

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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35 **Abstract**

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37 Northern Andes, in Colombia and Ecuador. Among its species, *Leschenius vulcanorum* stands
38 out as an important pest of potatoes in its parthenogenetic form, known as “tiroteador de la
39 papa”. In this study, the adult male and the larval stage (first and mature larvae) of *L.*
40 *vulcanorum* are described and illustrated for the first time. A description of the male
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42 *ventrilingulatus* sp. nov., described from Ecuador. An updated phylogenetic analysis was
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47 wide at base), the female has ventrite 4 with a posterior rounded projection, and posterior margin
48 of ventrite 5 subacute, not excavated. This paper also includes lectotype designation, a revised
49 key to all known species of *Leschenius*, habitus photos of males and females, illustrations of
50 genitalia, and a distribution map.

51

52

53 **Introduction**

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

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

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

81

82

83

84 Materials & Methods

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

90 ~~Immature specimens: 1 mature larva and 4 submature larvae collected with associated~~
91 ~~adults with the following data:~~ Colombia, Municipio de Sibaté, vereda el Romeral, 4°26'3" N,
92 74°14'8" O (3100 masl), J.E.C. Gomez leg., 2009; 10 first instar larvae ~~reared from eggs~~
93 ~~deposited by adults kept in captivity, with collection data as above.~~ The slide-mounted larval
94 specimens are deposited at the MLP. Techniques for dissection of larvae, terminology and
95 abbreviations herein applied corresponds to Marvaldi (1998).

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

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

106 The electronic version of this article in Portable Document Format (PDF) will represent a
107 published work according to the International Commission on Zoological Nomenclature (ICZN),
108 and hence the new names contained in the electronic version are effectively published under that
109 Code from the electronic edition alone. This published work and the nomenclatural acts it
110 contains have been registered in ZooBank, the online registration system for the ICZN. The
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114 available from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS.

115

116 **Phylogenetic analysis**

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

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

129 A cladistic analysis was conducted with **TNT** (Goloboff & Catalano, 2016), using the
130 “traditional search” algorithm, with 100 random addition sequences, Tree Bisection and
131 Reconnection (TBR) branch swapping, holding 10 trees during each replication. The most
132 parsimonious tree was rooted with *Melanocyphus lugubris*. Clade stability was evaluated with
133 1000 replication Bootstrap (BT) (Felsenstein, 1985), support values over 50 % were indicated
134 below branches. The total length (L), the consistency index (CI) (Kluge & Farris, 1969), and the
135 retention index (RI) (Farris, 1989) of the most parsimonious trees (MP tree) were calculated
136 excluding the uninformative characters. The character changes were mapped on the tree using
137 fast (ACCTRAN) optimization with WINCLADA1.00.08 (Nixon, 2002).

138
139

140 **Results**

141 **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
142 genus *Leschenius*, sharing the synapomorphies of the genus: the pre-epistome well developed
143 (character 10.1); the pronotal base ‘V’-shaped (character 17.2); the elytral humeri slightly
144 prominent to absent (character 23.1); and the procoxae almost contiguous with anterior margin of
145 prosternum (character 29.0). 

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

161 The other subclade includes *L. rugicollis* and *L. manueli* and is supported by the rostrum and
162 forehead coarsely strigose (character 3.3), and pronotum foveolate-granulose (character 4.2),
163 ~~with strongly convex eyes (character 11.0), and apex of median lobe evenly rounded (character~~
164 ~~47.3).~~

165

166 **Taxonomy**

167 ***Leschenius* del Río 2012**

168

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

171

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

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

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

212
213 **Remarks.** The characters mentioned above for the first larva, newly hatched, are exclusive of the
214 first instar (see also *Marvaldi & Loiácono, 1994*). Additional differences between early and older
215 instar larvae involve relative dimension of structures, like the antennae, which are relatively
216 much larger in the first instar; the pigmentation and level of sclerotization of body areas tend to
217 increase in successive instars; the differences in length between setae of body areas are higher in
218 early instars.

219
220 **Comparative notes.** The larval characters given herein for the genus *Leschenius* are in full
221 agreement with those defining the tribe Naupactini (*Marvaldi & Loiácono, 1994*) or *Naupactus*
222 and allied genera (*Marvaldi, 1998*). Two apparently distinct features of the mature larva studied

223 of *L. vulcanorum* are the *des1* well developed (in known mature larvae of other Naupactini *des1*
224 is minute or very small); also, setae *x* and *y* of pedal areas of thoracic segments are subequal (in
225 other Naupactini as *Naupactus*, seta *x* is distinctly smaller than *y*). Larval characters deemed as
226 diagnostic for the species are given below.

227

228

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

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

231 *Canephorus vulcanorum* Kirsch 1889: 17; Strand 1943: 96 (*Canephorulana*);
232 Kuschel 1955: 277 (*Amitrus*); Kuschel in Wibmer & O'Brien 1986: 53 (*Asymmathetes*) (Fig.
233 4A).

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

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

240 *Caulostrophus aequatorialis* Kirsch 1889: 13; Dalla Torre, Emden & Emden 1939: 319
241 (*Macrostylus (Amphideritus)*); Kuschel in Wibmer & O'Brien 1986: 53 (*Asymmathetes*) (Fig.
242 4D). **Syn. n.**

243

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

245

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

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

255

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

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

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

270

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

273 **Paralectotype**, Ecuador, Sangay, 3500m, ~~cotypus, MTD~~. ~~Lectotype of *Caulostrophus*~~
274 ~~*aequatorialis* Kirsch, female, Cotopaxi, 5688, Typus, MTD, here designated (Fig. 4D).~~
275 ~~Lectotype of *Amphideritus brevis* Oliff, female, Ecuador feet, Ed. Whymper, MNHN, here~~
276 ~~designated (Fig. 4B).~~ ~~Lectotype of *Amphideritus pigmaeus* Oliff, female, Chimborazo, Ecuador,~~
277 ~~12-13000 feet, Ed Whymper, MNHN, here designated (Fig. 4C).~~

