

On the Andean genus *Leschenius* (Coleoptera: Curculionidae: Entiminae): updated phylogeny, with a new species from Ecuador, discovery of males, and larval description of the potato weevil *Leschenius vulcanorum* (#67992)

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On the Andean genus *Leschenius* (Coleoptera: Curculionidae: Entiminae): updated phylogeny, with a new species from Ecuador, discovery of males, and larval description of the potato weevil *Leschenius vulcanorum*

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The weevil genus *Leschenius* del Río (Curculionidae: Entiminae: Naupactini) is distributed in the Northern Andes, in Colombia and Ecuador. Among its species, *Leschenius vulcanorum* stands out as an important pest of potatoes in its parthenogenetic form, known as “tiroteador de la papa”. In this study, the adult male and the larval stage (first and mature larvae) of *L. vulcanorum* are described and illustrated for the first time. A description of the male of *Leschenius bifurcatus* is also provided. A new bisexual species was discovered, *Leschenius ventrilingulatus* sp. nov., described from Ecuador. An updated phylogenetic analysis was performed, including the new species, with results indicating a sister group relationship between *Leschenius ventrilingulatus* sp. nov. and *L. vulcanorum*. They can be distinguished because the former is usually of smaller size and is dressed with denser and thicker setae, it has shorter antennae, a subcylindrical shape of the pronotum, shorter elytra (about 1.5x longer than wide at base), the female has ventrite 4 with a posterior rounded projection, and posterior margin of ventrite 5 subacute, not excavated. This paper also includes lectotype designation, a revised key to all known species of *Leschenius*, habitus photos of males and females, illustrations of genitalia, and a distribution map.

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Abstract

The weevil genus *Leschenius* del Río (Curculionidae: Entiminae: Naupactini) is distributed in the Northern Andes, in Colombia and Ecuador. Among its species, *Leschenius vulcanorum* stands out as an important pest of potatoes in its parthenogenetic form, known as “tiroteador de la papa”. In this study, the adult male and the larval stage (first and mature larvae) of *L. vulcanorum* are described and illustrated for the first time. A description of the male of *Leschenius bifurcatus* is also provided. A new bisexual species was discovered, *Leschenius ventrilingulatus* sp. nov., described from Ecuador. An updated phylogenetic analysis was performed, including the new species, with results indicating a sister group relationship between *Leschenius ventrilingulatus* sp. nov. and *L. vulcanorum*. They can be distinguished because the former is usually of smaller size and is dressed with denser and thicker setae, it has shorter antennae, a subcylindrical shape of the pronotum, shorter elytra (about 1.5x longer than wide at base), the female has ventrite 4 with a posterior rounded projection, and posterior margin of ventrite 5 subacute, not excavated. This paper also includes lectotype designation, a revised key to all known species of *Leschenius*, habitus photos of males and females, illustrations of genitalia, and a distribution map.

Introduction

The weevils of the South American genus *Leschenius* del Río (Curculionidae, Entiminae, Naupactini) range in the highlands of Colombia and Ecuador, at approximately 1800 to 5000 m.a.s.l. (del Río, Marvaldi & Lanteri, 2012). Along with other Naupactini distributed in the Andes, the genus *Leschenius* belongs to the so-called “Andean group” according to the phylogenetic analysis of the Naupactini tribe performed by Lanteri & del Río (2017). It belongs to a more inclusive clade that includes most genera often related to *Pantomorus sensu lato* (e.g. *Atrichonotus*, *Aramigus*, *Phacepholis*, *Parapantomorus*) plus the “Andean group” (*Asymmathetes* to *Trichocyphus*), defined by the reduction of the elytral humeri and metathoracic wings. The monophyly of the “Andean group” is mainly supported by the pro-femora about as wide as meta-femora and by some features of the vestiture like the scarcity of scales and the elytral setae being either erect and long or absent.

The genus *Leschenius* is recognized by the black, denuded, and shiny integument, the well-developed pre-epistome, the elytral base curved backward, the reduction of the metathoracic

wings, and by the procoxae separated and situated much closer to the anterior than to the posterior margin of the prosternum. Mixed in the series of *Leschenius vulcanorum*, we found some specimens which are very similar to this species (del Río, Marvaldi & Lanteri, 2012) but different in some diagnostic characters such as the length of the elytra, the density of the vestiture, and the shape of the female ventrite 4. After close examination, we concluded that these specimens correspond to a new bisexual species close to *Leschenius vulcanorum*. We also found male specimens, previously unnoticed, as belonging to *L. vulcanorum*. Finally, and despite its great economic importance as a potato pest, we realized there was not a detailed larval description for this species, or any representative of *Leschenius*.

The purpose of this contribution was to provide a systematic update of the genus *Leschenius*, including descriptions of a new species, the larva of *L. vulcanorum*, the males of *L. vulcanorum* and *L. bifurcatus*, along with lectotype designations, updated phylogenetic analysis and a revised key to all known species of the genus.

Materials & Methods

The study was based upon the examination of adult specimens borrowed from the following institutions: Charles O'Brien collection, now housed at Arizona State University (AZUCOB, Tempe, USA), The Natural History Museum (BMNH, London, UK), Museo de La Plata (MLPC, La Plata, Argentina), Muséum National d'Histoire Naturelle, (MNHN, Paris, France), Museum für Tierkunde, (MTD, Dresden, Germany), Museum für Naturkunde (ZMB, Berlin, Germany).

Immature specimens: 1 mature larva and 4 submature larvae collected with associated adults with the following data: Colombia, Municipio de Sibaté, vereda el Romeral, 4°26'3''N, 74°14'8'' O (3100 masl), J.E.C. Gomez leg., 2009; 10 first instar larvae reared from eggs deposited by adults kept in captivity, with collection data as above. The slide-mounted larval specimens are deposited at the MLP. Techniques for dissection of larvae, terminology and abbreviations herein applied corresponds to Marvaldi (1998).

Dissections of female and male genitalia were made according to standard entomological techniques. Characters of the genitalia were drawn using a camera lucida adapted to a stereoscopic microscope Nikon SMZ800. Measurements were taken with an ocular micrometer

attached to this microscope. Measurements with their abbreviations used in the description are as follows: L, maximum length; LA, length of antennae; LB, length of body; LE, length of elytra; LP, length of pronotum; W, maximum width; WRa, width of rostrum measured across apex (excluding scrobes); WRb, width of rostrum at anterior margins of eyes. The terminology used for the morphological structures follows *Marvaldi et al. (2014)*, *Lanteri & del Río (2017)* and the glossary of weevil characters by *Lyal (2021)*. The terminology used for the sculpture follows that of *Harris (1979)*.

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Phylogenetic analysis

For the phylogenetic analysis of *Leschenius*, the list of morphological characters and the data matrix by *del Río, Marvaldi & Lanteri (2012)* were ~~modified~~ to include the new species as terminal taxon as well as new information ~~about the~~ males of *Leschenius vulcanorum* and *L. bifurcatus*.

For the inclusion of the new species in the present analysis, four characters from the list by *del Río, Marvaldi & Lanteri (2012)* were redefined (chars. 5, 41, 47, and 48), and a new one of the male genitalia was added (Table 1). The new list consisted of 50 morphological characters of the adults, including 36 from the external morphology and 14 from the female (9) and male terminalia (5). The data matrix herein analyzed includes 12 terminal taxa, corresponding to seven species of *Leschenius* plus five outgroup taxa (Table 2) ~~chosen because they are deemed as~~ closely related to *Leschenius* according to *Lanteri & del Río (2017)*. All characters were treated as non-additive and analyzed under equal weights.

A cladistic analysis was conducted with TNT (Goloboff & Catalano, 2016), using the “traditional search” algorithm, with 100 random addition sequences, Tree Bisection and Reconnection (TBR) branch swapping, holding 10 trees during each replication. The most parsimonious tree was rooted with *Melanocyphus lugubris*. Clade stability was evaluated with 1000 replication Bootstrap (BT) (Felsenstein, 1985), support values over 50 % were indicated below branches. The total length (L), the consistency index (CI) (Kluge & Farris, 1969), and the retention index (RI) (Farris, 1989) of the most parsimonious trees (MP tree) were calculated excluding the uninformative characters. The character changes were mapped on the tree using fast (ACCTRAN) optimization with WINCLADA1.00.08 (Nixon, 2002).

Results

Cladistics. The analysis yielded one most parsimonious tree (L=155 steps, CI= 0.56, RI= 0.53) (Fig. 1). In the cladogram the new species, *Leschenius ventrilingulatus* belongs to the genus *Leschenius*, sharing the synapomorphies of the genus: the pre-epistome well developed (character 10.1); the pronotal base ‘V’-shaped (character 17.2); the elytral humeri slightly prominent to absent (character 23.1); and the procoxae almost contiguous with anterior margin of prosternum (character 29.0).

