inadequate taxonomic attention, and that there were many undescribed species similar to the heterogenous genus *Columbisoga* Muir. Bartlett & Kunz (2015) noted that 3 undescribed Tropidocephalini were found in Costa Rica, which was the first published report of Neotropical Tropidocephalini outside of South America. *Malaxa* is uncommonly encountered, but is easily diagnosed among New World Tropidocephalini as the only genus with very long antennae (reaching apex of mesonotum; segment I several times longer than wide).

The phylogenetic work of Huang *et al.* (2017), obtained from a maximum likelihood analysis of 4 genes (cox1, cytb, 16S rDNA, and 28S rDNA), places *Malaxa* (using the Chinese *Malaxa semifusca* Yang & Yang) sister to *Lauriana* Ren & Qin, with both in turn sister to a clade of *Malaxella* Ding & Hu, *Specinervures* Kuoh & Ding, and *Bambusiphaga maculata* Chen & Li (which had failed to group with 8 other *Bambusiphaga* Huang & Ding species). Superficial similarities between *Lauriana* and *Malaxa* appear to recommend this proposed relationship.

There were no New World taxa included in these analyses and the relationships among Old and New World Tropidocephalini remain entirely unexplored. This same work placed the split between Saccharosydnini and Tropidocephalini at 82 MYA and estimates the origin of *Malaxa* at about 48 MYA. These results, at minimum, suggest that dispersal (rather than vicariance) would need to be invoked to support a close relationship between Old and New World species of *Malaxa*.

The features of Tropidocephalini were reviewed by Bartlett (2009) following Asche (1990), and the tribe is diagnosed by a thickened calcar, which is concave on the inner surface, and lacking teeth on the trailing margin, as found on most other advanced Delphacidae. The central 'sperm-conducting tube' of the membranous aedeagus is within a sclerotized theca (forming a phallotheca, although it is usually less accurately called the aedeagus in descriptive taxonomy). The phallotheca and anal segment are in close functional contact (in contrast to the Delphacini), with the base of the phallotheca mostly integrated into the ventral side of the anal segment. The base of the phallotheca is usually asymmetrically twisted and often bears a slender process from the base (Asche 1990, Bartlett 2009) that is rarely found in Delphacini (with few exceptions, such as *Abbrosoga* Caldwell).

Most Tropidocephalini with reported plant associations feed on bamboo (reported as 78% by Wilson *et al.* 1994), with all the remaining associated with other grasses (e.g., Wilson *et al.* 1994, Chen 2003, Chen & Tsai 2009, Qin & Zhang 2010). Exceptions to bamboo feeding include species of *Tropidocephala* Stål on *Andropogon* L. (e.g., Nickel 2003), *Jassidaeus lugubris* (Signoret) on *Festuca* L. (Asche & Hoch 1982, Wilson *et al.* 1994), and interestingly, *Columbisoga* Muir (3 species), *Macrocorupha gynerii* Muir, and *Malaxa occidentalis* Muir (from the New World) on *Gynerium* P. Beauvois (Poaceae: Panicoideae: Gynerieae; e.g., Soreng *et al.* 2015). *Gynerium* P. Beauvois, known as (e.g.) caña brava, giant reed, or wildcane, as currently understood, consists of a single species, *G sagittatum* (Aublet) P. Beauvois, distributed from the Caribbean and southern Mexico to tropical Argentina (Sánchez-Ken & Clark 2001). The species is a reed-like grass, and among the tallest grasses, excluding woody bamboos, reaching 10-15 m in height (Sánchez-Ken & Clark 2001), and is a pioneer species of floodplain forests along whitewater rivers with rapid channel migration rates (Kalliola *et al.* 1992). While *Gynerium* is not phylogenetically close to the bamboos (e.g., Soreng *et al.* 2015), it is physiognomically similar, and if *Gynerium* is a correctly reported plant association, its distribution hints that *Malaxa* (and the Tropidocephalini) may be more widely distributed in the New World than hitherto reported.

Here, we review the New World species of *Malaxa*, in comparison to the type species (*Malaxa acutipennis*) with reference to the amended genus diagnosis as presented by Hou *et al.* (2013). This work was initiated to reassess the genus-level standing of New World *Malaxa*, questioned by Bartlett (2009), and to assess the species-level standing of *Malaxa* specimens extracted from various collections among undetermined Neotropical Tropidocephalini.

Materials and methods

All available *Malaxa* specimens were examined, with emphasis on the New World, from available collections, including specimens extracted from unsorted material, and online photographs (e.g., from the Dept. of Biology, National Museum of Natural Science (NMNS), Taichung, Taiwan and National Chung Hsing University NCHU Museum of Entomology, Taichung City, Taiwan). Examined specimens were provided with 2D barcode labels and data captured using "Arthropod Easy Data Capture" (Schuh *et al.* 2010, Schuh 2012, Arthropod Easy Capture 2013) in the NSF-sponsored "Tri-Trophic Thematic Collection Network" (http://tcn.amnh.org/). These data are visualized at Discover Life (www.discoverlife.org) and are available via the iDigBio (www.idigbio.org) specimen portal. Planthopper nomenclature follows Bartlett *et al.* (2014), except forewing venation following Bourgoin *et al.* (2015). We have interpreted the Sc+RA and MP longitudinal veins to originate near the leading margin of the basal cell, whereas CuA originates from the trailing margin. Examined specimens were deposited in the following collections:

BPBM—Bernice P. Bishop Museum, J. Linsley Gressitt Center for Research in Entomology, Honolulu, HI; INHS—Illinois Natural History Survey, University of Illinois, Champaign, IL;

LBOB—Lois O'Brien collection (LBOB, Green Valley, Arizona; affiliated with the University of Arizona); NCSU—North Carolina State University, Department of Entomology, Raleigh, NC;

TAMU—Texas A & M University, College Station, TX; UDCC—University of Delaware, Dept. of Entomology and Wildlife Ecology, Newark, DE; UKIC—University of Kentucky, Department of Entomology, Lexington, KY; USNM—Smithsonian Institution, National Museum of Natural History, Washington, D.C.

