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A NEW SPECIES OF *LOXANDRUS* LECONTE (COLEOPTERA:CARABIDAE: LOXANDRINI) FROM SOUTH AMERICA

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ABSTRACT

***Loxandrus semperfidelis*, new species** (Carabidae: Loxandrini), is described from its type locality, Orellana Province, Ecuador, and distributional range extending to Peru. This large and robustly–built South American species is distinguished from all other loxandrines by the unequal widths of the elytral intervals, in which odd–numbered intervals are as much as twice as wide as even–numbered ones. Males are distinctive in having a ventral abdominal process, or "keel", which is not known from any other species of Carabidae. Both adult and first instar larval characteristics are described.

KEY WORDS: Neotropical Coleoptera, Pterostichitae, secondary sexual characters

INTRODUCTION

As presently circumscribed *Loxandrus* LeConte includes 229 recognized species (Lorenz 2005), with the vast majority found in South America. Based on casual observation of material presently in collections, the actual species–level diversity is likely to be three times this number or more. Recent works treating portions of *Loxandrus* or loxandrines (Moore 1965; Allen 1972; Allen and Ball 1980; Straneo 1991), which were not intended to test higher–level phylogenetic relationships, assumed *Loxandrus* to be monophyletic. However this is not the case, as *Loxandrus* is presently recognized by a combination of plesiomorphic morphological states, and the genus is rendered paraphyletic by other loxandrine genera (Will unpublished data). Despite recognizing the genus as paraphyletic, the complexity of the group and the large number of undescribed species precludes a meaningful reclassification at this time. Even with flux in the higher classification, I believe it is appropriate and necessary to describe well–defined species (e.g., Straneo 1991; Will 2005), and to name species that have already been used in various investigations such as those on pygidial gland secretions (Will et al. 2000), and that are important exemplars in an ongoing phylogenetic analysis of generic–level taxa in the tribe (Will unpublished data).

MATERIAL AND METHODS

Methods for examination, dissection, description, and illustration of adults follows Will and Liebherr (1997). Digital images were taken using a Microptics XLT digital imaging system. Verbatim type–specimen label data are enclosed in quotation marks. All specimen data have been entered into the EMEC data base and individual records can be accessed online using the database numbers that are included on each specimen as listed below, e.g., EMEC1003639.

The larva used for the description below was reared from an egg produced by one of a series six females collected at Yasuni Station, Ecuador. The adult females were initially placed on dirt and leaf litter from the collection site and then moved to moist sphagnum. Soil and sphagnum were inspected every few days for eggs, which were removed to a small container with soil, sphagnum, or tissue, and kept at various moisture levels and temperatures. In some cases eggs were left untouched in the container with the adults. Although about 20 eggs were found, only a single egg hatched. No sign of development was seen in other eggs, i.e., no embryonic structures were visible through the chorion. The single emerged larva has a slight asymmetry of the head capsule and the urogomphi appear collapsed or shriveled, suggesting that even this emergence was under suboptimal conditions. Soon after the larva emerged from the egg, it was placed into near boiling water for one minute and then cleared in warm 10% KOH. The cleared specimen was neutralized with 10% acetic acid and then washed with water. The specimen was then placed into a larger volume of 4% glycerine and placed on a slide warmer for several days to slowly evaporate the water (Goulet 1977). The glycerine–impregnated larval cuticle was examined under a compound microscope. Illustrations were composed using both camera lucida and by overlaying digital images using standard computer drawing software. The chaetotaxy system, morphological nomenclature, and general form of description follow Bousquet and Goulet (1984) and Bousquet (1985). Institutions that provided material for this study or where material will be deposited include: **CMNH**, Section of Invertebrate Zoology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (R.L. Davidson); **BMNH**, Department of Entomology, The Natural History Museum, London; **CUIC**, Department of Entomology, Cornell University, Ithaca, New York (J.K. Liebherr); **EMEC**, Essig Museum of Entomology, Berkeley, University of

Fig. 1.—Holotype specimen of *Loxandrus semperfidelis*, new species.

California, Berkeley, California (C. Barr); **QCAZ**, Catholic Zoology Museum, Pontificia Universidad Catolica del Ecuador, Quito, Ecuador (G. Onore); **UASM,** Strickland Museum, University of Alberta, Edmonton, Alberta, Canada (D. Shpeley, G.E. Ball); **USNM**, Department of Entomology, United States National Museum of Natural History, Smithsonian Institution (T.L. Erwin).