The genus *Leschenius* has two main clades, named A and B in Fig. 1. Clade A is well supported and includes the new species, *L. ventrilingulatus* as sister of *L. vulcanorum*, a relationship supported by the very short rostrum (character 5.2), the relatively wide pronotum (character 14.1), the penis with its apex tapering into a long acute projection (character 47.0), dorsally slightly recurved (character 49.1), with a long flagelum like sclerotization in the endophallus (character 48.2). Clade B includes the remaining five species of the genus, supported by the rostral sulcus exceeding posterior margin of eyes (character 7.1), corbel of metatibial apex narrow, setose or denuded (character 31.2); penis apodemes half as long as than penis body (character 45.1). In clade B, *Leschenius bifurcatus* is the sister of the remaining species, which form a clade defined by the elytral base strongly curved backwards and by the humeral angle of males anteriorly projected. They are grouped in two sister subclades, one including *L. nigrans* and *L. silviae*, defined by the obtuse angle between the longitudinal axis of penis and its apodemes (character 46.1), funicle segment 2 more than 1.5 times longer than segment 1 (character 13.0), apical comb of metatibiae longer than dorsal comb (character 32.0).

The other subclade includes *L. rugicollis* and *L. manuli* and is supported by the rostrum and forehead coarsely strigose (character 3.3), and pronotum foveolate-granulose (character 4.2), ~~with strongly convex eyes (character 11.0), and apex of median lobe evenly rounded (character 47.3).~~

Taxonomy

Leschenius del Río 2012

Most characters of the following larval description, based on specimens of *Leschenius vulcanorum*, may apply to the genus *Leschenius*.

Description of larvae. Mature larva. Body robust, widest at thorax and first abdominal segments. Cuticle asperities present on ventral areas, and absent on lateral and dorsal areas.

Head (Fig. 2A) deeply retracted into thorax, longer than wide; posterior margin ogival; posterior half unpigmented, with softer integument and without setae; all setae shifted anteriorly, placed on anterior third. Epicraneal line more than 0.5 the length of head capsule. Frontal lines and endocarina absent. Hypopharyngeal bracon with paramedian maculae. Postoccipital condyles obtuse, hyaline. Setae (Fig. 2A): *fs4,5*, *des5*, and *les2* long, subequal situated on anterior cephalic fifth; *des1*, *des3* shorter but well developed; *fs1,2,3*, *des4*, *pes1-4* minute; *les1* reduced; *vcs1* longer than *vcs2*, both short. Stemmata absent. Antenna (Fig. 2B) with sensorium about 2.5 x wider than long, truncate at apex. Labrum (Fig. 2C) with *lms1,2,3*, subequal, *lms1* slightly less widely separated than *lms2*. Epipharynx (Fig. 2D) with *mes1* less separated than *mes2*; epipharyngeal sensilla as single units (not as sensillum clusters), one pair between *mes1* and *mes2* but closer to *mes2*, and another pair close to bases of labral rods; labral rods (Fig. 2D) ax shaped, bifurcate, with one arm reaching *mes1* and the other *mes2*. Mandibles (Fig. 2E) with *mds1* slightly longer than *mds2*, both transversely placed within the scrobe; *mds2* exterior and slightly basal to *mds1*. Maxillae (Fig. 2F-G) with spinules on dorsal surface of external margin of estipes and below mala and palpus; maxillary mala with a row of 8 *dms* and with 4 *vms*. Labium (Fig. 2F) with premental sclerite well sclerotized, with posterior extension truncate and expanded at apex, anterior extension slender. **Thorax** (Fig. 3A). Spiracle (Fig. 3E) ellipsoidal, without airtubes. Pronotum (Fig. 3A) with 9 setae. Meso- and metathorax with *pds3* distinctly longer

than others; alar area with 2 *as*. Pedal areas of thoracic segments (Figs. 3A–B) each with 9 setae: seta *z* conspicuous; setae *x* and *y* subequal; *u* smaller than *v*; *v* smaller than *w*; seta *v'* present and rather conspicuous; small *x'* distinct; a pair of additional anterosternal microsetae occasionally present in front of each pedal area. **Abdomen** (Figs. 3C–D, F): Spiracles (Fig. 3E) elliptical, 2x smaller than thoracic one, without airtubes. Segments AI–VII (Figs. 3A, C) with 5 *pds*, *pds3* and *pds5* the longest; spiracular area with only *ss2* distinct and progressively placed closer to postdorsum, *ss1* vestigial or absent. AVIII with 4 *pds*, lacking the homologous *pds2* of preceding segments; *ss* indistinct. Abdominal apex (Fig. 3D) modified, with transverse posterior sclerotized ridges on dorsum, pleura and sternum of AIX; AIX with 4 *ds* including a seta *ds'*, placed lateral to *ds1*; laterally with 2 *ls* strongly unequal, the longest on sclerotized ridge; AX terminal, 4-lobed, each lateral anal lobe with 3 minute setae, the outermost stronger.

First instar larva (Figs. 2H–J, 3E). **Head** (Figs. 2H–I) only slightly retracted into thorax, slightly longer than wide; major cephalic setae placed on anterior half, *des2* and *les1* less reduced than in older larvae; *des1* minute (smaller than in mature larvae). Frontal lines weakly distinct. Anterior and posterior stemmata distinct, as dark pigmented spots. Antennal sensorium prominent and projected outwards. Mandibles (Fig. 2J) with *mds1,2* strongly unequal, *mds1* about 5x longer than *mds2*. **Thorax**. Spiracle (Fig. 3F) bicameral with annulated airtubes; pedal area with setae *z*, and *v'* relatively small, seta *w* relatively very long and spatulate or blunt at apex. **Abdomen**. Spiracles (Fig. 3F) bicameral, with airtubes having a smaller number of rings than thoracic one; abdominal apex not distinctly sclerotized.

Remarks. The characters mentioned above for the first larva, newly hatched, are exclusive of the first instar (see also *Marvaldi & Loiácono, 1994*). Additional differences between early and older instar larvae involve relative dimension of structures, like the antennae, which are relatively much larger in the first instar; the pigmentation and level of sclerotization of body areas tend to increase in successive instars; the differences in length between setae of body areas are higher in early instars.

Comparative notes. The larval characters given herein for the genus *Leschenius* are in full agreement with those defining the tribe Naupactini (*Marvaldi & Loiácono, 1994*) or *Naupactus* and allied genera (*Marvaldi, 1998*). Two apparently distinct features of the mature larva studied

of *L. vulcanorum* are the *desI* well developed (in known mature larvae of other Naupactini *desI* is minute or very small); also, setae *x* and *y* of pedal areas of thoracic segments are subequal (in other Naupactini as *Naupactus*, seta *x* is distinctly smaller than *y*). Larval characters deemed as diagnostic for the species are given below.

***Leschenius vulcanorum* (Kirsch, 1889)**

(Figs. 2, 3, 4, 5A, 6G, K)

Canephorus vulcanorum Kirsch 1889: 17; Strand 1943: 96 (*Canephorulana*); Kuschel 1955: 277 (*Amitrus*); Kuschel in Wibmer & O'Brien 1986: 53 (*Asymmathetes*) (Fig. 4A).

Amphideritus brevis Oliff 1891: 68; Dalla Torre, Emden & Emden 1936: 14 (*Macrostylus*); Kuschel 1955: 277 (*Amitrus*) (syn. of *vulcanorum*); Kuschel in Wibmer & O'Brien 1986: 53 (*Asymmathetes*); del Río, Marvaldi & Lanteri 2012: 60 (*Leschenius*) (Fig. 4B).

Amphideritus pigmaeus Oliff 1891: 68; Dalla Torre, Emden & Emden 1936: 14 (*Macrostylus*); Kuschel 1955: 277 (*Amitrus*) (syn. of *vulcanorum*); Kuschel in Wibmer & O'Brien 1986: 53 (*Asymmathetes*) (Fig. 4C).

Caulostrophus aequatorialis Kirsch 1889: 13; Dalla Torre, Emden & Emden 1939: 319 (*Macrostylus* (*Amphideritus*)); Kuschel in Wibmer & O'Brien 1986: 53 (*Asymmathetes*) (Fig. 4D). **Syn. n.**

Diagnosis and description of female in del Río, Marvaldi & Lanteri (2012).

Description of male (Fig. 5A). Smaller than female (4.0-6.3 mm; females 5.3-8.7 mm); rostrum shorter (L/Wa: 0.76-0.84); less convergent towards apex (Wb/Wa, 1.15-1.30); antennal club more elongate (L/W, 2.5-2.8); pronotum (W/L: 1.25-1.35), wider respecting the elytra and longer than females, with sides more arcuate; elytra slightly shorter (L/W, 1.32-1.40) with apex not divided, more rounded; metatibiae with larger mucro than in females; posterior margin of ventrite 5 blunt. Genitalia (Figs 6G, K). Median lobe slightly curved in lateral view, tapering towards apex, with subacute, dorsad slightly recurved hook-like apex; penis as long as abdomen;

apodemes slightly shorter than median lobe (0.7x); endophallus armed with minute spicules and with a slightly sclerotized flagellum.

Larval stage. After comparison with larvae known for other species in tribe Naupactini (Marvaldi & Loaiácono, 1994; Marvaldi, 1998) the following combination of characters can be suggested as diagnostic for the species *L. vulcanorum*.