In the descriptions, we have utilized the same features, in a similar sequence and with the same measurements, as those used by Hou *et al.* (2013). For clarity, we specify that the body length measurement included in genus- and species-level descriptions extends (in dorsal view) from the distal apex of the head to the tip of the tegmina. All ratios are calculated from measurements taken from the same specimen. In the descriptions, "genitalia" should be understood to include the terminal abdominal segments. Label data were recorded for all included specimens. For primary types, labels were quoted verbatim using "/" to indicate a line break and "//" to indicate a new label and with supplemental information given in brackets. For other material examined, label data were rewritten to maintain consistency in pattern, beginning with the country, state or province, and more specific locality, followed by the collection date, collector, and lastly the number, sex of specimens, and specimen depository given in parentheses. Abbreviations in label data were expanded for clarity, except when their meaning was unclear. The distribution map was created using SimpleMappr (Shorthouse 2010).

Photographs and measurements were taken using a digital imagery system consisting of a Nikon SMZ1500 microscope, Nikon Digital Sight DS-U1 camera and NIS Elements Imaging software (version 3.0). Line art was digitally traced from photographs. All measurements are in millimeters (mm).

Results

We found substantive differences among the New and Old World *Malaxa* species, detailed below, and segregate the New World species into two new genera. We also found differences between the Chinese *Malaxa* (as described by Hou *et al.* 2013) and the type species *Malaxa acutipennis* suggesting that the composition of Old World *Malaxa* may require reconsideration. Diagnostic features distinguishing the taxa examined in this work are presented below, and the following keys are provided to summarize these features.

Key to genus for Malaxa and related groups examined in this work (males)

1.	Forewings apically pointed (Figs. 2, 35), arched on leading margin (giving wings a spatulate appearance); anal tube of male simple (not bearing processes; Fig. 5) and opening of male pygofer without processes; recorded from Philippines
1'-	Forewings apically rounded (Figs. 36–37), leading margin straight; anal tube of male either simple (e.g., Fig. 14) or with 1–2
	processes; opening of pygofer with processes of varying sorts (e.g., Figs. 13, 25, 27) 2
2.	Anal tube with 1–2 processes; opening of pygofer usually bearing two broad lamellate medioventral processes, between them
	a V-like emargination; recorded from China
2'-	Anal tube simple (Fig. 14); opening of pygofer either with a small midventral forked process (Figs. 13, 25, 41), or a broad,
	scoop-like projection plus a pair of lateral teeth (Fig. 27); Neotropical
3.	Antennae very long (exceeding mesonotum), segment I several times as long as broad (Figs. 10, 12); pygofer bearing a mid-
	ventral forked process (Figs. 13, 25, 41); aedeagus caudally directed bearing poorly sclerotized terminal process (Figs. 26, 38);
	hind leg spinulation 5-7-5 or 5-6-5 Lamaxa n. g.
3'-	Antennae shorter, not exceeding mesonotum, segment I about 2x as long as wide and approximately 1/3 length of segment II
	(Figs. 19–20); pygofer opening with broad, median scoop-like projection and pair of rounded lateral teeth (Fig. 27); aedeagus
	robust and strongly downcurved (Figs. 28, 39); hind leg spinulation 5-6-4

Key to Genera of New World Tropidocephalini (revised from Bartlett 2009).

1	Body strongly dorsoventrally flattened (Fig. 34); frons rather square, median carinae of frons forked ventrally near lower mar-
	gin of eyes (Fig. 35) Procidelphax Bartlett
-	Body not flattened (e.g., Fig. 16), frons rectangular, median carinae not forked (e.g., Fig. 17), except dorsally near fastigium in
	some species
r	Vortey much (as 1.5x) longer than broad rounded enteriorly in dersel view (Fig. 20); modion carine of vertey unbroached

2 Vertex much (ca. 1.5x) longer than broad, rounded anteriorly in dorsal view (Fig. 30); median carina of vertex unbranched...

	<i>Macrocorupha</i> Muir
-	Vertex shorter (Figs. 31–32), more truncate anteriorly; median carina of vertex variable
3	Antennae very long (Figs. 10, 12), exceeding posterior margin of mesothorax; both segments long (much longer than wide)
	with segment I nearly ½ length segment II
-	Antennae not as long (Figs 19-20), not exceeding mesothorax; generally segment I somewhat longer than wide and 1/3 or less
	length of II 4
4	Lateral carinae of pronotum reaching hind margin (Fig. 31); the Y-carina of vertex not distinct, sometimes forming a rounded
	areolet at apex of the median carina; anal tube with or without processes (a heterogeneous taxon, often strongly marked on
	body and wings) Columbisoga Muir
-	Lateral carinae of pronotum not attaining hind margin (Fig. 32); the Y-carinae of vertex distinct, rounded areolet not present;
	anal tube without processes
5	Wings clear and unmarked (except fuscous at wing base in C. caresi); head and body uniformly colored (Fig. 32); ventral mar-
	gin of pygofer with broad forked process (also with a pair of lateral projections in the type species C. lloydi); aedeagus cau-
	dally directed or somewhat twisted, not strongly curved ventrad Columbiana Muir
-	Wings clear, strongly marked with fuscous (Fig. 21); body dark, marked with pale (especially on head; Fig. 23); ventral margin
	of pygofer with broad scoop-like projection (not apically forked; Fig. 27) and a pair of lateral teeth; aedeagus strongly down-
	curved

Descriptive taxonomy

Genus Malaxa Melichar, 1914: 275

Type species. Malaxa acutipennis Melichar, 1914.

Malaxa Melichar 1914: 275; Muir 1926: 7; Metcalf 1943: 103; Fennah 1945: 429; Yang & Yang 1986: 56; Ding *et al.* 1999: 443; Chen *et al.* 2006: 160; Ding 2006: 150; Bartlett 2009: 387; Hou *et al.* 2013: 864.