278

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

284 *radiata*, adults feed, Lopez col (1f USNM); Guamote, 3-7-1969, en cocoons of alfalfa plants (1f
285 USNM); Guaslam prov, 1-22-60-on bucts of young corn, Merino (2f USNM); Quimiag on
286 maize, Jan 1979 Kirckhy (2f BMNH); Riobamba, 3-VII-1905, unter steinen, Ohaus (17f ZMB),
287 20-XI-05 (1f ZMB), 27-XI-05 (2f ZMB); Riobamba, Ause de Cubillin, 3500, 5-Vii-05 Ohaus
288 (42f ZMB). **Cotopaxi:** 71 km W Latacunga under stones May 1, 1978, O'Brien & Marshall (1f
289 1m MLP; 45 km W Latacunga, under stones May1 1978, Obrien & Marshall (8f MLP); 21 km S
290 Latacunga, April 25 1978, CW&L Obrien & Marshall (1f MLP); 6 km W Latacunga, under
291 stones, May1 1978, Obrien & Marshall (3f MLP); Latacunga, XI 1981 Onore Brit Mus 1990-214
292 (1f BMNH); 15 km W entrance PN Cotopaxi, April 30 1978, Obrien & Marshall (4f MLP); 14
293 km W entrance PN Cotopaxi, April 30 1978, Obrien & Marshall (1f MLP); Cotopaxi, P. 13 km S
294 Latacunga along PanAma, XI-3-77, G Noonan, M. Moffett, under clumps soil and grass, rocks,
295 debris-in green grassy field w green short grass ca 2600m. (13f 1m MLP); Tilipulo, V-III-1981,
296 G. Onore Brit Mus 1985-254 (4f BMNH). **Bolivar:** Guaranda, X-I-1955, on new corn (7f
297 USNM). **Loja.** Loja, Ohaus (2f ZMB). **Pichincha:** 38.8km NE Quito on PanAm XI-8-77, G
298 Noonan, M. Moffett, under rocks on dirt clumps, in areas with sparse to very sparce short grass
299 ca 2200m. (1f MLP). **Tungurahua:** SE end Ambato, XI-1-77, G Noonan, M. Moffett, under
300 rock in fields w short sparce grass, soil dry under stones, ca 2500m. (2f MLP); 13km NE Baños,
301 April 26 1978, Obrien & Marshall (1f MLP); Baños, 1800m, 9-V-37 Brundage (2f USNM);
302 Baños, X-4-44, EJ Hambleton (1f USNM); Pomasqui, X-7-54, Merino, orange trees (4f USNM);
303 Totoras, 7 km SE Ambato, April 26 1978, Obrien & Marshall (3f MLP). Plus, the material listed
304 in *del Río, Marvaldi & Lanteri (2012)*.

305

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

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

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

318

319

320 ***Leschenius ventrilingulatus* del Río & Marvaldi, sp. n.**

321 **(Figs 5B-F; 6A-F, H, L)**

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

332

333 **Description. Female** (Figs. 5B, D–F). Species medium-sized (LB, 5.0–6.0mm). Tegument
334 visible, dark brown to reddish brown, shiny. Vestiture composed of disperse, pale ocher to cream
335 setae, moderately dense, creamy decumbent setae-like scales, devoid of them on middle (forming
336 wide lateral stripes) on pronotum; grouped on patches on elytra in some cases devoid of scales
337 on middle line; also present on venter and legs (more abundant on distal third of femora).

338 Rostrum very short (Fig. 5F) (L/Wa, 0.73–0.83), sides moderately convergent towards apex
339 (Wb/Wa, 1.31–1.43), dorsum moderately convex. Forehead foveolate–strigose, with longitudinal
340 striae. Vertex sparsely punctuate. Antennae (Fig. 6A) of medium length (LB/LA, 2.50–2.85);
341 scape reaching to slightly exceeding posterior margin of eyes. Funicle with segment 2 about as
342 long as segment 1, both elongated; funicle segments 3–6 slightly longer than wide, and funicle
343 segment 7 as long as wide; club slightly fusiform (L/W, 2.3–2.4). Pronotum (Fig. 5B) slightly
344 subcylindrical, moderately wider than long (W/L, 1.30–1.35), with anterior margin as wide as
345 posterior margin; median groove absent. Scutellar shield subtriangular, large and wide

346 (surrounded by elevated edges), denuded. Elytra (Fig. 5B, E) short (L/W, 1.23–1.33), with
347 maximum width on anterior third, slightly convex; base slightly curved backwards on middle;
348 striae with medium-size punctures; striae 9–10 slightly closer on posterior two-thirds; intervals
349 flat, about twice as long as striae; elytral apex acute, entire, not projected or bifurcate. Legs.
350 Procoxae much closer to anterior than posterior margin of prosternum; protibiae with row of six
351 or seven acute small denticles (on distal two-thirds of tibiae) and medium sized mucro; meso and
352 metatibiae without denticles and with small mucro; metatibial apex with narrow corbel covered
353 with disperse small elongate cream scales; apical and dorsal combs subequal. Abdomen (Fig.
354 5D). Intercoxal portion of ventrite 1 slightly broader than metacoxal cavities (1.10–1.15x);
355 ventrite 2 longer than ventrites 3 and 4 combined (1.60x without projection; 1.10 along midline);
356 ventrite 4 with a posterior rounded projection; posterior margin of ventrite 5 subacute not
357 excavated; tergites I–VII membranose. Terminalia. Sternite VIII (Figs. 6B–C) with plate sub-
358 rhomboidal, not elongate, with tuft of medium-sized and coarse setae, and with shorter setae on
359 apical third; ‘V’-shaped sclerotization with lateral arms reaching two-thirds of plate, and lateral
360 margins sclerotized; apodeme 2.8–3.0x longer than plate. Ovipositor (Figs. 6D–E) as long as
361 ventrites 1–5; with scattered fine short setae on sides of baculi on anterior third; ventral baculi
362 subparallel; styli wide. Spermathecal body (Fig. 6F) sub-cylindrical; collum (duct-lobe) conical,
363 short; ramus (gland-lobe) indistinct; cornu long; spermathecal duct (Fig. 6D) short, half as long
364 as ovipositor, or 3x the maximum width of spermatheca, membranous, moderately wide.
365 Male (Fig. 5C). Same size as female (4.8–5.5 mm); rostrum less conical (Wb/Wa, 1.32–1.37);
366 antennal club more elongate (L/W, 2.6–2.7); elytra slightly more elongate (L/W, 1.30–1.35);
367 metatibia with larger mucro than in female; ventrite 4 without posterior projection; posterior
368 margin of ventrite 5 blunt. Genitalia (Figs. 6H, L). Penis (median lobe) slightly curved in lateral
369 view, tapering towards apex, with dorsad recurved hook-like apex; penis as long as abdomen;
370 penis apodemes slightly shorter than penis body (0.8x); endophallus armed with minute spicules
371 and with a sclerotized flagellum, with a denticulated blade (Fig. 6H).
372 Morphometrics. Holotype, female: rostrum L/Wa: 0.77, Wb/Wa: 1.31; antenna LB/LA: 2.85,
373 antennal club L/W: 2.31; pronotum W/L: 1.34; elytra L/W: 1.33; LE/LP: 2.6.
374
375 **Etymology.** The specific name refers to the tongue-like projection of the female venter.
376