Mature larva (Figs. 2–G, 3A–E). Maximum head width 2.2 mm. Setae fine, brown. Head yellowish, intense yellow on anterior margin of frons, about 1.3 x longer than wide. Cephalic setae (Fig. 2A): *des1* well developed (although shorter than *des3* and those placed on anterior third, *fs4*, *fs5*, *des5*, and *les2*). Ephipharynx with spinules anteriad and posteriad to the labral rods; epipharyngeal sensilla not in clusters but apparently fusionated into single units. Pronotum pigmented with pattern of brownish maculae (Fig. 3A). Abdominal apex (AIX) with transverse sclerotized ridges in dorsum, pleura and sternum (Fig. 3D).

Larva 1 (Figs. 2H–J, 3F). Maximum head width 0.2 mm. Head (Fig. 2A) with *des1* minute (like *des 4*), cephalic setae well developed are *des2*, *des3*, *des5*, *fs4*, *fs5*, *les1*, and *les2*; *des1* slightly more widely separated than *fs4*. Clypeus with setae subequal. Labrum with *lms2* somewhat more widely separated than *lms1*.

Type material examined. Lectotype of *Canephorus vulcanorum* Kirsch, female, Ecuador Tunguragua, 3800, *Canephorus vulcanorum* typus Kirsch, MTD, here designated (Fig. 4A).

~~Paralectotype, Ecuador, Sangay, 3500m, cotypus, MTD. Lectotype of *Caulestrophus aequatorialis* Kirsch, female, Cotopaxi, 5688, Typus, MTD, here designated (Fig. 4D).~~

~~Lectotype of *Amphideritus brevis* Oliff, female, Ecuador feet, Ed. Whympers, MNHN, here designated (Fig. 4B). Lectotype of *Amphideritus pigmaeus* Oliff, female, Chimborazo, Ecuador, 12-13000 feet, Ed Whympers, MNHN, here designated (Fig. 4C).~~

Other material examined. COLOMBIA. No loc., int. Miami, 5-2-85, with cut flowers of *Dianthus* sp (1f USNM). **ECUADOR.** No loc., 11-11-93 (2f USNM). **Chimborazo:** Chimborazo, S side of Mt, elev 11600 nr Snowline, 19 june 1975 (1f USNM); Colta, 3-VI-05, Ohaus, 9-VII-05 (27f ZMB); Interandin-Hochland, Colta 3500-4000m, 8-10-VII-1905 Ohaus (1f ZMB), 2,8-VII-1905 Ohaus (2f ZMB); Faldas del Chimborazo, jan-1983, in pine leaves *Pinus*

radiata, adults feed, Lopez col (1f USNM); Guamote, 3-7-1969, en cocoons of alfalfa plants (1f USNM); Guaslam prov, 1-22-60-on buets of young corn, Merino (2f USNM); Quimiag on maize, Jan 1979 Kirckhy (2f BMNH); Riobamba, 3-VII-1905, unter steinen, Ohaus (17f ZMB), 20-XI-05 (1f ZMB), 27-XI-05 (2f ZMB); Riobamba, Ause de Cubillin, 3500, 5-Vii-05 Ohaus (42f ZMB). **Cotopaxi**: 71 km W Latacunga under stones May 1, 1978, O'Brien & Marshall (1f MLP); 45 km W Latacunga, under stones May1 1978, Obrien & Marshall (8f MLP); 21 km S Latacunga, April 25 1978, CW&L Obrien & Marshall (1f MLP); 6 km W Latacunga, under stones, May1 1978, Obrien & Marshall (3f MLP); Latacunga, XI 1981 Onore Brit Mus 1990-214 (1f BMNH); 15 km W entrance PN Cotopaxi, April 30 1978, Obrien & Marshall (4f MLP); 14 km W entrance PN Cotopaxi, April 30 1978, Obrien & Marshall (1f MLP); Cotopaxi, P. 13 km S Latacunga along PanAma, XI-3-77, G Noonan, M. Moffett, under clumps soil and grass, rocks, debris-in green grassy field w green short grass ca 2600m. (13f 1m MLP); Tilipulo, V-III-1981, G. Onore Brit Mus 1985-254 (4f BMNH). **Bolivar**: Guaranda, X-I-1955, on new corn (7f USNM). **Loja**. Loja, Ohaus (2f ZMB). **Pichincha**: 38.8km NE Quito on PanAm XI-8-77, G Noonan, M. Moffett, under rocks on dirt clumps, in areas with sparse to very sparce short grass ca 2200m. (1f MLP). **Tungurahua**: SE end Ambato, XI-1-77, G Noonan, M. Moffett, under rock in fields w short sparce grass, soil dry under stones, ca 2500m. (2f MLP); 13km NE Baños, April 26 1978, Obrien & Marshall (1f MLP); Baños, 1800m, 9-V-37 Brundage (2f USNM); Baños, X-4-44, EJ Hambleton (1f USNM); Pomasqui, X-7-54, Merino, orange trees (4f USNM); Totoras, 7 km SE Ambato, April 26 1978, Obrien & Marshall (3f MLP). Plus, the material listed in *del Río, Marvaldi & Lanteri (2012)*.

Remarks. In the revision of the genus *Leschenius* (*del Río, Marvaldi & Lanteri, 2012*), the type material of the species *Asymmathetes aequatorialis* (Kirsch 1889), was not seen and we mentioned that this species may also belong to the genus *Leschenius*. Herein, based on the observation of the type material of all the ~~names~~ related to *Leschenius vulcanorum* (Fig. 4A-D), including *Caulostrophus aequatorialis* Kirsch (Fig. 4D), we establish the synonymy of this name with *Leschenius vulcanorum* (Fig. 4A). This species is only known from the type material and corresponds to a phenotype within the great variation observed in *L. vulcanorum* (see figs 4A-D).

Bisexual populations of *Leschenius vulcanorum* was so far only seen in Ecuador, near Latacunga locality (Cotopaxi province), and in Ambato locality (Tungurahua province).

Differences noted between the bisexual and the parthenogenetic ones are related with the body size and morphometrics of the elytra. The bisexual form is usually smaller with slightly shorter elytra.

***Leschenius ventrilingulatus* del Río & Marvaldi, sp. n.**
(Figs 5B-F; 6A-F, H, L)

Diagnosis. *Leschenius ventrilingulatus* is easily distinguished from the remaining species of *Leschenius* (except *L. vulcanorum*) by possessing a shorter and less conical rostrum with sides not thickened and elevated, and apex not projected. It is very similar to *L. vulcanorum*, but distinguished by its size usually small, vestiture of denser and thicker setae (mainly on head, legs and elytra), shorter antennae (with funicular segments 1 and 2 subequal); shape of the pronotum, subcylindrical with anterior margin as wide as posterior margin; elytra shorter (about 1.5x longer than wide at base, regarding 2x in *L. vulcanorum*); the metatibial apex with narrow corbel; female with ventrite 4 with a posterior rounded projection; and posterior margin of ventrite 5 subacute not excavated. Female genitalia with plate of sternite VIII sub-rhomboidal not elongate with longer apodeme.

Description. Female (Figs. 5B, D–F). Species medium-sized (LB, 5.0–6.0mm). Tegument visible, dark brown to reddish brown, shiny. Vestiture composed of disperse, pale ocher to cream setae, moderately dense, creamy decumbent setae-like scales, devoid of them on middle (forming wide lateral stripes) on pronotum; grouped on patches on elytra in some cases devoid of scales on middle line; also present on venter and legs (more abundant on distal third of femora). Rostrum very short (Fig. 5F) (L/Wa, 0.73–0.83), sides moderately convergent towards apex (Wb/Wa, 1.31–1.43), dorsum moderately convex. Forehead foveolate–strigose, with longitudinal striae. Vertex sparsely punctuate. Antennae (Fig. 6A) of medium length (LB/LA, 2.50–2.85); scape reaching to slightly exceeding posterior margin of eyes. Funicle with segment 2 about as long as segment 1, both elongated; funicle segments 3–6 slightly longer than wide, and funicle segment 7 as long as wide; club slightly fusiform (L/W, 2.3–2.4). Pronotum (Fig. 5B) slightly subcylindrical, moderately wider than long (W/L, 1.30–1.35), with anterior margin as wide as posterior margin; median groove absent. Scutellar shield subtriangular, large and wide