Diagnosis. Description from Hou et al. (2013: 286–287, with comments in square brackets) "Body slender and elongate, length (from apex of vertex [~coryphe] to tip of tegmina): male 3.7–4.8 mm, female 4.3–5.1 mm, often with blackish brown markings. Head with eyes narrower than pronotum. Vertex longer or slightly shorter in middle than broad at base (0.95–1.24: 1), apex projected in front of eyes. Submedian carinae uniting before apex, greatest length of basal compartment shorter than wide at base of vertex (0.48–0.81: 1). Frons [~metope] relatively long, longer in middle line than wide at widest part (about 2.73-3.00: 1), widest at middle or apex. Rostrum reaching mesothoracic trochanters. Antennae cylindrical, very long, surpassing apex of clypeus, basal segment longer in middle than wide at apex (3.67–5.22: 1), shorter than from in middle line (0.49–0.74: 1), shorter than second segment (0.40–0.56: 1). Pronotum shorter than vertex in middle line (0.58–0.96: 1), lateral carinae attaining hind margin. Mesonotum longer in middle line than vertex and pronotum together (1.33–2.05: 1). Tegmina elongate, longer in middle line than wide at widest part (1.76–3.16: 1), much longer than abdomen, hyaline, cross vein deposited medially, apical margin acutely rounded. Spinal formula of hind tibia 5-6-4. Post-tibial spur large and thick, concave on inner surface, without teeth along the hind margin, with an apical tooth. Anal segment of male short, ring-like, left lateroapical angle produced into process. Pygofer with two broad lamellate medioventral processes, between of them with a V-like emargination. Genital styles broad in basal half, forked or with process at apex. Aedeagus with or without phallobase, phallus tubular, curved C-like and directed segmental venter."

Etymology. Melichar (1914) provided no indication of the derivation of the genus name *Malaxa*. Its derivation could be from a geographical locality (e.g., the village or landform on Crete), from a surname (e.g., of the Romanian engineer Nicolae Malaxa), from an arbitrary combination of letters or from some other source; but none of those can obviously be recommended as the derivation of the name. We suggest that *Malaxa* be treated as an arbitrary combination of letters that is feminine in gender because of past usage and the name termination (-*a*).

Malaxa acutipennis Melichar, 1914

(Figures 1-6)

Type locality. Luzon, Laguna, Los Baños.

Amended Diagnosis. *Color*. Body color generally stramineous, thorax and abdomen darker in lateral compartments. *Structure*. Body length female 3.96 mm (3.81–4.10 mm, n=3; males dissected and not available for

measurement). Head including eyes narrower than pronotum (in dorsal view; Fig. 1), with vertex projecting slightly in front of eyes, narrowing distally, vertex length subequal to width at base. Submedian carinae distinct, uniting before fastigium, median carinae obscure. Frons long, parallel-sided, widest just before frontoclypeal suture (width of frons dorsally and at frontoclypeal suture equal; Fig. 4); 1:w ratio 3.6-4.5:1. Rostrum just reaching mesothoracic trochanters. Antennae long and cylindrical except groove on front ventral portion of segment I; long, reaching or surpassing apex of clypeus (Fig. 4), but not exceeding apex of mesothorax; antennal segment II about 2x length I (ratio I:II 0.43–0.46: 1). Pronotum length at midline nearly equal to length of vertex; all carinae (lateral and median) attaining hind margin. Mesonotum longer in middle line than vertex and pronotum together (1.41-1.82: 1). Tegmina much longer than abdomen, clear with fuscous veins; apex of forewing distinctly pointed, leading margin arced so that wing width greatest near midlength (Figs 2, 35). Nodus just preceding midlength; Sc+RP separated from MP at basal cell, fork of SC+RA from RP near nodal line; Cu fork just past midlength of clavus; PCu+1A joined in basal third of clavus. Spinulation of hind leg 5-6-4 (Fig. 3); calcar large and thick, concave on inner surface, without teeth along the hind margin, with an apical tooth. Pygofer roughly quadrate in lateral view, slightly longer ventrally than dorsally (Fig. 5). Ventral margin of pygofer opening simple. Gonostyli forceps-like, with simple, acutely-pointed apex. Aedeagus strongly downcurved and divided into four spine-like projections. Anal segment of male short, ring-like, without process.



FIGURES 1–6. *Malaxa acutipennis* (Luzon, Philippines; female, except 5); 1, habitus dorsal view; 2, habitus lateral view; 3, hind tarsus, calcar and apex of tibia (ventral view); 4, face, frontal view; 5, male terminalia, left lateral view; 6, specimen label.

Remarks. Several differences can be observed between *Malaxa acutipennis* and the Chinese species in that genus. The most salient of these are that *M. acutipennis* has an apically pointed forewing (rounded in all other *Malaxa*) with the leading margin arced (giving the wing a spatulate appearance; parallel-sided in all other *Malaxa*); the more elongate pronotum with the carinae clearly reaching the hind margin (most other *Malaxa* with a relatively

shorter pronotum with lateral carinae not reaching); and the genitalia with a simple ventral margin of the pygofer opening (vs. having projections on the opening of the pygofer); and the simple anal tube (most Chinese Malaxa bear a single, large, asymmetrical projection on the anal tube). Also, it appears that in Malaxa acutipennis, the from is widest just above the frontoclypeal margin and the first antennal segment is longitudinally grooved on the ventral portion of the front. We did not examine other non-Chinese Malaxa outside of M. acutipennis (i.e., M. javanensis Muir, M. nigra Muir, and M. obtusipennis Muir); however, Malaxa javanensis (see Muir 1919: 532, figure 3 [from Indonesia: Java]), has a large asymmetrical process on the anal tube and an acuminate midventral process on the opening of the pygofer. Malaxa nigra [Philippine Islands; Luzon], was described by Muir as having a midventral process on the pygofer and a large spine on the left side of the anal tube. Malaxa obtusipennis [Malaysia: Sabah] was described from 3 females, and so the features of the male terminalia are not available for consideration. Given our observations, it is reasonable to question the monophyly of Malaxa in the Old World, but at this time it is not clear whether the observed differences represent a sequence of autapomorphies for M. acutipennis, or alternatively that the genus-composition of Old World Malaxa requires reconsideration. However, our purpose was to contrast Malaxa from the Old World to those from the Neotropics. As presented below, we find that the Neotropical Malaxa differ from those in the Old World in a number of respects, and have here segregated them into two new genera.

Specimens examined (*Malaxa*). *Malaxa acutipennis* Melichar, 1914: Philippines, Laguna, Mt. Makiling, Luzon, Baker [no date provided] (USNM; 3 females, 2 males).

Malaxa fusca Yang & Yang, 1986: Taiwan, Nantou, Sin Shan forest road, 1 km W jct rt 66, 700 m, 23 54'39"N, 120 53'2"E, 11 June 2004, C. H. Dietrich, 07-1, vacuum (INHS; 3 females).

Malaxa sp.: Thailand, Phetchabun P[rovince], Pha hong Cave, 17.vi.1997, C. W. & L. B. O'Brien (1 female, UDCC).