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

384

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

390

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

393

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

396

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

398

399 **Description of male** (Fig. 5H). Similar size as female, slightly smaller (Fig. 5G) (10-13 mm);
400 rostrum (L/Wa, 1.0-1.1; Wb/Wa, 1.30–1.45); antennal club slightly more elongate (L/W, 3.1–
401 3.4); pronotum (W/L, 1.17-1.19); elytra (L/W, 1.60–1.65) with projected apex but not bifurcated,
402 only slightly divided; ventrites 3-5 not bulged as female, posterior margin of ventrite 5 blunt.
403 Genitalia (Figs 6I, J, M). Penis body slightly curved in lateral view, tapering towards apex (Fig.
404 6M), with dorsad strongly recurved hook-like apex (Fig. 6J); penis longer than abdomen (1.25–
405 1.30); penis apodemes much shorter than median lobe (0.4x); endophallus armed with minute
406 spicules and with two long wing-shaped sclerites (Fig. 6I).

407

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

415

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

420

421

422 **Key to species of *Leschenius***

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

424

- 425 1. Size 4–8mm (usually 5–7mm, exceptionally more than 8mm but never more than 9mm).
426 Rostrum very short (L/W less than 0.95, usually near 0.8); pronotum with setae forming two
427 feeble lateral stripes; elytral apex not
428 projected..... 2
- 429 1'. Size 8–12.5mm. Rostrum moderately short (L/W more than 0.96, usually 1); pronotum
430 without or with scattered setae, never forming lateral stripes; elytral apex projected
431 backwards..... 3
- 432 2. Elytra with creamy decumbent setae like scales grouped on patches on entire elytra. Pronotum
433 subcylindrical, with anterior margin as wide as posterior margin. Metatibial apex with narrow
434 corbel. Female with ventrite 4 with a posterior rounded
435 projection..... *ventrilingulatus, n. sp* (Figs. 5B–F)
- 436 2'. Elytra devoid of creamy decumbent setae like scales, or if present, limited to the margin
437 (intervals 9–10). Pronotum slightly subconical, with posterior margin wider than anterior
438 margin. Metatibial apex with moderately broad corbel (width: 1/3 of the length of the tibial

439 apex). Female with ventrite 4 without a posterior rounded
440 projection.....*vulcanorum* (Figs. 4A–D, 5A, see fig. 1 of *del Río, Marvaldi &*

441 *Lanteri, 2012*)

442 3. Pronotum with posterior margin as wide as anterior margin. Elongate elytra (3X or more the
443 length of pronotum). Elytral apex, in females strongly projected backwards and distinctly
444 bifid or divided; in males, moderately projected and rounded to slightly
445 divided.....*bifurcatus* (see figs. 2–3 of *del Río, Marvaldi & Lanteri, 2012*)

446 3'. Pronotum with posterior margin distinctly wider than anterior margin. Oval elytra (less than
447 2.8x the length of pronotum, usually between 2.2–2.7x). Elytral apex of both males and
448 females moderately projected, entire to slightly divided.....4

449 4. Corbel plate of metatibia broad (width: almost half the diameter of apex of
450 tibiae).....*nigrans* (see figs. 9–10 of *del Río, Marvaldi &*

451 *Lanteri, 2012*)

452 4'. Corbel plate of metatibia narrow (less than quarter apex of tibiae).....5

453 5. Body length 8.4–9.3mm, moderate sized. Pronotum as wide as elytra in males. Elytra 2.2–
454 2.45x the length of pronotum. Spermatheca with nodulus not
455 constricted.....6

456 5'. Body length 7.8–8.4mm, small. Pronotum distinctly narrower than elytra in both sexes. Elytra
457 2.5–2.75x the length of pronotum. Spermatheca with tubular nodulus, constricted near
458 spermathecal body.....*silviae* (see figs. 11–12 of *del Río, Marvaldi &*

459 *Lanteri, 2012*)

460 6. Pronotum slightly wider than long (W/L: 1.10–1.25). Ovipositor without setae on sides of
461 baculi. Apex of penis slightly pointed.....*rugicollis* (see figs. 4–5 of *del Río,*
462 *Marvaldi & Lanteri, 2012*)

463 6'. Pronotum of males strongly wider than long (W/L: 1.30–1.35). Ovipositor with conspicuous
464 setae on sides of baculi. Apex of penis rounded.....*manueli* (see figs. 6–8 of *del*
465 *Río, Marvaldi & Lanteri, 2012*)

466

467

468 **Discussion**

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

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

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

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

488 Of particular interest is the occurrence of parthenogenesis within the genus *Leschenius*, and this
489 mode of reproduction was suggested by *del Río, Marvaldi & Lanteri (2012)* for the species *L.*
490 *vulcanorum* and *L. bifurcatus*, based on the apparently absence of males in their populations.
491 The examination of additional material in the present study provided new evidence that suggest
492 *L. bifurcatus* is not parthenogenetic, leaving *Leschenius vulcanorum* as the only parthenogenetic
493 species. The parthenogenesis of *L. vulcanorum* was confirmed by laboratory rearing (*del Río,*
494 *Marvaldi & Lanteri, 2012*). Nonetheless, in the present study, we discovered males of *L.*
495 *vulcanorum*, indicating that this species also has bisexual populations, so far only seen in three
496 localities in Cotopaxi and Tungurahua provinces of Ecuador. The existence of both sexual and
497 parthenogenetic populations within the species supports the idea of a special kind of
498 parthenogenesis, called “geographical parthenogenesis” (Lanteri & Normark, 1995). In *L.*
499 *vulcanorum*, as in other species having this kind of reproduction, the sexual and parthenogenetic
500 forms have different distribution ranges, being the parthenogenetic one more widespread than the

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

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

525 Concerning the immature stages, the study of the larvae of *Leschenius* lead us to confirm
526 that the tribe Naupactini is very homogeneous in larval morphology, as suggested by *Marvaldi*
527 (1998). Also, there seem to be no particular features that could be suggestive as adaptive traits to
528 arid environments. This is not unexpected, since *Leschenius* larvae, like those of most entimines,
529 are subterranean (i.e., endophagous) and then “preadapted” to live in harsh environments.
530 Finally, additional research with molecular tools will be very important to find out the genetic
531 divergence and evolution of the group, and the role of the parthenogenesis. Moreover, the study

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

534

535

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538 examination of the material in their collections.