SYSTEMATIC ACCOUNT

Order Coleoptera Linnaeus, 1758
Family Carabidae Latreille, 1802
Subfamily Harpalinae Bonelli, 1810
Tribe Loxandrini Erwin and Sims, 1984
Genus ***Loxandrus*** LeConte, 1852

Loxandrus semperfidelis, new species

Etymology.—It is with great pleasure that I name this species *Loxandrus semperfidelis* with the specific epithet based on the Latin phrase "*semper fidelis"* as used by the United States Marine Corps. I do this as a salute to George E. Ball for his faithful service as a Marine and to his undiminished Marine Corps bearing that he brings to all that he does.

Type Material.—HOLOTYPE. Male, labeled: "00°40'36"S 76°24'2"W, ECUADOR, Napo Prov., Yasuni Scientific Station, 20:IV:1998,210m,Col.K.Will,Headlamp.U.C.Berkeley,EMEC1003639". [red label] "Holotype, Loxandrus semperfidelis, K.Will 2006" [handwritten]. (EMEC). **ALLOTYPE**. Female Labeled: "00°40'36"S 76°24'2"W, ECUADOR,Napo Prov., Yasuni Scientific Station, 13:IV:1998, 210m,Col.K.Will, Headlamp. U.C.Berkeley, EMEC1003639". [red label] "Allotype, Loxandrus semperfidelis K.Will 2006" [handwritten] (EMEC). **PARATYPES**. EMEC database numbers EMEC1003641—EMEC1003654 and USNM1003655—USNM1003657. **ECUADOR: Orellana Prov**.: Yasuni Scientific Station, 00°40'36"S 76°24'02"W. 13–25:IV:1998, 210m,Coll.K.Will, Headlamp searching at night, terra firme tropical forest (1 male, 1 female QCAZ, 1 male CUIC, 1 male BMNH, 1 male CMNH, 1 male UASM, 5 males, 3 females EMEC, 1 male as DNA voucher–associated numbers DRM936 and KWWECU1998/95). Onkone Gare Camp 00°39'10"S 76°26'00"W, 3–8:x:1995, 220m, terra firme forest, along trail at night under leaf litter, Colls. G. Ball and D. Shpeley (1 female USNM). Res. Ehnica Waorani, 1km S. Onkone Gare Camp, Trans. Ent. 00°39'10"S 76°26'00"W, 30:vi:1994, 220m, running on muddy Q–trail near intersection of x–trans. 8 and main transect, Coll. T.L.Erwin (1 female USNM). Res. Ethnica Waorani, NPF, 00 39'10"S 076 26'00"W, 6:x:1995, 220m, T.L. Erwin et al., Trail across road, fig fall, terra firme forest at night (1 male USNM). **PERU**: Madre de Dios, Tambopata Res. Zone Explorer's Inn, 12°50'S 069°17'W, 22:x:1982, 290m, Coll. DL Pearson, along main trail (1 male USNM).

Type locality.—Ecuador, Orellana Province (previously part of Napo Province), Yasuni Scientific Station.

Distributional Range.—Ecuador and Peru.

Diagnosis.—Specimens will key to *Loxandrus* in Straneo's (1979) key to genera and individuals share characteristics of Straneo's (1991) group–1 or group–2 as follows: base of the pronotum bordered at the sides, upper surface shiny, elytra without red or yellow spots or patterns, pronotum with the sides rounded and slightly convergent to the base, base of the pronotum impunctuate, anterior submarginal sulcus ("border" of Straneo 1991) narrowly interrupted medially (group–2) or entire (group–1). Members of this species are among the largest individuals of all loxandrine species. The smallest individuals of *L. semperfidelis* (12.0mm) overlap in length with the largest individuals of several other species, e.g., *L. sulcatus* Bates, *L. pseudomajor* Straneo, *L. major* Straneo, *L. assimilis* Dejean, but are easily distinguished from all other loxandrines by the unequal widths of the elytral intervals, in which odd numbered intervals are as much as twice as wide as even ones (Fig. 1). The ventral abdominal process, or "keel" in males is unique in Carabidae (Fig. 2A).