Lamaxa, new genus

(Figures 7–18, 25–26, 36, 38, 40–42)

Type species. Malaxa occidentalis Muir, 1926.

Description. Color. Brownish-orange with brown and paler markings; wings clear with characteristic dark (and sometimes pale) markings. Structure. Body slender and elongate; length (from apex of vertex to tip of tegmina) males $\bar{x} = 4.97$ mm (4.71–5.33 mm, n=5); females $\bar{x} = 5.31$ mm (5.10–5.62 mm, n=6). Head much narrower than pronotum (Figs. 7, 10), carinae concolorous. Lateral carinae of clypeus, frons (~metope) and vertex (~coryphe) distinct, other carinae obscure, especially near fastigium. Frons elongate and parallel-sided, widest near frontoclypeal suture, narrowed to fastigium (Figs. 9, 12; 1:w $\overline{x} = 2.6:1$). Vertex longer than broad at base (1:w $\overline{x} =$ 1.4:1), distally narrowing and projected slightly in front of eyes; submedian carinae uniting before fastigium, basal compartments longer than wide. Rostrum reaching or exceeding metathoracic trochanters. Antennae cylindrical, both segments very long (Figs. 10, 12), surpassing apex of clypeus (and apex of mesonotum), segment I close to half length of II (ratio I:II 0.4–0.5:1), length antennal segment I \bar{x} =0.47 mm, II \bar{x} = 1.05 mm. Pronotum shorter than vertex in middle line, lateral carinae usually not attaining hind margin. Mesonotum longer in middle line than vertex and pronotum together. Wings elongate, much longer than abdomen, nodus at about 2/3 length, apex acutely rounded (Fig. 36). Spinal formula of hind leg 5-7-5 (or 5-6-5). Calcar thick, concave on inner surface, without teeth along the hind margin, with an apical tooth. Pygofer irregularly quadrilateral in lateral view (Fig. 26). In caudal view, opening carinate, with midventral forked process (Figs. 13, 25), broad lamellate medioventral processes absent. Dorsocaudal margins of pygofer expanded and inflected to partially enclose anal tube (Fig. 42), diaphragm evident, armature absent. Gonostyli broad basally, basal angles prominent, diverging and narrowed distally to apically to blunt or acute apex (Figs. 25, 40). Aedeagus elongate and tubular with large, flattened, poorly sclerotized subapical process (Figs. 14, 38; representing a flagellum?). Anal tube (anal segment) small, without processes.

Remarks. *Lamaxa* differs from *Malaxa acutipennis* in having a parallel-sided wing with a rounded apex (vs. pointed with an arched leading wing edge in *Malaxa acutipennis*); antennae are similar in proportion but nearly twice as long in *Lamaxa* than *Malaxa acutipennis* (and lacking the ventral carina on I); the genitalia of *Lamaxa*

bear a forked projection on the pygofer opening, whereas *Malaxa acutipennis* is simple; and the dorsocaudal margin of the pygofer is expanded in *Lamaxa* but not in *Malaxa*. The aedeagus of *Lamaxa* is slightly curved and caudally directed, bearing weakly sclerotized apical projections (vs. downcurved in *Malaxa acutipennis*).

Lamaxa differs from the Chinese *Malaxa* in structural proportions along with distinctive features of the male genitalia. *Lamaxa* is larger than the Chinese *Malaxa*, the vertex is more elongate, the lateral carinae of the pronotum are laterally curved, usually not reaching the hind margin, and the spinulation of the hind leg is 5-7-5 (or 5-6-5) (instead of 5-6-4). More distinctly, in *Lamaxa*, the anal tube is without processes, whereas in Chinese *Malaxa*, the anal tube bears a single (sometimes 2), large usually strongly asymmetrical process(es). In *Lamaxa*, the dorsocaudal angle of the pygofer is projected (simple in Chinese *Malaxa*), and the midventral portion of the pygofer opening bears a forked process, whereas in Chinese *Malaxa*, there are "two broad lamellate medioventral processes, between of them with a V-like emargination" (Hou *et al.* 2013: 867), although these are reduced in some species. In Chinese *Malaxa*, the aedeagus is downcurved and C-shaped, whereas in *Lamaxa* the aedeagus is slightly curved and caudally directed, bearing weakly sclerotized apical projections, missing from Chinese *Malaxa*.

Species included are *Lamaxa gracilis* (Fennah, 1945) and *Lamaxa occidentalis* (Muir, 1926). Two female specimens, probably representing additional species of *Lamaxa* were examined (listed below under 'females tentatively assigned to *Lamaxa*'). One was a specimen from Honduras that was similar to the coloration of *Lamaxa occidentalis*, except that the face (frons, genae, clypeus) were broadly black except for a strongly contrasting pale stripe above the frontoclypeal suture, also bearing more substantially embrowned wings. The second, from southern Brazil, was very pale yellowish with weakly marked wings, a dark longitudinal line along both segments of the antennae, and partially embrowned legs.

Etymology. The new genus name "*Lamaxa*" is an anagram of "*Malaxa*", and is to be understood as feminine in gender.

Lamaxa occidentalis (Muir, 1926), New combination

= Malaxa occidentalis Muir, 1926: 7. (Figures 7–14, 25–26, 36, 38)

Type locality. Napo River near Tena, Ecuador.