539

540

541

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576

Figure 1

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

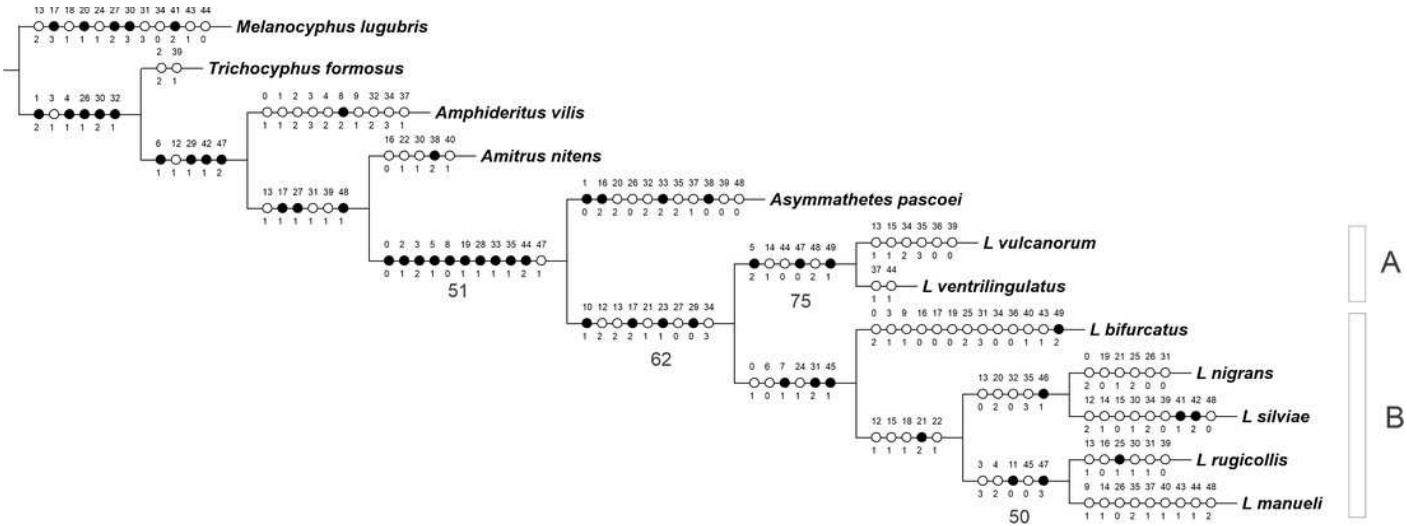


Figure 2

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.

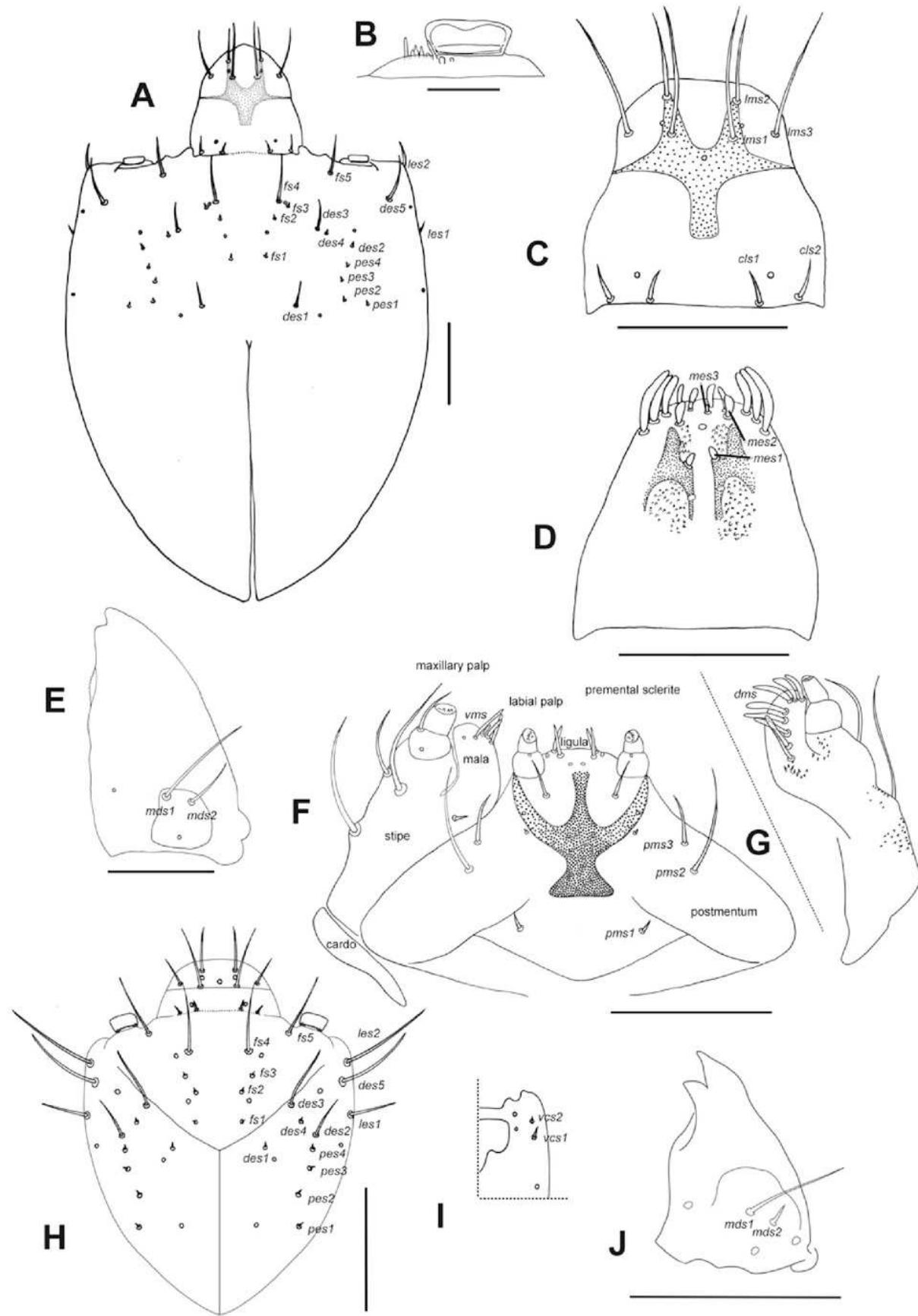


Figure 3

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.