(surrounded by elevated edges), denuded. Elytra (Fig. 5B, E) short (L/W, 1.23–1.33), with maximum width on anterior third, slightly convex; base slightly curved backwards on middle; striae with medium-size punctures; striae 9–10 slightly closer on posterior two-thirds; intervals flat, about twice as long as striae; elytral apex acute, entire, not projected or bifurcate. Legs. Procoxae much closer to anterior than posterior margin of prosternum; protibiae with row of six or seven acute small denticles (on distal two-thirds of tibiae) and medium sized mucro; meso and metatibiae without denticles and with small mucro; metatibial apex with narrow corbel covered with disperse small elongate cream scales; apical and dorsal combs subequal. Abdomen (Fig. 5D). Intercoxal portion of ventrite 1 slightly broader than metacoxal cavities (1.10–1.15x); ventrite 2 longer than ventrites 3 and 4 combined (1.60x without projection; 1.10 along midline); ventrite 4 with a posterior rounded projection; posterior margin of ventrite 5 subacute not excavated; tergites I–VII membranose. Terminalia. Sternite VIII (Figs. 6B–C) with plate sub-rhomboidal, not elongate, with tuft of medium-sized and coarse setae, and with shorter setae on apical third; ‘V’-shaped sclerotization with lateral arms reaching two-thirds of plate, and lateral margins sclerotized; apodeme 2.8–3.0x longer than plate. Ovipositor (Figs. 6D–E) as long as ventrites 1–5; with scattered fine short setae on sides of baculi on anterior third; ventral baculi subparallel; styli wide. Spermathecal body (Fig. 6F) sub-cylindrical; collum (duct-lobe) conical, short; ramus (gland-lobe) indistinct; cornu long; spermathecal duct (Fig. 6D) short, half as long as ovipositor, or 3x the maximum width of spermatheca, membranous, moderately wide. Male (Fig. 5C). Same size as female (4.8–5.5 mm); rostrum less conical (Wb/Wa, 1.32–1.37); antennal club more elongate (L/W, 2.6–2.7); elytra slightly more elongate (L/W, 1.30–1.35); metatibia with larger mucro than in female; ventrite 4 without posterior projection; posterior margin of ventrite 5 blunt. Genitalia (Figs. 6H, L). Penis (median lobe) slightly curved in lateral view, tapering towards apex, with dorsad recurved hook-like apex; penis as long as abdomen; penis apodemes slightly shorter than penis body (0.8x); endophallus armed with minute spicules and with a sclerotized flagellum, with a denticulated blade (Fig. 6H). Morphometrics. Holotype, female: rostrum L/Wa: 0.77, Wb/Wa: 1.31; antenna LB/LA: 2.85, antennal club L/W: 2.31; pronotum W/L: 1.34; elytra L/W: 1.33; LE/LP: 2.6.

Etymology. The specific name refers to the tongue-like projection of the female venter.

Material examined. Holotype. Female, 5 mm long, with labels as follows “ECUADOR, Totoras,/ 7km SE. Ambato/Apr. 26, 1978 C&L/ O’Brien & Marshall” (MLP). **Paratypes.** Same data as holotype (1m **AZUMOC**); ECUADOR, 6 km W/ Latacunga under/ stones May 1, 1978/ O’Brien & Marshall (1f, 1m MLP, dissected with genitalia in vial with glicerine); ECUADOR/ Latacunga/ IX- 1981 Onore/ Brit. Mus./ 1990-214 (3f 2m BMNH); ECUADOR, 5km SE./ Pelileo, April/ 26, 1978 CW&LB/ O’Brien & Marshall (1m **AZUMOC**); ECUADOR/ Catamayo B./ Loja 5.9.05/ F. Ohaus (1f ZMB).

Geographic distribution (Fig. 7). *Leschenius ventrilingulatus* is endemic of Ecuador, known for Cotopaxi, Loja, and Tungurahua provinces. It is distributed on the interandean region on river basins, between 1250 and 2750 meters above sea level (unlike *L. vulcanorum* which is distributed in higher altitudes 2600-5000 m. a. s. l.). It is sympatric with *L. vulcanorum* (Fig. 7) in Latacunga (Cotopaxi province) and Totoras (Tungurahua province) at 2600-2750 m. a. s. l.

Remarks. *Leschenius ventrilingulatus* is the sister species of *Leschenius vulcanorum*, according to results of the cladistics analysis herein undertaken (Fig. 1).

***Leschenius bifurcatus* del Río, Marvaldi & Lanteri 2012** (Figs 5G-H, 6 I, J, M)

Diagnosis and description of female in *del Río, Marvaldi & Lanteri (2012)*.

Description of male (Fig. 5H). Similar size as female, slightly smaller (Fig. 5G) (10-13 mm); rostrum (L/Wa, 1.0-1.1; Wb/Wa, 1.30–1.45); antennal club slightly more elongate (L/W, 3.1–3.4); pronotum (W/L, 1.17-1.19); elytra (L/W, 1.60–1.65) with projected apex but not bifurcated, only slightly divided; ventrites 3-5 not bulged as female, posterior margin of ventrite 5 blunt. Genitalia (Figs 6I, J, M). Penis body slightly curved in lateral view, tapering towards apex (Fig. 6M), with dorsad strongly recurved hook-like apex (Fig. 6J); penis longer than abdomen (1.25-1.30); penis apodemes much shorter than median lobe (0.4x); endophallus armed with minute spicules and with two long wing-shaped sclerites (Fig. 6I).

Material examined. ECUADOR. No loc, intercept. Port Miami, 16-VI-2004 (1f USNM).
Pichincha: Conocoto, 31-Jan-1992, Alvaro Barragan (1m MLP); Pomasqui, Runicucho, 2400
m., 6 Dec-1993, E. Volbracht (1m PUCE). **Imbabura:** 3.9 km N. Ibarra on Pan Am, XI-II-77,
Moffet collr, under rocks by rd. in dry area, with sparse grass ca. 2300 (1f, 3m AZUCOB; 1f, 2m
MLPC;); Urcuqui, 14-III-62, Merino & Vasquez, in soil nr cotton plants (2m USNM); El Chotar,
Mr. Juncal, 1 june-1961, Merino & Vasquez, reared from larvae doing damage to roots of bean
plants (1m USNM). Plus, the material listed in *del Río, Marvaldi & Lanteri (2012)*.

Remarks. The specimens of population of Ibarra (Imbabura) are slightly different from the type,
the female (Fig. 5G) has a wider and shorter pronotum and the elytral apex only slightly
bifurcated but strongly projected posteriad; the males have also a wider and shorter pronotum
and the penis with a shorter ostium area and a more recurved apex (Fig. 6J).

Key to species of *Leschenius*

Modified from *del Río, Marvaldi & Lanteri (2012)*.

1. Size 4–8mm (usually 5–7mm, exceptionally more than 8mm but never more than 9mm).
Rostrum very short (L/W less than 0.95, usually near 0.8); pronotum with setae forming two
feeble lateral stripes; elytral apex not
projected.....2
- 1'. Size 8-12.5mm. Rostrum moderately short (L/W more than 0.96, usually 1); pronotum
without or with scattered setae, never forming lateral stripes; elytral apex projected
backwards.....3
2. Elytra with creamy decumbent setae like scales grouped on patches on entire elytra. Pronotum
subcylindrical, with anterior margin as wide as posterior margin. Metatibial apex with narrow
corbel. Female with ventrite 4 with a posterior rounded
projection..... ***ventrilingulatus*, n. sp** (Figs. 5B–F)
- 2'. Elytra devoid of creamy decumbent setae like scales, or if present, limited to the margin
(intervals 9-10). Pronotum slightly subconical, with posterior margin wider than anterior
margin. Metatibial apex with moderately broad corbel (width: 1/3 of the length of the tibial

- apex). Female with ventrite 4 without a posterior rounded projection.....*vulcanorum* (Figs. 4A–D, 5A, see fig. 1 of *del Río, Marvaldi & Lanteri, 2012*)
3. Pronotum with posterior margin as wide as anterior margin. Elongate elytra (3X or more the length of pronotum). Elytral apex, in females strongly projected backwards and distinctly bifid or divided; in males, moderately projected and rounded to slightly divided.....*bifurcatus* (see figs. 2–3 of *del Río, Marvaldi & Lanteri, 2012*)
- 3'. Pronotum with posterior margin distinctly wider than anterior margin. Oval elytra (less than 2.8x the length of pronotum, usually between 2.2–2.7x). Elytral apex of both males and females moderately projected, entire to slightly divided.....4
4. Corbel plate of metatibia broad (width: almost half the diameter of apex of tibiae)..... *nigrans* (see figs. 9–10 of *del Río, Marvaldi & Lanteri, 2012*)
- 4'. Corbel plate of metatibia narrow (less than quarter apex of tibiae).....5
5. Body length 8.4–9.3mm, moderate sized. Pronotum as wide as elytra in males. Elytra 2.2–2.45x the length of pronotum. Spermatheca with nodule not constricted.....6
- 5'. Body length 7.8–8.4mm, small. Pronotum distinctly narrower than elytra in both sexes. Elytra 2.5–2.75x the length of pronotum. Spermatheca with tubular nodule, constricted near spermathecal body.....*silviae* (see figs. 11–12 of *del Río, Marvaldi & Lanteri, 2012*)
6. Pronotum slightly wider than long (W/L: 1.10–1.25). Ovipositor without setae on sides of baculi. Apex of penis slightly pointed.....*rugicollis* (see figs. 4–5 of *del Río, Marvaldi & Lanteri, 2012*)
- 6'. Pronotum of males strongly wider than long (W/L: 1.30–1.35). Ovipositor with conspicuous setae on sides of baculi. Apex of penis rounded.....*manueli* (see figs. 6–8 of *del Río, Marvaldi & Lanteri, 2012*)

Discussion

The description of a new species and more complete information about male characters, allowed

us to propose an updated phylogenetic hypothesis of *Leschenius*, which differs from the previous study by *del Río, Marvaldi & Lanteri (2012)* regarding the position of *L. bifurcatus* and relationships within clade B (Fig. 1). In the new phylogeny *L. bifurcatus* is the sister species of a subclade that contains *L. nigrans* sister of *L. silviae* and *L. rugicollis* sister of *L. manueli*. Also, the present study led to the discovery of the sister species of *L. vulcanorum* and the pair *L. ventrilingulatus* – *L. vulcanorum* is proposed as the sister group of all remaining species of *Leschenius*.