Amended diagnosis. Color. Brownish-orange with characteristic paler and deep brown markings (Figs. 7–12); paler on disc of pronotum, above the frontoclypeal suture, and on middle portion of antennal segment II; dark brown on dorsal portion of clypeus, distal portion of antennal segment I, proximal and apical portion of antennal segment II, pronotal paratergites [often also marked with white], dorsum or mesonontum and the ventral portion of mesopleuron (details varying intraspecifically). Wings clear, usually with white marking along PCu in clavus (often faded in older specimens) and a broad dark, transverse, crescent-shaped marking, opened proximad [sometimes inclosing whitish patch], and a narrow dark crescent opening caudally along nodal line and trailing margin of wing to near wing apex; sometimes also a dark bar from nodal line diagonally to the near wing midline; sometimes also darkened near apex of clavus; details and extent of markings varied by species and locality. Structure. Body slender and elongate; length (from apex of vertex to tip of tegmina) males $\bar{x} = 4.97$ mm (4.71–5.33 mm, n=4); females $\bar{x} = 5.31$ mm (5.10–5.62 mm, n=6). Head much narrower than pronotum (Figs. 7, 10), carinae concolorous. Lateral carinae of clypeus, frons and vertex distinct, other carinae obscure, especially near fastigium. Frons elongate and parallel-sided, widest at frontoclypeal suture, narrowed to fastigium (Figs. 9, 12; 1:w $\bar{x} = 2.6:1$, range 2.3–3.2:1, n=10). Vertex longer than broad at base (1:w \overline{x} = 1.4:1, range 1.2–1.5:1, n=10), distally narrowing and projected slightly in front of eyes; submedian carinae uniting before fastigium, basal compartments longer than wide. Rostrum reaching metathoracic coxae. Antennae cylindrical, both segments very long (Figs. 10, 12), surpassing apex of clypeus (and apex of mesonotum; Figs. 10, 12), segment I close to half length of II (ratio I:II 0.4–0.5:1), length antennal segment I \bar{x} = 0.47 mm (range 0.41–0.52, n=10), II \bar{x} = 1.05 (range 0.95–1.11, n=10) (segment I about 0.67×length of frons, II 1.49× length of frons). Pronotum shorter than vertex in middle line (0.44–0.71: 1), lateral carinae usually not attaining hind margin. Mesonotum longer in middle line than vertex and pronotum together (1.21–1.72:1). Wings elongate (\bar{x} = 4.3 mm, range 3.9–4.6, n=9), much longer than abdomen, nodus at about 2/3 length, wing apex acutely rounded (Fig. 36); apparently, Sc, RA, RP and MP unbranched, CuA 3-branched; fork of SC+RA from RP distad of fork of CuA (inner subapical cell longer than outer subapical cell);

fusion of PCu with AA in basal third of clavus. Spinulation of hind legs 5-7-5 (or 5-6-5). Pygofer irregularly quadrilateral in lateral view (Fig. 26), in caudal view opening carinate, midventrally with forked process (Figs. 13, 25, 41), dorsocaudal margins expanded and inflected to partially enclose anal tube (Fig. 42). Diaphragm of pygofer evident, armature absent. Gonostyli broad basally, basal angles prominent, diverging and narrowed distally to apically to blunt or acute apex (similar to Fig. 40). Aedeagus elongate and tubular (Figs. 14, 26, 38) with large, flattened, rather membranous subapical ventral process, with (as oriented in Figure 14) anterior teeth on margin of flattened process and elongate spine near midlength of anterior margin. Anal tube (anal segment) small, without processes.



FIGURES 7–14. *Lamaxa occidentalis* (7–9, 13–14 paratype male, Napo River, Ecuador; 10–12 La Selva Biological Station Costa Rica); 7, habitus dorsal view; 8, habitus lateral view; 9, frontal view; 10 habitus dorsal view; 11, habitus lateral view; 12, frontal view; 13, pygofer, caudal view (embedded in balsam); 14, aedeagus, connectives, gonostyli and anal tube, left lateral view (embedded in balsam).

Plant associations. Label reads "ex: Cana / silvestre", and Muir (1926) reports this as *Gynerium* sp. (Poaceae); however, the common name is also used for the exotic grasses *Arundo donax* L. or *Saccharum spontaneum* L., although we assume that Muir correctly reported the plant association.

Distribution. Bolivia, Ecuador, Colombia, Costa Rica; tentatively also Peru.

Remarks. A male paratype (barcode UDCC_TCN 00042688) examined here was evidently the reference subject for Muir's (1926) figure 6 (compare with Figure 14). The specimen has had the abdomen removed and cleared, the parts of the male terminalia disarticulated and mounted in balsam between to microscope cover slips, which in turn are inserted into a cardboard holder and pinned beneath the specimen. This technique was frequently used for specimens studied by Muir (possibly by W. Giffard).

Specimens varied noticeably in coloration, especially in the extent and intensity of the dark patterning; but no substantive genitalic differences were found among specimens. Some specimens were noticeably faded, particularly the oldest specimens and these that had been collected into alcohol.

Material examined. Paratypes "Napo, River / Ecuador / Apr. 5-10, 1923 // F. X. Williams / Collector /

Paratype // [handwritten, partly illegible] Napo R. / ex Cana silvestre" (1 male, 3 females BPBM; 1 female USNM). Other Material Examined. **COSTA RICA**: Heredia, near Puerto Viejo, La Selva Biological Station, 18–19 Aug. 2003, C. R. Bartlett (1 female, UDCC); same 20 Aug 2003 (1 male, UDCC); same 28 Feb. 2004 (1 female, UDCC); Limon, 24 km SE of Limon, 4 Aug 1990, W. F. Chamberlain (1 male, TAMU). **BOLIVIA**: Santa Cruz, 3.7 km SSE Buena Vista, Hotel Flora & Fauna, 14–28 Oct 2000, M. C. Thomas (2 female, UDCC); Santa Cruz, nr. Buena Vista, 13-Nov-09, G. J. Svenson (1 male, UDCC). **COLOMBIA**: Choco [Department], PNN Utría Centro de Visitantes, 15–30 Oct, 2000, J. Perez, Malaise Trap sample m.816 (2 male, UKIC); same, 30 June 2000–5 July 2000, M. Sharkey, Malaise trap (1 female, UKIC), same, J. Perez, 15 Sept 2000–7 Sept 2000, Malaise trap m.820 (1 female, UKIC); Meta, Villavicencio, vic. Gunaviche Estadero, nr Rio Guatiquía; 4.1751, -73.63722, 1465 ft [447 m], 3-5.vii.2013, J E Eger & A A Calixto, MV Light (3 male, UDCC). Tentatively included: **PERU**: Huanuco, 5 km s. Tingo Maria, P[uen]te Perez, 600m, 9 20'51"S, -75 58'51"W, 25 Oct 2002, C. H. Dietrich, [sample] 02-41-1, merc. vapor light (1 female, INHS).

Lamaxa gracilis (Fennah, 1945), New combination

= Malaxa gracilis Fennah, 1945: 430. (Figures 15–18)

Type locality. Caracas, Venezuela.

Plant associations. None reported.

Distribution. Venezuela.