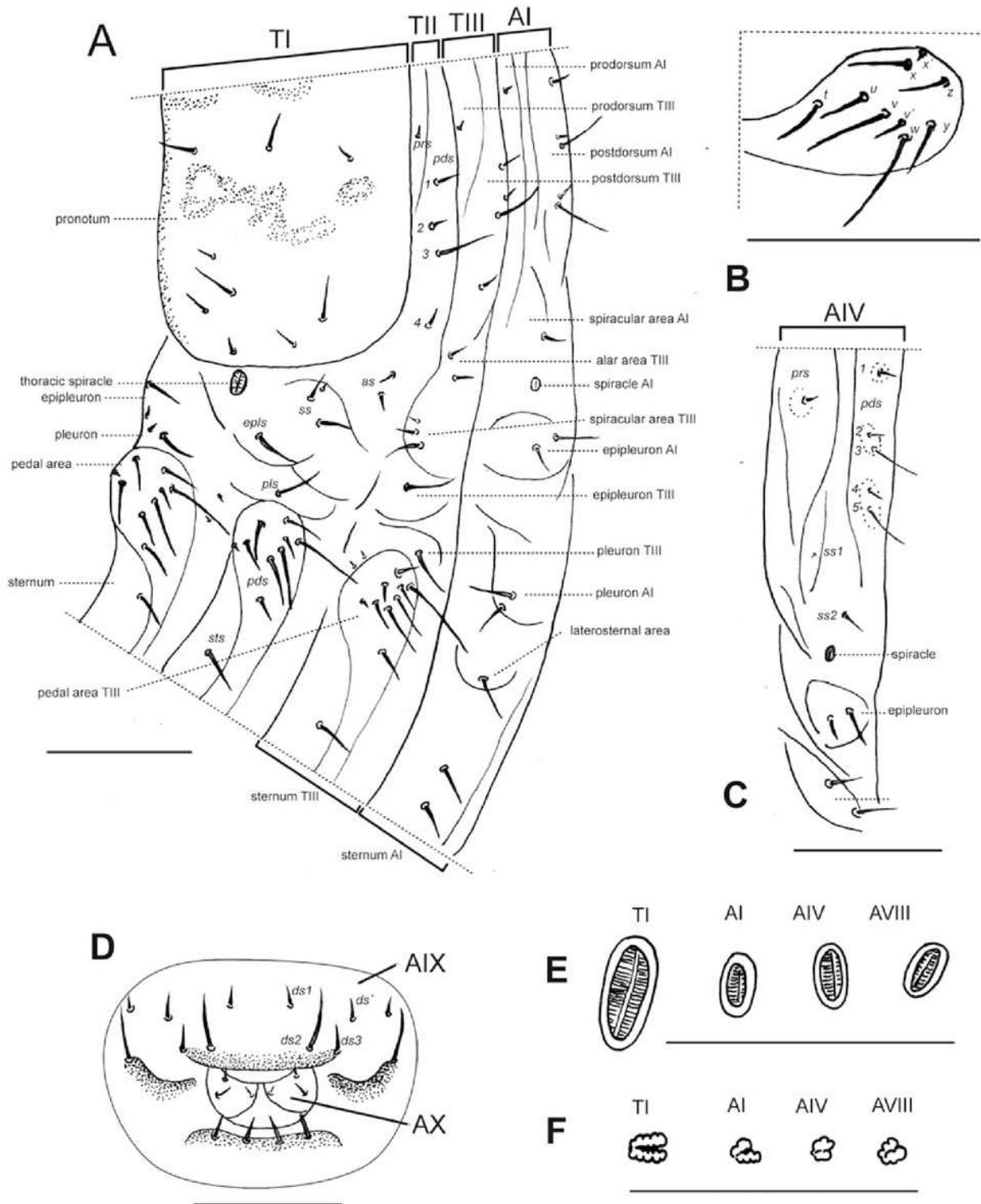


Figure 4

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.