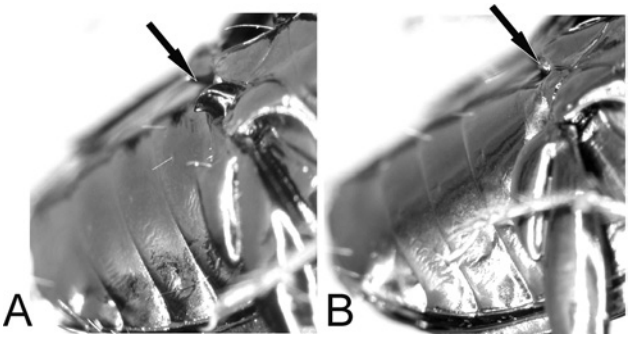

Fig. 2.—*Loxandrus semperfidelis*, ventral view of abdomen showing medial sternal process or "keel" in **A**, male, and the unmodified sternum in **B**, female.

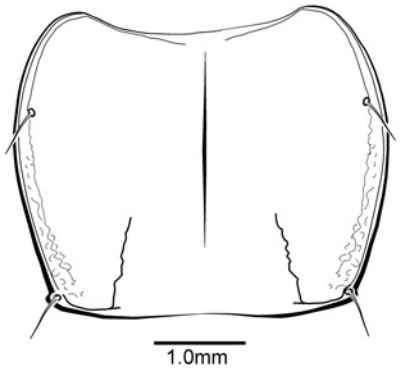

Fig. 3.—Pronotum of *Loxandrus semperfidelis*.

Description.—Large size, overall length 12.0–14.0mm. Deep black color and shiny throughout body, dorsally and ventrally. Coxae, tarsi, labrum, maxillary and labial palps paler brunneous. Mandibles and antennae black, paler at bases.

Head.—Ocular ratio (width over eyes/width between eyes) 1.67, two pairs supraorbital setae; microsculpture on disc shallow, fine reticulate microlines (evident at 25x); frontal impressions short, rounded, converging posteriorly, but poorly delimited; mentum clearly broader than long, anterior margin moderately emarginate, epilobes prominent, triangular, reflexed dorsally; mentum tooth simple, blunt, very slightly emarginate and medially impressed at apex; single pair of fine setae paramedially near anterior margin at base of mentum tooth; paramedial pits deep, sharply defined; suture present between mentum and submentum; submentum with two pairs of lateral setae; maxillary stipes with seta near base, palpifer with setae near apex; palpomeres glabrous, fusiform, all nearly equal in length; maxillary galea fusiform; lacinia large with thick, curved apical digitus and medial field of spines and setae; labial palpi fusiform, palpomere 2 longer than 3 and with 2 large medial setae and 2 small apical setae, palpomere 3 with scattered small setae; ligula with glossal sclerite broadly rounded at apex, edge shelf–like, sloping ventrally, apex with 2 large setae; paraglossae long and free; labrum with 6 setae on apical margin; clypeus slightly tumescent; mandible retinaculum discrete, premolar and molar teeth small; antennae long, extended beyond base of pronotum, antennomere 1–3 glabrous except for large seta on dorsum of 1 and anterior face of 2 and apex of 3 with ring of 6 setae, antennomeres 4–11 with dense short pubescence and 4–6 longer setae in ring around apices.

Thorax. Pronotum quadrate (Fig. 3), widest at or just anterad middle; side margins slightly and evenly rounded to hind angles, basal margin straight, anterior margin with front angles only slightly protruded, anterior submarginal sulcus entire, or interrupted medially; hind angles obtuse, minutely, but evidently denticulate; two pairs of lateral setae, one pair just anterad middle set in groove adjacent to pronotal disc, one pair in lateral bead at hind angles; lateral marginal bead continuous from front angles to hind angles and along base to level of posterior

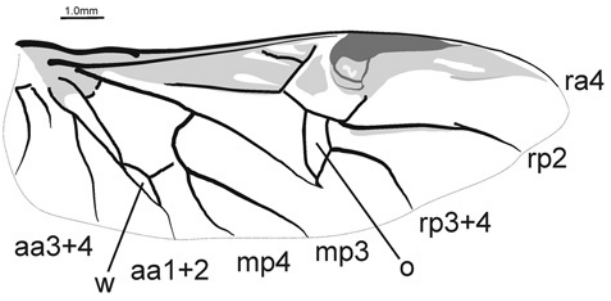

Fig. 4.—Right flight wing of *Loxandrus semperfidelis*, dorsal view.