Remarks. This species was described from a single male that remains undissected (Figs. 15–18). Fennah (1945: 431) stated that "[t]his species differs from *occidentalis* Muir in the shape of the genitalia, especially the penis", which he had earlier in the same page described as "[p]enis narrowly tubular basally, with a wide, pendent, laterally compressed semimembranous appendage, devoid of teeth, arising sub-apically and reflected anteriorly ventrad" (see Fennah 1945, figures 88–89 in contrast to Muir 1926, figure 6). The holotype is externally very similar to *occidentalis*. We suspect that *gracilis* and *occidentalis* may be the same species, with the difference cited by Fennah (1945) a result of the apex of the aedeagal process getting broken off; however, because we have only the holotype available, which is geographically segregated from the available specimens of *occidentalis* (Fig. 43), we cannot determine with confidence whether the two taxa represent the same or different species.



FIGURES 15–18. Lamaxa gracilis (holotype); 15, habitus, dorsal view; 16, habitus, lateral view; 17 frontal view; 18, labels.

Material examined. Holotype "Coll. No. 3009/ Holotype ♂ MALAXA / GRACILIS Fennah / Coll. J. G. Myers, Caracas, Venezuela Dec 6, 1930 // TypeNo 56682 / USNM"

Females tentatively assigned to Lamaxa.

BRAZIL, Santa Caterina, Nova Teutonia, 25 Aug 1950, Fritz. Plaumann (1 female, NCSU). **HONDURAS**, Ocotepeque, 14 mi. NE Nueva Ocotepeque, 25-Jul-74, C & L O'Brien & Marshall (1 female, UDCC).

Xalama, new genus

(Figures 19-24, 27-29, 37, 39)

Type species. Malaxa microstyla Muir, 1930: 211

Description. Color. Brownish with distinctive paler markings, especially on head; wings clear with strong fuscous markings (Figs. 19–21, 23–24). Structure. Body slender and elongate; length males $\bar{x} = 4.69$ mm (n=5); females not available (only males examined). Head narrower than pronotum (Figs. 19, 23), carinae concolorous. Carinae of head distinct although median carina of vertex weaker. Frons elongate and parallel-sided, narrowed between eyes, widest near frontoclypeal suture (Figs. 20, 24; l:w \bar{x} = 2.5:1, n=5). Vertex narrowing distally, slightly projecting in front of eyes, vertex broader along hind margin than along midline; submedian carinae distinct, uniting before fastigium, basal compartments longer than wide. Rostrum reaching hind coxae. Antennae cylindrical, segment II long; nearly surpassing apex of clypeus; segment I about 1/3 length of II (Figs. 20, 24; ratio I:II 0.37:1), length antennal segment I $\bar{x} = 0.13$ mm (n=5), II $\bar{x} = 0.34$ (n=5). Pronotum subequal or just shorter than vertex along midline, lateral carinae usually not attaining hind margin. Mesonotum longer in middle line than vertex and pronotum together. Wings elongate (\bar{x} = 3.8 mm, n=5), much longer than abdomen, predominately clear with distinctive dark markings, nodus at about 2/3 length, wing apex rounded. Spinal formula of hind leg usually 5-6-4. Calcar thick, concave on inner surface, without teeth along the hind margin, bearing an apical tooth. Pygofer roughly triangular in lateral view (Figs. 27, 39), elongate ventrally and strongly narrowed dorsally; pygofer opening and lateral margins with projections (in *microstyla*, midventral projection is a broad, rounded scoop in caudal view, lateral projections just below midlength in form of rounded tooth in lateral view); diaphragm from lateral projections of pygofer broadly concave beneath gonostyli (weak or absent above gonostyli). Gonostyli (Figs. 27, 28) flattened and curled (apically scoop-like), irregularly parallel-sided, curved medially; bearing low, rounded tooth medially near midlength; apically broader and more flattened, somewhat angular, bearing find, irregular serrulations on inner apical margin fine, irregularly placed setae. Aedeagus (Figs. 27, 39) elongate and robust, strongly downcurved into long, sclerotized structure, slightly twisted, bearing an irregular row of teeth on left and right sides and long, downward projecting process at curve. Anal tube (anal segment) small and simple.

Etymology. The new genus name "*Xalama*" is an anagram of "*Malaxa*", and is to be understood as feminine in gender.

Remarks. The new genus is similar to *Malaxa acutipennis* in having a simple anal tube and a strongly downcurved aedeagus; also, the gonostyli may be considered grossly similar in appearance. They differ in that *Xalama* has projections (lateral and midventral) on the opening of the pygofer (vs. simple), the proportions of the antennae, and the shape of the wings and details of the wing venation.

Xalama differs from the Chinese *Malaxa* in having a simple anal tube, and the projections on the opening of the pygofer is different; also, although it is not entirely clear from all the illustrations of Chinese *Malaxa*, it appears that the diaphragm is much more complete in *Malaxa* than in *Xalama*. Also, *Xalama* has much shorter antennae which are differently proportioned between the two segments.

Xalama differs most obviously from *Lamaxa* in the nature and proportions of the antennae (much shorter in *Xalama*), and in the downcurved aedeagus (versus caudally-projecting with apical membranous flagella), and the nature of the processes on the opening of the pygofer.

Xalama microstyla Muir, 1930: 211 (Figures 19–24, 27–29, 37, 39)

Type locality. San Fermin, Bolivia.

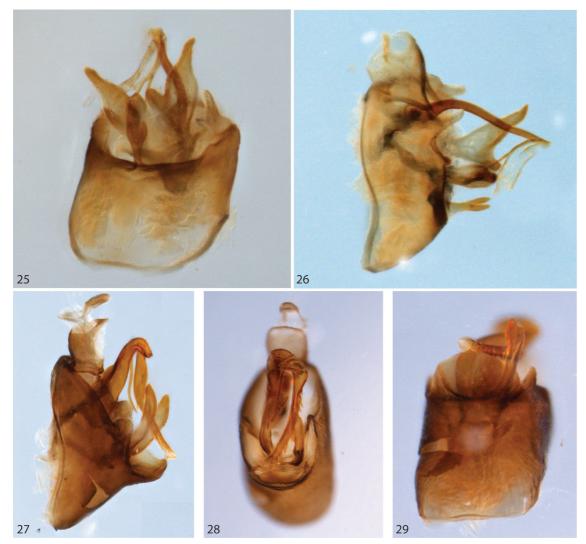


FIGURES 19–24. Xalama microstyla (19–22 holotype; 23–24 Peru); 19, habitus, dorsal view; 20, frontal view; 21, habitus lateral view; 22, labels; 23, habitus, dorsal view; 24, frontal view.