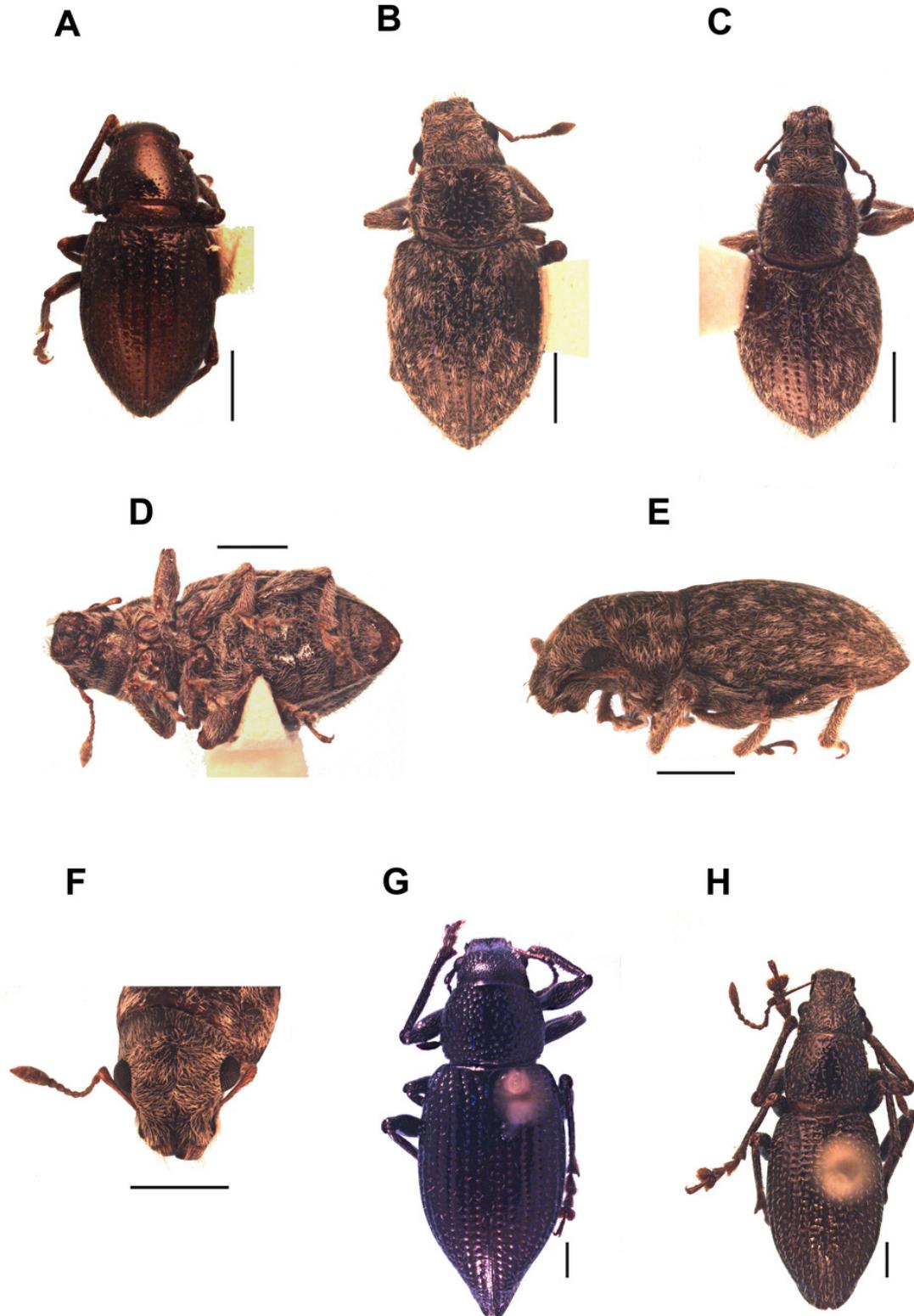


Figure 6

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.

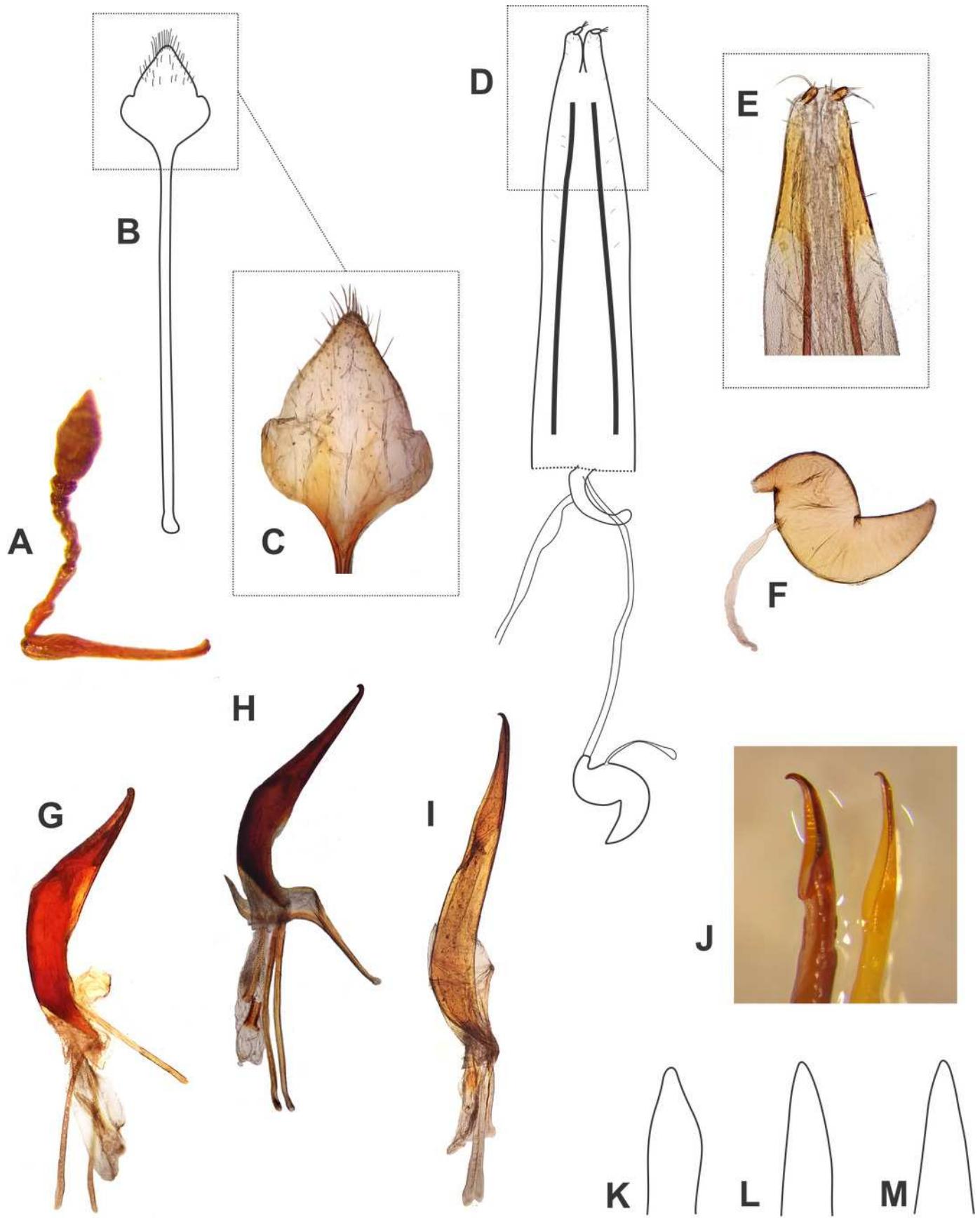


Figure 7

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. manueli* white triangle; *L. bifurcatus* black star; *L. silviae* black triangle; *L. ventrilingulatus* white star.