The genus *Leschenius* is distributed in the Northern Andes of Ecuador and northern Colombia, approximately 1800– 5000 m.a.s.l (Fig. 7), corresponding to the North Andean Páramo province of the South American transition Zone (*Morrone, 2006*). All species included have a narrow distribution range in Ecuador, except *L. vulcanorum* that is widely distributed from central to northern Ecuador and extend to southern Colombia. The latter species, *L. vulcanorum*, along with *L. ventrilingulatus*, *L. bifurcatus*, and *L. nigrans* inhabit in northern Ecuador, and they have been found in sympatry (Fig. 7). The other three species, *L. silviae*, *L. manueli*, and *L. rugicollis* are distributed in the southern provinces of Ecuador.

The new species *Leschenius ventrilingulatus* is distributed on the inter-Andean region on river basins (Fig. 7), and is sympatric with *L. vulcanorum* at 2500-2750 m.a.s.l., that corresponds to the lowest altitude for *L. vulcanorum*.

Of particular interest is the occurrence of parthenogenesis within the genus *Leschenius*, and this mode of reproduction was suggested by *del Río, Marvaldi & Lanteri (2012)* for the species *L. vulcanorum* and *L. bifurcatus*, based on the apparently absence of males in their populations.

The examination of additional material in the present study provided new evidence that suggest *L. bifurcatus* is not parthenogenetic, leaving *Leschenius vulcanorum* as the only parthenogenetic species. The parthenogenesis of *L. vulcanorum* was confirmed by laboratory rearing (*del Río, Marvaldi & Lanteri, 2012*). Nonetheless, in the present study, we discovered males of *L. vulcanorum*, indicating that this species also has bisexual populations, so far only seen in three localities in Cotopaxi and Tungurahua provinces of Ecuador. The existence of both sexual and parthenogenetic populations within the species supports the idea of a special kind of parthenogenesis, called “geographical parthenogenesis” (*Lanteri & Normark, 1995*). In *L. vulcanorum*, as in other species having this kind of reproduction, the sexual and parthenogenetic forms have different distribution ranges, being the parthenogenetic one more widespread than the

respective sexual forms (*Vandel, 1931*). So far, exemplars of both sexes of this species were collected in just three localities. Morphological differences between the bisexual and the parthenogenetic form are noticed in body size and morphometrics of the elytra, being the bisexual form usually smaller and with slightly shorter elytra. It is important to remark that within the parthenogenetic form the variation in body size and morphometrics is extremely wide (Figs. 4A-D). Same as other parthenogenetic weevils, including the around 30 parthenogenetic species of the tribe Naupactini (*Lanteri & Normark 1995*), in *L. vulcanorum* the parthenogenesis is also associated with the wingless condition and xeric habitats.

An interesting feature observed in females of the new species described, *L. ventrilingulatus* (sexually dimorphic) is the ventrite 4 with its posterior margin produced medially into a tapered lamina or tongue-like projection. This characteristic seems to be unique within the tribe Naupactini, and so far, also unknown among Neotropical Entiminae. Although unusual, a modified ventrite 4 is also present in genera of Entiminae inhabiting montane areas of other regions of the world (see *Brown, 2017* and reference therein): New Zealand [*Austromonticola* Brown 2017, *Chalepistes* Brown 2017, and *Nicaeana* Pascoe 1877], Solomon Islands [*Platyacus* Faust, 1897 (Celeuthetini)], Mauritian Islands [*Syzygops* Schönherr, 1826 (Ottistirini)]; Chinese Himalayas [*Trichalophus caudiculatus* (Fairmaire, 1886) (Tropiphorini)], Kashmir and Himalayas [*Leptomias* Faust, 1886 (Tanymecini)], and Central America [*Sciomias* Sharp, 1911 (Sciaphilini)]. These structures are hypothesized to have evolved in response to oviposition needs in and beside cushion plants or selected to mitigate the female costs of prolonged mating (*Brown, 2017*). Although the function was not studied yet, the first suggestion that these ventral structures may assist in the preparation of oviposition sites in close-packed vegetational structures seems highly plausible, the cushion growth form is a common feature of the alpine vegetation worldwide where the weevil species with this trait are found.

Concerning the immature stages, the study of the larvae of *Leschenius* lead us to confirm that the tribe Naupactini is very homogeneous in larval morphology, as suggested by *Marvaldi (1998)*. Also, there seem to be no particular features that could be suggestive as adaptive traits to arid environments. This is not unexpected, since *Leschenius* larvae, like those of most entimines, are subterranean (i.e., endophagous) and then “preadapted” to live in harsh environments.

Finally, additional research with molecular tools will be very important to find out the genetic divergence and evolution of the group, and the role of the parthenogenesis. Moreover, the study

of the biology and behavior of *L. ventrilingulatus* will offer insights into the function of the abdominal structures of the female.

Acknowledgements

We thank all the specialists and curators that loaned us specimens for study and/or facilitated the examination of the material in their collections.

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576

Figure 1

MP tree for the genus *Leschenius* showing the phylogenetic position of the new species, *Leschenius ventrilingulatus*. 

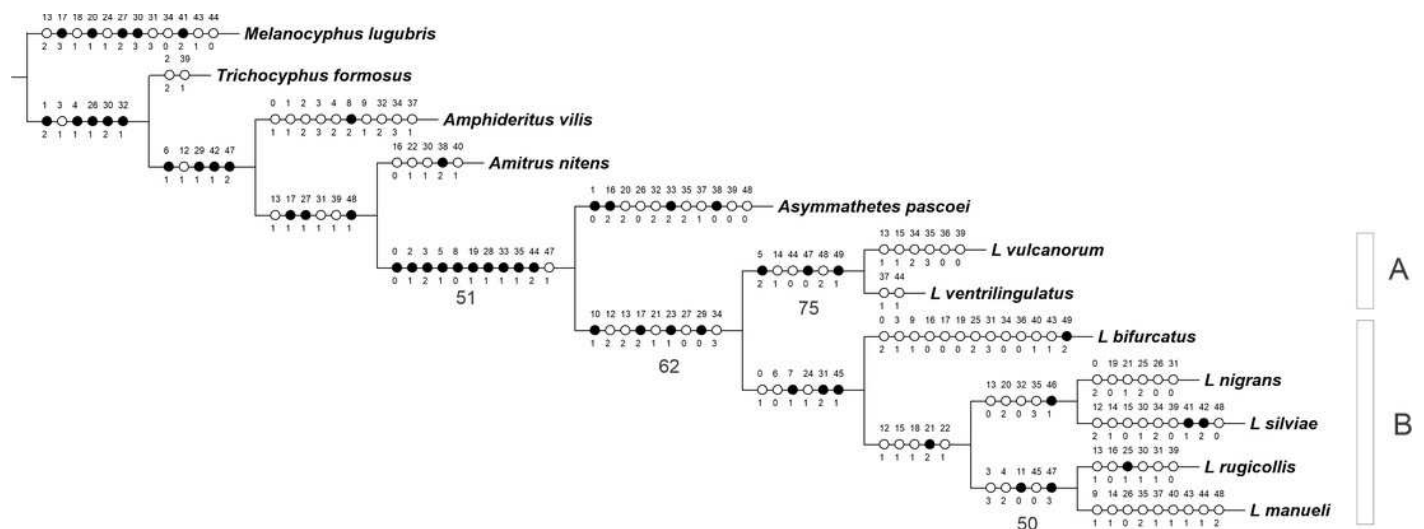


Figure 2

Leschenius vulcanorum, larva.

(A—G) Mature larva. (A) Head, dorsal. (B) Left antenna. (C) Clypeus and labrum. (D) Epipharynx. (E) Mandible, dorsal. (F) Maxilla and labium, ventral. (G) Maxilla, dorsal. (H—J) First instar larva. (H) Head, dorsal. (I) Head, partial, ventral. (J) Mandible, dorsal. Scales A, C—G= 0.5mm; B, H—J= 0.1mm.