Amended diagnosis. Color. Body generally deep brown (Figs. 19, 21, 23); head, legs and dorsum of pronotum paler; carinae concolorous; vertex and dorsal portion of frons and genae orangish (bearing pale middorsal vitta on posterior vertex, extending posteriorly onto pronotum); ventral portions of frons and genae cream color; antennae stramineous. Disc of pronotum orangish brown except paler median vitta. Legs stramineous except darker proximally; venter of abdomen orangish. Wings clear with strong fuscous markings, one brown bar across apex of clavus to past fork of CuA; a second elongate curved marking extending diagonally along nodal line to wing margin, then diagonally across wing apex to costal margin. Structure. Body slender and elongate; length (from apex of vertex to tip of tegmina) males $\bar{x} = 4.69$ mm (4.40–4.88 mm, n=5); females not available. Head narrower than pronotum (Figs. 19, 23), carinae concolorous. Carinae distinct although median carina of vertex weaker. Frons elongate and parallel-sided (Fig. 24; 1:w \bar{x} = 2.5:1, range 2.4–2.8:1, n=5), narrowed between eyes (width \bar{x} = 0.17, n=5), widest near frontoclypeal suture (w \bar{x} = 0.22, n=5). Vertex narrowing distally, slightly projecting in front of eyes, vertex broader caudally than long along midline (1: [basal] width $\bar{x} = 0.74$:1, range 0.65–0.91:1, n=5); submedian carinae distinct, uniting before fastigium, basal compartments longer than wide. Rostrum reaching hind coxae. Antennae cylindrical, segment II long, nearly surpassing apex of clypeus (Figs. 20, 24); segment I about 1/3 length of II (ratio I:II 0.37:1, range 0.28–0.45:1, n=5), length antennal segment I $\bar{x} = 0.13$ mm (range 0.10–0.17, n=5), II \bar{x} =0.34 (range 0.31–0.37, n=5). Pronotum subequal or just shorter than vertex along midline, lateral carinae usually not attaining hind margin. Mesonotum longer in middle line than vertex and pronotum together (1.91-2.33:1, n=5). Wings elongate ($\bar{x}=3.8$ mm, range 3.2-4.1, n=5), much longer than abdomen, predominately

clear with distinctive dark markings, wing apex rounded (Fig. 37); nodus at about 2/3 length; Sc, RA and RP unbranched; MP branched near wing apex, CuA 3-branched; junction of PCu + AA near midlength of clavus; fork of MP+CuA at near 2/3 length of clavus; fork RA+SC and RP near claval apex (thus inner subapical cell longer than outer subapical cell). Spinulation of hind leg 5-6-4. Pygofer roughly triangular in lateral view (Figs. 27, 39), elongate ventrally and strongly narrowed dorsally; in caudal view, pygofer opening with midventral and lateral projections; midventral projection large and rounded, scoop-like; lateral projections just below midlength in form of rounded tooth in lateral view. Diaphragm extending from level of lateral projections and broadly concave beneath gonostyli (weak or absent above gonostyli). Gonostyli flattened and curled (apically scoop-like), irregularly parallel-sided, curved medially, bearing low, rounded tooth medially near midlength; apically broader and more flattened, somewhat angular, bearing find, irregular serrulations on inner apical margin fine; irregularly placed setae. Aedeagus elongate and robust, strongly downcurved into long, sclerotized structure, slightly twisted, bearing an irregular row of teeth on left and right sides and long, downward projecting process at curve. Anal tube (anal segment) small and simple.

Remarks. Differences between *Xalama*, *Lamaxa*, and *Malaxa* have been previously provided in the remarks under the later 2 genera. The much shorter and differently proportioned antennae and the very different form of the genitalia (viz. the strongly downcurved aedeagus and the projections on the ventral and lateral opening of the pygofer) are the most diagnostic features of the genus.



FIGURES 25–29. Male genitalia of *Lamaxa occidentalis* (25–26) and *Xalama microstyla* (27–29); 25, pygofer, semiventral view (note shape of process on ventral margin of pygofer opening); 26, pygofer, left lateral view; 27, pygofer, left lateral view; 28 pygofer, near caudal view; 29, pygofer, ventral view (note shape of process on ventral margin of pygofer opening).



FIGURES 30–34. New World Tropidocephalini genera; dorsal view of head and thorax (30–32), frontal view (33), lateral view of head and thorax (34); 30, *Macrocorupha* sp. (probably new species, Colombia); 31, *Columbisoga saracura* (holotype); 32, *Columbiana* sp. (probably new species, Colombia); 33–34 *Procidelphax dejecta* (paratype).

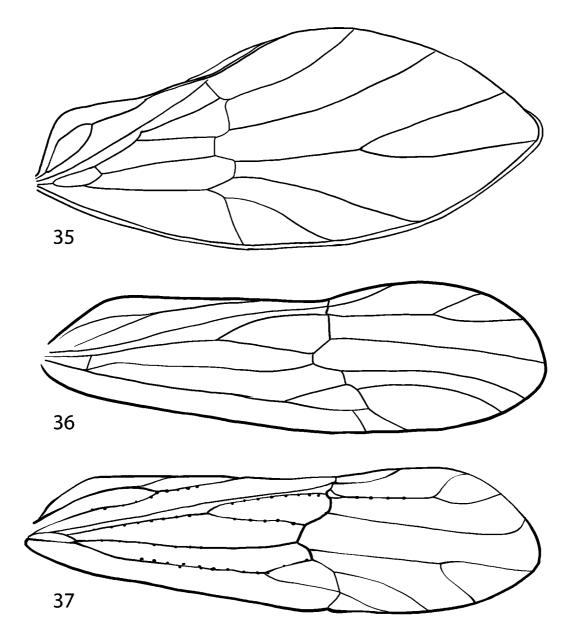
Material examined. *Type material.* Holotype (Fig. 22) "S. Fermin / Boliv. // N. Holmgren // Typus [red paper] // Malaxa / microstylus / [male symbol] Muir [handwritten] // 79 / 81 / Riksmuseum / Stockholm / NHRS-GULI / 000011301". *Other material examined.* **PERU**: Chanchamayo, San Ramon, 11.12083°S 75.35361°W, 800 m, 17 Oct 2002, R. Rakitov & C. H. Dietrich (6 males, INHS).