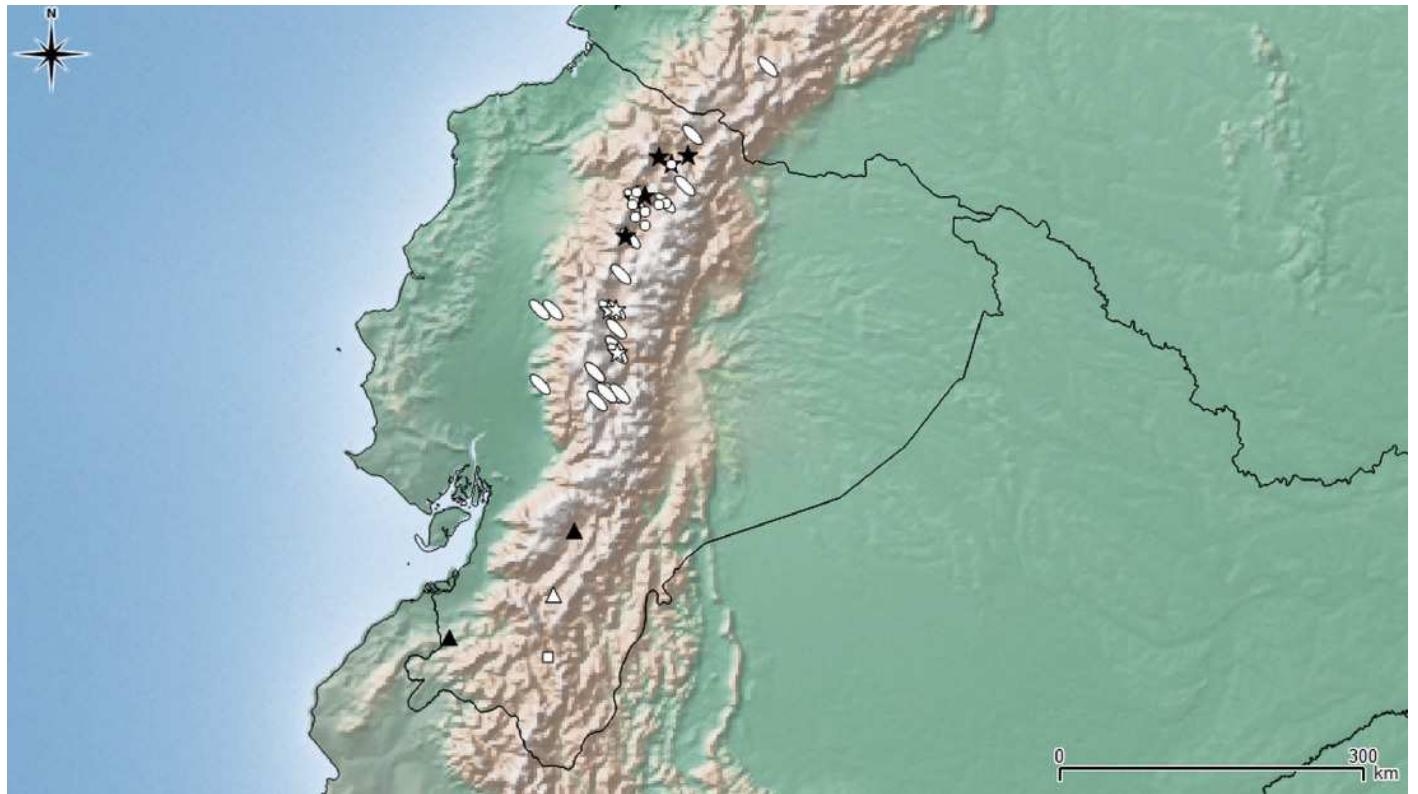


Table 1(on next page)

List of characters, character states and coding.

1 **Table 1. List of characters, character states and coding**

2

3 *External morphology*

4

- 5 0. Body size (length in dorsal view, from apex of rostrum to apex of elytra): **small** (less than 8
6 mm long) (0); **medium sized** (between 8-10 mm) (1); **large** (over 10 mm long) (2).
- 7
- 8 1. **Elytral vestiture**: **squamose** (0); **setose** (1); **scarce or absent** (2).
- 9
- 10 2. **Elytral setae**: **absent** (0); **short, suberect** (1); **long, erect** (2).
- 11
- 12 3. Rostrum and forehead: smooth (0); punctuate or foveolate (1); foveolate-strigose (2);
13 coarsely strigose (3)
- 14
- 15 4. Pronotum: smooth (0); punctuate or foveolate (1); foveolate-granulose (2); tuberculate (3).
- 16
- 17 5. Relative length of rostrum: $LR \setminus WRa$ more than 1 (0); $LR \setminus WRa$ 0.96-1 (1) less than 0.95 (2).
- 18
- 19 6. Sides of rostrum: slightly convergent towards apex ($WRb \setminus WRa$ less than 1.4) (0); moderately
20 convergent towards apex ($WRb \setminus WRa$ more than 1.4) (1)
- 21
- 22 7. Rostral sulcus: reaching forehead (0); exceeding posterior margin of eyes (1).
- 23
- 24 8. Size of epistome: narrow (0); moderately wide (1); very wide (2).
- 25
- 26 9. Epistome: depressed (0); elevated (1).
- 27
- 28 10. **Pre-epistome**: **absent or reduced** (0); **well developed** (1).
- 29
- 30 11. Eyes: strongly convex (0); moderately convex (1).
- 31
- 32 12. Length of antennal scape: short, not reaching posterior margin of eyes (0); reaching posterior
33 margin of eye (1); slightly exceeding posterior margin of eyes (2).
- 34
- 35 13. Ratio between length of funicle segments 2 and 1: $La2/La1$ more than 1.5 (0); between 1.1
36 and 1.49 (1); subequal (2).
- 37
- 38 14. Ratio between maximum width and length of pronotum: W/L : less than 1.3 (0); more than
39 1.3 (1).
- 40
- 41 15. Shape of pronotum: subcylindrical (0); slightly conical (1).
- 42
- 43 16. Sides of pronotum: almost straight to slightly curved (0); moderately curved (1); strongly
44 curved (2).
- 45
- 46 17. Pronotal base: straight (0); curved backwards (1); "V" shaped (2); bisinuate (3).