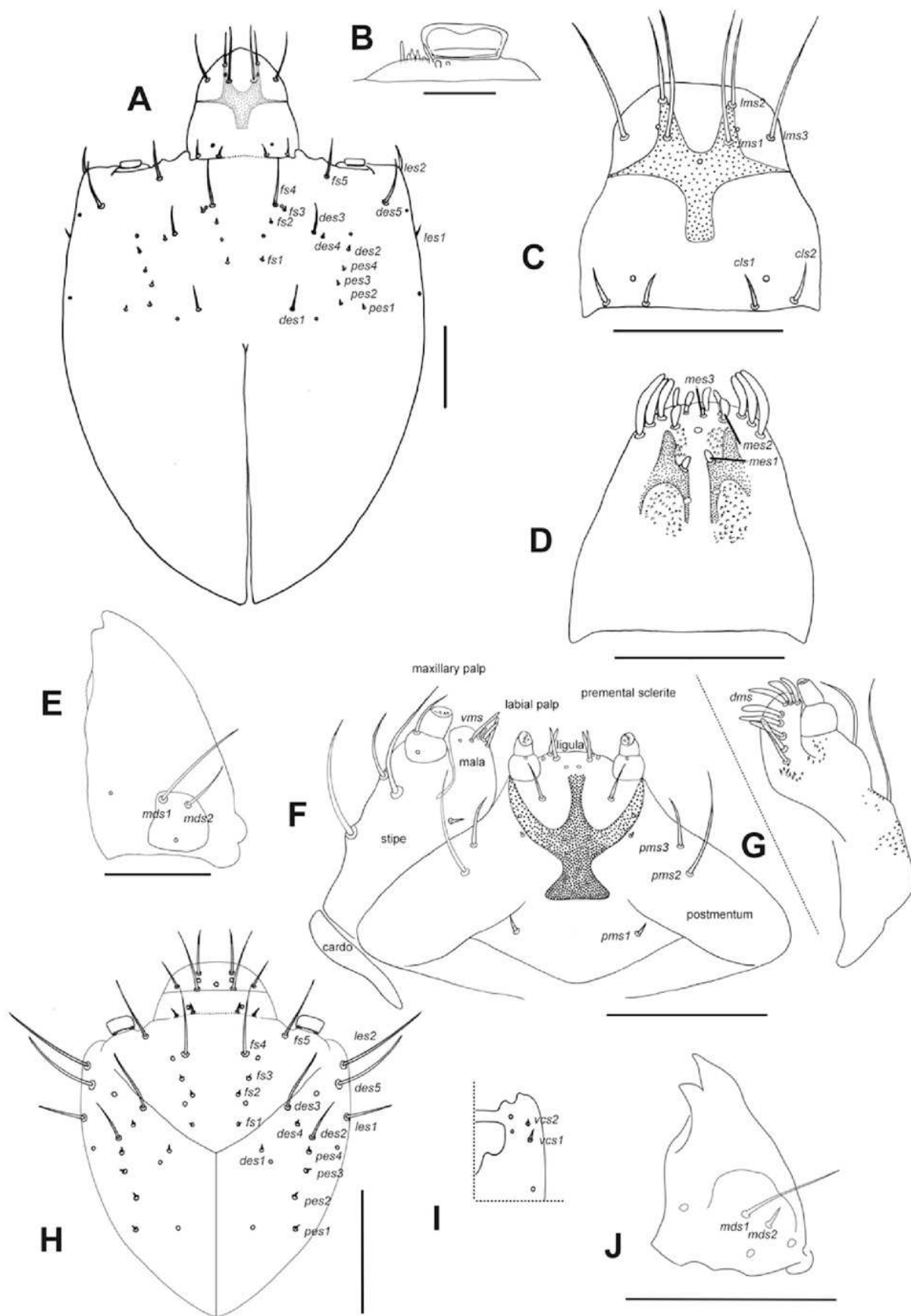


Figure 3

Leschenius vulcanorum, larva.

(A—D) Body parts and chaetotaxy, mature larva. (A) Prothorax, mesothorax, metathorax, and abdominal segment I, one side from mid-dorsum to mid-ventral. (B) Detail of pedal area. (C) Abdominal segment IV, dorso-lateral parts. (D) Abdominal apex, segments IX and X, caudal view. (E) Spiracles from thorax and abdominal segments I, IV, and VIII, ~~mature larva~~. (F) Spiracles from thorax and abdominal segments I, IV, and VIII, first instar larva. Scales A—D=1mm, E=0.5mm; F=0.1mm.

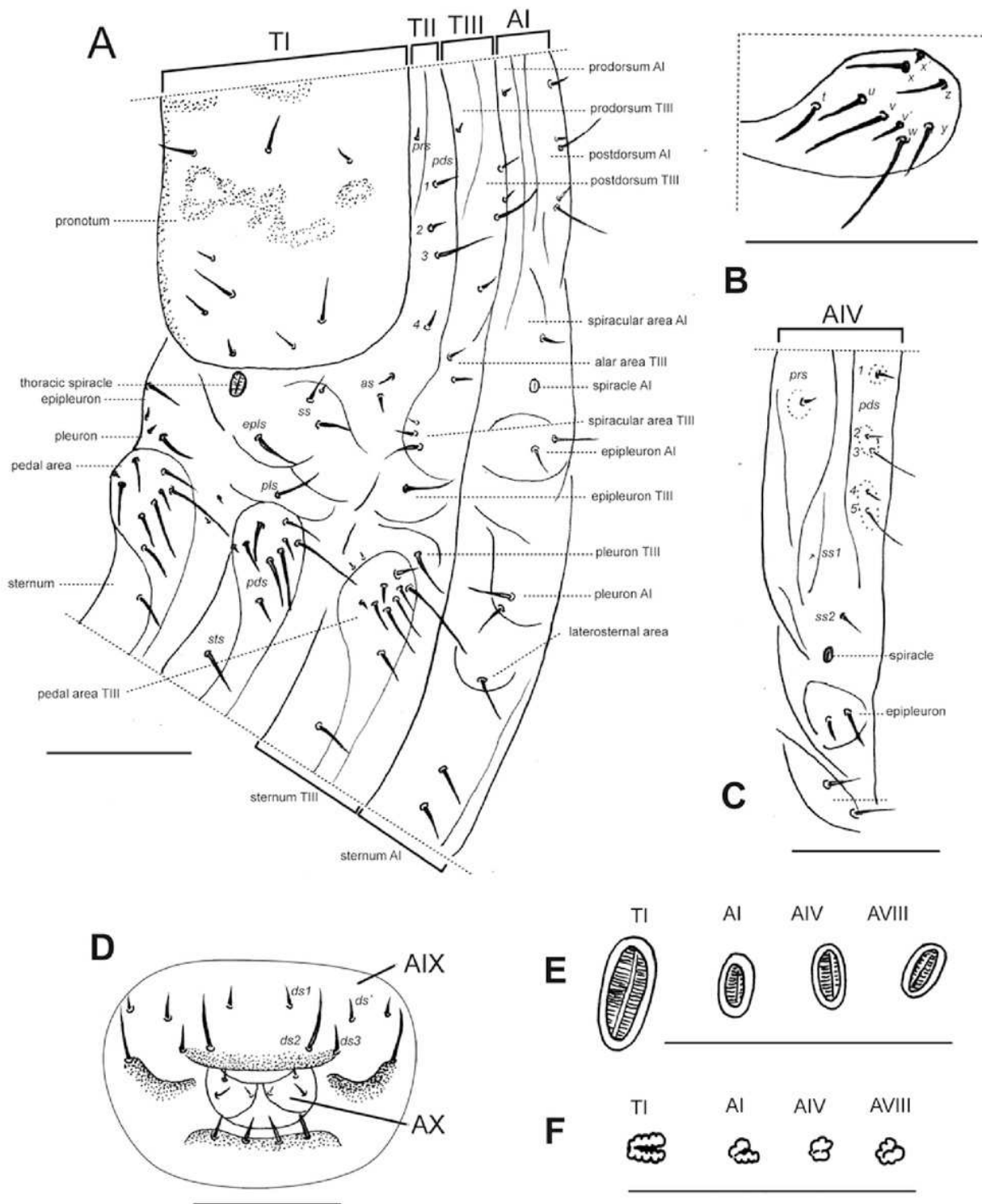


Figure 4

Types, females, corresponding to the four ~~species names~~ of *Leschenius vulcanorum*.

(A) Lectotype of *Canephorus vulcanorum* Kirsch 1889, MTD. (B) Lectotype of *Amphideritus brevis* Oliff 1891, MNHN. (C) Lectotype of *Amphideritus pigmaeus* Oliff 1891, MNHN. (D) Lectotype of *Caulostrophus aequatorialis* Kirsch 1889, MTD. Scales 1mm.



Figure 5

Photographs of *Leschenius* species.

(A) *Leschenius vulcanorum*, male, habitus dorsal view. (B-F) *Leschenius ventrilingulatus*. (B) holotype female, habitus dorsal view. (C) Paratype male, habitus dorsal view. (D) Holotype female, ventral view. (E) Holotype female, habitus lateral view. (F) Holotype female, head, frontal view. (G-F) *Leschenius bifurcatus*. (G) Female, habitus dorsal view. (H) Male, habitus dorsal view. Scales 1 mm.