Discussion

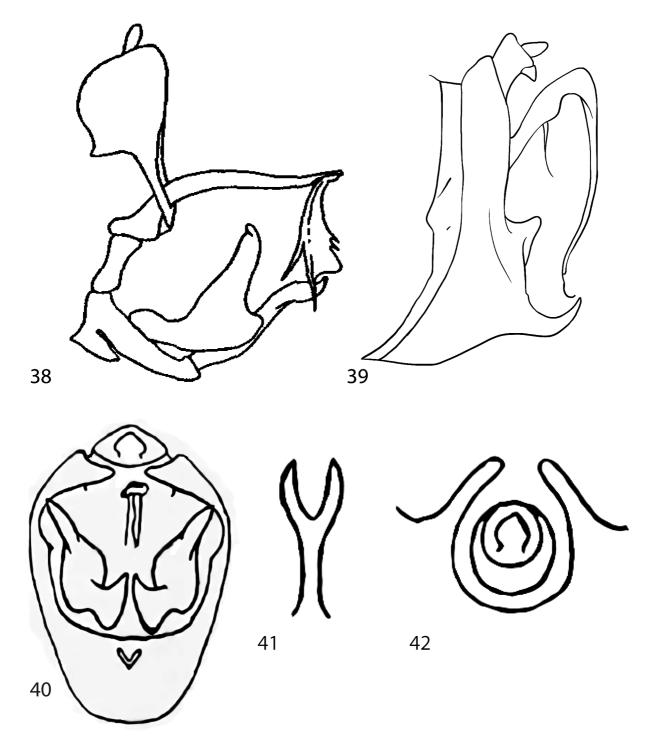
In our review of *Malaxa* and allies, we find that the associated Neotropical taxa form two distinctive groupings, which we have described as *Lamaxa* **n**. **g**. (for *gracilis* and *occidentalis*) and *Xalama* **n**. **g** (for *microstyla*). *Lamaxa* is superficially similar to some of the Chinese *Malaxa* (in having long antennae and in general body form), but differs substantively in details, and especially in features of the genitalia (see Remarks under *Lamaxa*). *Xalama microstyla* has relatively short antennae, genitalia that contrast with both *Lamaxa* and *Malaxa*, and seems to have been poorly placed in the *Malaxa*-group by Muir (1930).

In revising the key to genus for New World genera of Tropidocephalini (originally presented in Bartlett 2009), we found *Columbisoga zapote* Muir to possess structures on the ventral margin of the pygofer strikingly similar to those of *Columbiana*, and the coloration of this species is uniform and similar to that of *Columbiana lloydi* Muir (compare Muir 1919, fig. 7 and Muir 1926, fig. 22), suggesting that this species may belong to this genus. Upon further review, we found that the lateral carinae of the pronotum of *C. zapote* do reach the posterior margin, and the anal tube bears a (small) process, features not otherwise present in *Columbiana*. Furthermore, Muir (1926) noted that *C. zapote* seemed most closely related to *C. sacchari*, which is also a uniformly colored species (bearing some weak markings on the wings) that bears a strong process on the anal tube. From these observations, we suggest that the systematics and defining features of these genera deserves re-examination.

We found *Lamaxa* to be distributed in tropical South America north into Mesoamerica at least as far north as Costa Rica (the first tropidocephaline species reported from Mesoamerica). If the host association is properly reported, the genus could be much more widely distributed. Specimens of *Lamaxa* are relatively rare in collections, although we can only speculate on reasons for this. The genus is relatively distinctive and easily extracted from unsorted specimens, and at least sometimes come to lights (*pers. obs.*). We note that it is unclear whether *occidentalis* and *gracilis* are separate species, because the differences Fennah (1945) reported between the species could be the result of damage to the holotype of *gracilis*. Additional material of *Lamaxa* from Venezuela might be helpful in resolving this problem. *Lamaxa occidentalis* varies in details of coloration among localities, which initially seemed to suggest that we possessed representatives of undescribed species, but we did not observe any substantive differences in the genitalia among the specimens of *Lamaxa occidentalis* on hand.



FIGURES 35–37. Forewing, line art, leading margin ventrad; 35, Malaxa acutipennis; 36, Lamaxa occidentalis; 37, Xalama microstyla.



FIGURES 38–42. Redrawn line art; 38, *Lamaxa occidentalis*, aedeagal complex (aedeagus, connective, gonostyli) and anal tube from Muir 1926 (figure 6); 39 *Malaxa microstyla*, lateral view of terminalia, from Muir 1930 (figure 7); 40, *Lamaxa gracilis*, caudal view of pygofer (Fennah 1945, figure 94); 41, *Lamaxa gracilis*, median process of pygofer, ventral view (Fennah 1945, figure 91); 42, *Lamaxa gracilis*, anal segment and expanded dorsocaudal portion of male pygofer, posterodorsal view (Fennah 1945, figure 93).

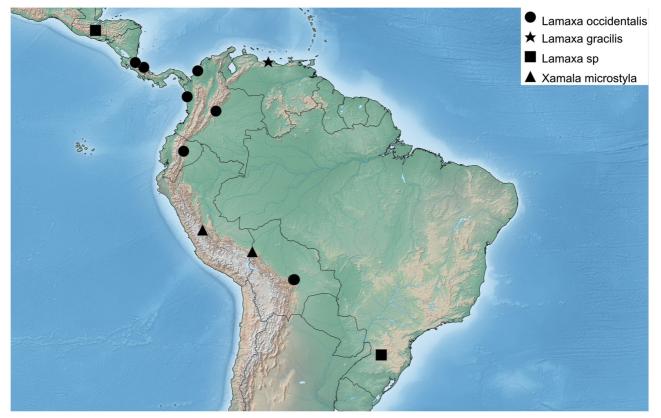


FIGURE 43. Distribution of New World species of Lamaxa and Xalama.

While the purpose of this work was to consider the systematics of Neotropical *Malaxa* as opposed to the Old World taxa, it is evident that the type species of *Malaxa*—*M. acutipennis*—exhibits differences from the Chinese fauna as reviewed by Chen *et al.* 2006 and Hou *et al.* 2013. Based on published descriptions, it appears that *Malaxa javanensis* and *M. nigra* may be allied with the Chinese fauna, but *M. obtusipennis* was described from females, which limits our ability to place this species. However, the composition of *Malaxa* in the Old World was not our purview and our observations should only be taken to indicate that the species composition of *Malaxa*, suggesting that additional undescribed species may be found among the Southeast Asian fauna.

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