47
48 18. Projection of lateral angles of pronotum of males: absent (0); present (1).
49
50 19. Ratio between maximum length and width of elytra: L/W more than 1.5 (0); less than 1.5 (1)
51
52 20. Maximum width of elytra: about middle (0); at posterior third (1); at anterior third (2).
53
54 21. Elytral base: bisinuate (0); straight to slightly curved backwards (1); strongly curved
55 backwards (2).
56
57 22. Humeral angles of males: not projected (0); anteriorly projected (1).
58
59 23. Elytral humeri: moderately prominent (0); slightly prominent to absent (1).
60
61 24. Apical projection of elytra: absent (0); present (1).
62
63 25. Elytral apex: entire (0); slightly divided (1); strongly divided or bifid (2).
64
65 26. **Elytral intervals:** slightly wider than striae (1.5-2x) (0); about same width of striae or slightly
66 slender (1).
67
68 27. **Elytral intervals:** flat to slightly convex (0); moderately convex (1); strongly convex (2).
69
70 28. Procoxae: contiguous to slightly separate (0); distinctly separate from each other (1).
71
72 29. **Procoxae:** almost contiguous with anterior margin of prosternum (0); about 2x closer to
73 anterior than to posterior margin (1); less than 2x closer to anterior than to posterior margin
74 of prosternum (2).
75
76 30. **Row of denticles on inner margin of tibiae:** present on three pairs of tibiae (0); present on
77 pro- and mesotibiae (1); present only on protibiae (2); absent on three pairs of tibiae (3).
78
79 31. Corbel of metatibial apex: broad, squamose (0); narrow to moderately broad, squamose (1);
80 narrow, setose or denuded (2); absent (3).
81
82 32. Apical setal comb of metatibiae: longer than dorsal comb (0); about as long as dorsal comb
83 (1); shorter than dorsal comb (2).
84
85 33. Ratio between length of ventrite 2 and ventrites 3+4 (L2/L3+4); subequal (0); between 1.25-
86 1.5 (1); more than 1.5x (2)
87
88 34. Posterior margin of ventrite 5 in females: rounded (0); blunt (1); excavate (2); slightly
89 pointed (3).
90
91 35. Posterior margin of ventrite 5 in males: rounded (0); bilobated (1); emarginate (2); blunt (3).
92

93 *Female terminalia*

94

95 36. Plate of female sternite VIII: subrhomboidal, elongate (basal half longer than apical half) (0);
96 subrhomboidal, not elongate (basal and apical half subequal) (1).

97

98 37. Apodeme of female sternite VIII: less than 2.7x longer than plate (0); more than 2.7x longer
99 than plate (1).

100

101 38. Ovipositor: about as long as to longer than ventrites 1-5 (0); 2\3 to 3\4 length of ventrites 1-
102 5 (1); about 1\2 or less the length of ventrites 1-5 (2)

103

104 39. Rows of setae along sides of baculi (ovipositor): absent (0); present (1).

105

106 40. Length of spermathecal duct: as long as half of the length of ovipositor (=medium-sized) (0);
107 shorter than half of the length of ovipositor (=short) (1).

108

109 41. Spermathecal body: subcylindrical (0); subglobose (1); globose (2).

110

111 42. Duct-lobe (collum) of spermatheca: conical, very short (0); truncate conical, short (1); tubular
112 (2)

113

114 43. Gland-lobe (ramus) of spermatheca: indistinct to slightly developed (0); well-developed (1).

115

116 44. Cornu of spermatheca: short (0); medium length to long (1); very long (2).

117

118 *Male genitalia*

119

120 45. Ratio between length of penis apodemes and length of penis body (LAp/Lml): apodemes
121 slightly shorter than penis body, (2\3-3\4) (0); about half as long as penis body (1).

122

123 46. Angle between longitudinal axis of penis body and its apodemes: almost flat (0); obtuse to
124 about 90° (1).

125

126 47. Apex of penis:  tapering into a long acute projection (0); slightly pointed (1); rounded, with a
127 pointed projection at apex (2); evenly rounded (3).

128

129 48. Endophallic armature: absent, no distinct sclerotized pieces (0); present, with wing-like
130 sclerotized pieces (1) with long sclerotization like flagellum (2).

131

132 49. Apex of penis:  not recurved (0); dorsally slightly recurved (1) dorsally strongly recurved (2)

133

Table 2(on next page)

Data matrix of *Leschenius* plus five outgroups.

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

2

	θ									I									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	0	1	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	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	0	1	0	1	
<i>Leschenius nigранs</i>	2	2	1	2	1	1	0	1	0	0	1	1	0	0	1	1	2	1	0	2	1	1	1	2	0	0	1	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	0	1	0	1	0	1	0	
<i>Leschenius manueli</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>Leschenius 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	0	1	0	1	0	1	0	

3

	3									4									9												
	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>	3	3	1	0	0	-	1	0	1	0	-	2	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Trichocyphus formosus</i>	0	0	0	0	1	-	1	0	1	1	0	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	0	0	2	1	0	0	0	2	1	0	
<i>Amphideritus vilis</i>	2	0	2	0	3	0	1	1	1	0	0	0	0	1	0	1	0	0	2	0	0	0	2	0	0	0	2	0	0		
<i>Asymathetes pascoei</i>	2	1	2	2	1	2	1	1	0	0	0	0	0	1	0	2	0	0	1	0	0	0	1	0	0	0	1	0	0	0	
<i>Leschenius rugicollis</i>	1	1	1	1	3	1	1	0	1	0	0	0	0	1	0	2	0	0	3	1	0	0	0	3	1	0	0	0	0	0	
<i>Leschenius nigранs</i>	2	0	0	1	3	3	1	0	1	1	0	0	0	0	1	0	2	1	1	1	1	0	0	0	2	1	1	1	0	0	0
<i>Leschenius vulcanorum</i>	2	1	1	1	2	3	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0
<i>Leschenius manueli</i>	2	2	1	1	3	2	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	3	2	0	0	0	0	0	0	0	
<i>Leschenius bifurcatus</i>	2	3	1	1	0	1	0	0	1	1	1	1	0	1	1	2	1	1	0	1	1	1	0	1	1	1	0	1	2	0	
<i>Leschenius silviae</i>	1	2	0	1	2	3	1	0	1	0	0	1	1	0	1	2	0	2	1	1	1	0	0	0	2	1	0	0	0	0	0
<i>Leschenius ventrilingulatus</i>	2	1	1	-	3	1	1	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0

4