A



B



C



D



E



F



G



H



Figure 6

Morphological characters, and female terminalia of *Leschenius ventrilingulatus*, and male terminalia of *Leschenius* species

Leschenius ventrilingulatus (A-F). (A) Female, left antenna. (B) Female, sternite VIII. (C) Detail of plate of sternite VIII. (D) Female genitalia, ventral view. (E) Detail of distal third of ovipositor. (F) Spermathecae with spermathecal duct. (G-I) Aedeagus, lateral view. (J) Detail of apex, lateral view, left: phenotype from Imbabura, right: typical phenotype. (K-M) terminal portion of tube, ventral view. (G, K) *L. vulcanorum*. (H, L) *L. ventrilingulatus*. (I, J, M) *L. bifurcatus*. Scales A = 1 mm; B-K = 0.5mm.

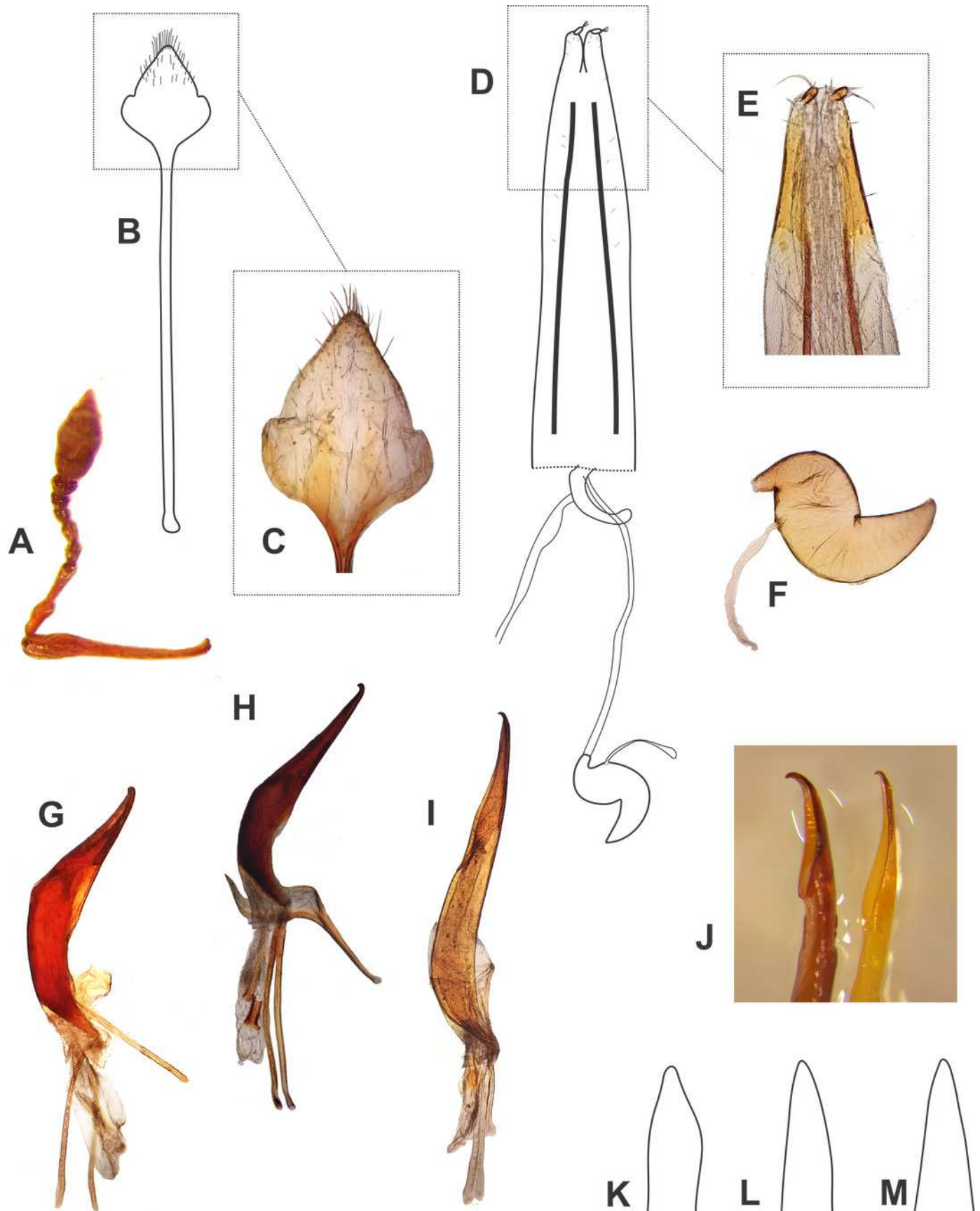


Figure 7

Distribution map of the seven species of *Leschenius*.

Ecuador and southern Colombia are shown in detail. Species references: *L. nigrans*, white circle; *L. rugicollis* white square; *L. vulcanorum*, parthenogenetic form white ellipse, bisexual form grey ellipse; *L. manuela* white triangle; *L. bifurcatus* black star; *L. silviae* black triangle; *L. ventrilingulatus* white star.

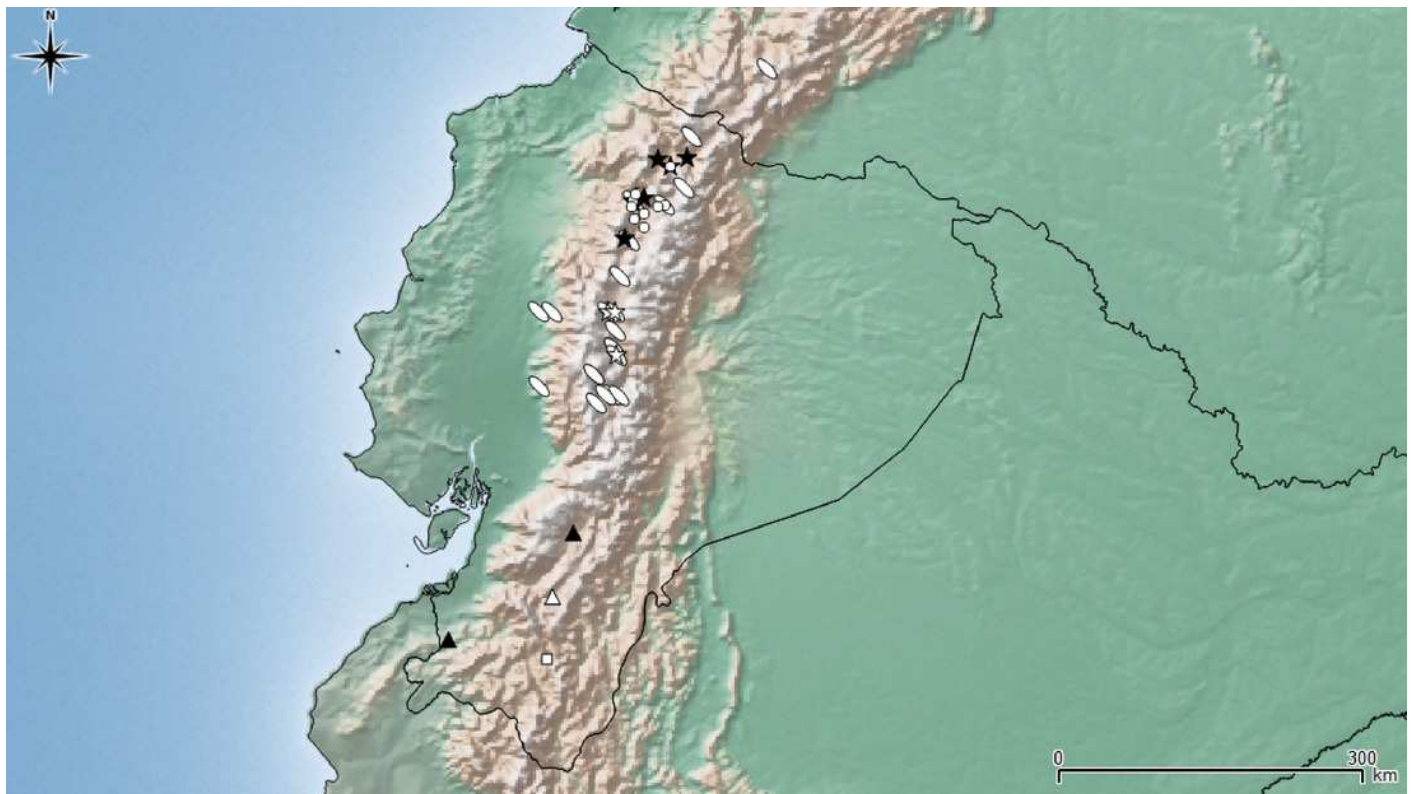


Table 1 (on next page)

List of characters, character states and coding.

Table 1. List of characters, character states and coding

External morphology

0. Body size (length in dorsal view, from apex of rostrum to apex of elytra): **small** (less than 8 mm long) (0); **medium sized** (between 8-10 mm) (1); **large** (over 10 mm long) (2).
1. **Elytral vestiture: squamose (0); setose (1); scarce or absent (2).**
2. Elytral setae: absent (0); short, suberect (1); long, erect (2).
3. Rostrum and forehead: smooth (0); punctuate or foveolate (1); foveolate-strigose (2); coarsely strigose (3)
4. Pronotum: smooth (0); punctuate or foveolate (1); foveolate-granulose (2); tuberculate (3).
5. Relative length of rostrum: LR\WRa more than 1 (0); LR\WRa 0.96-1(1) less than 0.95 (2).
6. Sides of rostrum: slightly convergent towards apex (WRb\WRa less than 1.4) (0); moderately convergent towards apex (WRb\WRa more than 1.4) (1)
7. Rostral sulcus: reaching forehead (0); exceeding posterior margin of eyes (1).
8. Size of epistome: narrow (0); moderately wide (1); very wide (2).
9. Epistome: depressed (0); elevated (1).
10. **Pre-epistome: absent or reduced (0); well developed (1).**
11. Eyes: strongly convex (0); moderately convex (1).
12. Length of antennal scape: short, not reaching posterior margin of eyes (0); reaching posterior margin of eye (1); slightly exceeding posterior margin of eyes (2).
13. Ratio between length of funicle segments 2 and 1: La2/La1 more than 1.5 (0); between 1.1 and 1.49 (1); subequal (2).
14. Ratio between maximum width and length of pronotum: W/L: less than 1.3 (0); more than 1.3 (1).
15. Shape of pronotum: subcylindrical (0); slightly conical (1).
16. Sides of pronotum: almost straight to slightly curved (0); moderately curved (1); strongly curved (2).
17. Pronotal base: straight (0); curved backwards (1); “V” shaped (2); bisinuate (3).

18. Projection of lateral angles of pronotum of males: absent (0); present (1).
19. Ratio between maximum length and width of elytra: L/W more than 1.5 (0); less than 1.5 (1)
20. Maximum width of elytra: about middle (0); at posterior third (1); at anterior third (2).
21. Elytral base: bisinuate (0); straight to slightly curved backwards (1); strongly curved backwards (2).
22. Humeral angles of males: not projected (0); anteriorly projected (1).
23. Elytral humeri: moderately prominent (0); slightly prominent to absent (1).
24. Apical projection of elytra: absent (0); present (1).
25. Elytral apex: entire (0); slightly divided (1); strongly divided or bifid (2).
26. **Elytral intervals**: slightly wider than striae (1.5-2x) (0); about same width of striae or slightly slender (1).
27. **Elytral intervals**: flat to slightly convex (0); moderately convex (1); strongly convex (2).
28. **Procoxae**: contiguous to slightly separate (0); distinctly separate from each other (1).
29. **Procoxae**: almost contiguous with anterior margin of prosternum (0); about 2x closer to anterior than to posterior margin (1); less than 2x closer to anterior than to posterior margin of prosternum (2).
30. **Row of denticles on inner margin of tibiae: present on three pairs of tibiae (0); present on pro- and mesotibiae (1); present only on protibiae (2); absent on three pairs of tibiae (3).**
31. Corbel of metatibial apex: broad, squamose (0); narrow to moderately broad, squamose (1); narrow, setose or denuded (2); absent (3).
32. Apical setal comb of metatibiae: longer than dorsal comb (0); about as long as dorsal comb (1); shorter than dorsal comb (2).
33. Ratio between length of ventrite 2 and ventrites 3+4 (L2/L3+4); subequal (0); between 1.25-1.5 (1); more than 1.5x (2)
34. Posterior margin of of ventrite 5 in females: rounded (0); blunt (1); escavate (2); slightly pointed (3).
35. Posterior margin of ventrite 5 in males: rounded (0); bilobated (1); emarginate (2) blunt (3).

Female terminalia

36. Plate of female sternite VIII: subrhomboidal, elongate (basal half longer than apical half) (0); subrhomboidal, not elongate (basal and apical half subequal) (1).
37. Apodeme of female sternite VIII: less than 2.7x longer than plate (0); more than 2.7x longer than plate (1).
38. Ovipositor: about as long as to longer than ventrites 1-5 (0); $2\frac{1}{3}$ to $3\frac{1}{4}$ length of ventrites 1-5 (1); about $1\frac{1}{2}$ or less the length of ventrites 1-5 (2)
39. Rows of setae along sides of baculi (ovipositor): absent (0); present (1).
40. Length of spermathecal duct: as long as half of the length of ovipositor (=medium-sized) (0); shorter than half of the length of ovipositor (=short) (1).
41. Spermathecal body: subcylindrical (0); subglobose (1); globose (2).
42. Duct-lobe (collum) of spermatheca: conical, very short (0); truncate conical, short (1); tubular (2)
43. Gland-lobe (ramus) of spermatheca: indistinct to slightly developed (0); well-developed (1).
44. Cornu of spermatheca: short (0); medium length to long (1); very long (2).

Male genitalia



45. Ratio between length of penis apodemes and length of penis body (LAp/Lml): apodemes slightly shorter than penis body, ($2\frac{1}{3}$ - $3\frac{1}{4}$) (0); about half as long as penis body (1).
46. Angle between longitudinal axis of penis body and its apodemes: almost flat (0); obtuse to about 90° (1).
47. Apex of penis  tapering into a long acute projection (0); slightly pointed (1); rounded, with a pointed projection at apex (2); evenly rounded (3).
48. Endophallic armature: absent, no distinct sclerotized pieces (0); present, with wing-like sclerotized pieces (1) with long sclerotization like flagelum (2).
49. Apex of penis  not recurved (0); dorsally slightly recurved (1) dorsally strongly recurved (2)

Table 2(on next page)

Data matrix of *Leschenius* plus five outgroups.

1 Table 2. Data matrix of *Leschenius* plus five outgroups.
2

	0										1										2									
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
<i>Melanocyphus lugubris</i>	2	2	0	1	1	0	0	0	1	0	0	1	0	2	0	0	1	3	1	0	1	0	0	0	1	0	1	2	0	2
<i>Trichocyphus formosus</i>	2	1	2	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	-	0	0	0	-	0	0	0	0	0	0	2
<i>Amitrus nitens</i>	2	2	0	1	[1 3]	0	1	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1
<i>Amphideritus vilis</i>	1	1	2	3	2	0	1	0	2	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Asymathetes pascoei</i>	0	0	1	2	1	1	1	0	0	0	0	1	1	1	0	0	2	1	0	1	2	0	0	0	0	0	0	1	1	1
<i>Leschenius rugicollis</i>	1	2	1	3	2	1	0	1	0	0	1	0	1	1	0	1	0	2	1	1	0	2	1	1	1	1	1	0	1	0
<i>Leschenius nigrans</i>	2	2	1	2	1	1	0	1	0	0	1	1	1	0	0	1	1	2	1	0	2	1	1	1	1	2	0	0	1	0
<i>Leschenius vulcanorum</i>	0	2	1	2	1	2	1	0	0	0	1	1	2	1	1	1	1	2	0	1	0	1	0	1	0	0	1	0	1	0
<i>Leschenius manuli</i>	1	2	1	3	2	1	0	1	0	1	1	0	1	2	1	1	1	2	0	1	0	2	1	1	1	0	0	0	1	0
<i>Leschenius bifurcatus</i>	2	2	1	1	1	1	0	1	0	1	1	1	2	2	0	0	0	0	-	0	0	1	0	1	1	2	1	0	1	0
<i>Leschenius silviae</i>	1	2	1	2	1	1	0	1	0	0	1	1	2	0	1	0	1	2	1	1	2	2	1	1	1	0	1	0	1	0
<i>Lescheniu ventrilingulatus</i>	0	[1 2]	1	2	1	2	1	0	0	0	1	1	2	2	1	0	1	2	0	1	0	1	0	1	0	0	1	0	1	0

3

	3										4									
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
<i>Melanocyphus lugubris</i>	3	3	1	0	0	-	1	0	1	0	-	2	0	1	0	0	0	1	0	0
<i>Trichocyphus formosus</i>	0	0	0	0	1	-	1	0	1	1	0	0	0	0	1	-	-	-	-	-
<i>Amitrus nitens</i>	1	1	1	0	[0 1]	0	1	0	2	1	1	0	1	0	1	0	0	2	1	0
<i>Amphideritus vilis</i>	2	0	2	0	3	0	1	1	1	0	0	0	1	0	1	0	0	2	0	0
<i>Asymathetes pascoei</i>	2	1	2	2	1	2	1	1	0	0	0	0	1	0	2	0	0	1	0	0
<i>Leschenius rugicollis</i>	1	1	1	1	3	1	1	0	1	0	0	0	1	0	2	0	0	3	1	0
<i>Leschenius nigrans</i>	2	0	0	1	3	3	1	0	1	1	0	0	1	0	2	1	1	1	1	0
<i>Leschenius vulcanorum</i>	2	1	1	1	2	3	0	0	1	0	0	0	1	0	1	0	0	0	2	1
<i>Leschenius manuli</i>	2	2	1	1	3	2	1	1	1	1	1	0	1	1	1	0	0	3	2	0
<i>Leschenius bifurcatus</i>	2	3	1	1	0	1	0	0	1	1	1	0	1	1	2	1	0	1	1	2
<i>Leschenius silviae</i>	1	2	0	1	2	3	1	0	1	0	0	1	2	0	2	1	1	1	0	0
<i>Leschenius ventrilingulatus</i>	2	1	1	-	3	1	1	1	1	1	0	0	1	0	1	0	0	0	2	1

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