impression, bead shallowly interrupted by lateral seta at hind angle; microsculpture not evident, very shiny and iridescent throughout; surface punctate in posterior impressions and along marginal channels from hind angles to anterolateral setae. Prosternal process glabrous and smoothly rounded, not margined. Prosternum and proepisternum glabrous, shiny. Mesosternum glabrous, very shiny and iridescent. Metasternum laterally with few (ca. 6–16), scattered coarse, shallow punctulae; metepisternum form elongate (length of lateral edge/length of anterior edge = 1.33), uniformly with coarse, shallow punctulae; metepimeron large, broadly rounded.

Elytra.—(Fig. 1). Parallel–sided, slightly convex, broadly rounded at apex with prominent externally visible plica; microsculpture not evident, very shiny and iridescent; striae deeply impressed, sharply punctate, punctulae shallower in apical third, absent at apex; parascutellar stria connected to and continuous with stria 1 and elytral basal margin, base of stria 1 absent though unilaterally and incompletely impressed in two individuals, striae 2 and 3 extended to basal margin or nearly so, striae 4–9 not extended to basal margin; basal margin entire; intervals convex throughout; intervals 3, 5, and 7 broader than all others, specifically 1, 8, and 9 of average relative width for typical *Loxandrus*; 2 and 4 very narrow; 6 narrow, slightly wider than 2 and 4; intervals 3 and 5 four times width of 2 and 4; 7 wider than 6 and 8 but narrower than 3 and 5; both 8 and 9 average relative width for typical *Loxandrus*; single dorsal setigerous puncture on disc of each elytron.

Flight Wing.—(Fig. 4). Large, venation typical for Carabidae.

Legs.—Protrochanter with medial seta; profemur anterior face with

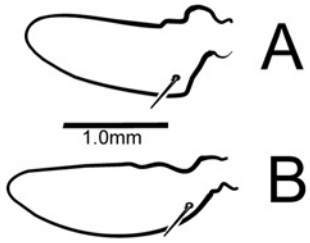

Fig. 5.—Right metatrochanters of *Loxandrus semperfidelis*. Ventral view of **A**, male, and **B**, female.

basal, medial (near ventral edge) and apical setae, dorsal face with 3–6 scattered setae, ventral face glabrous, posterior face with 2–5 scattered setae; protibial antennal cleaning organ well developed and with two clip setae, cleaner setal row extended dorsally, terminating 1–2 setae beyond larger medial seta, ventral ctenidia prominent, both proximal and distal spurs long and sharply pointed and smooth–edged; female protarsomeres symmetrical, 1 equal to length of 2+3, 1 with stout and 4 with long, fine ventral setae mesad and laterad, 2–3 with stout lateral row of ventral setae mesad and two longer setae laterad, 1–4 with four dorsoapical setae; male protarsomeres asymmetrical, 1 slightly shorter than length of 2+3, lobed mesad, 1 with stout, 4 with long fine and 2–3 with two pairs longer ventral setae mesad and laterad, 1–4 with four dorsoapical setae, 1–3 with two rows of articulo–setae; tarsomere 5 ventrally glabrous in both sexes, dorsolaterally with one pair of setae; tarsal claws of all legs smooth; mesocoxa with one seta mesad, one laterad; mesotrochanter with one subapical seta; mesofemur anterior face with medial, subapical (near ventral edge) and 2–3 subdorsal setae, dorsal face with 9–10 setae in row along length, 2–4 additional setae near apex, ventral face glabrous, posterior face with 4–5 baso–ventral setae in row and 2–3 subdorsal–apical setae; mesotibia with four rows of stout spines and mesal row of finer, denser spines, two apical spurs and ctenidium well–developed; mesotarsomeres elongate, 1 equal to length of 2+3, 1–4 with external sulci, two rows ventral setae, 5 glabrous; metacoxa with one seta mesad, one laterad; anterior sulcus complete, straight, appressed to anterior margin; metatrochanter with one basal seta, male metatrochanter with mesobasal corner produced to a nearly acute angle, apex conical

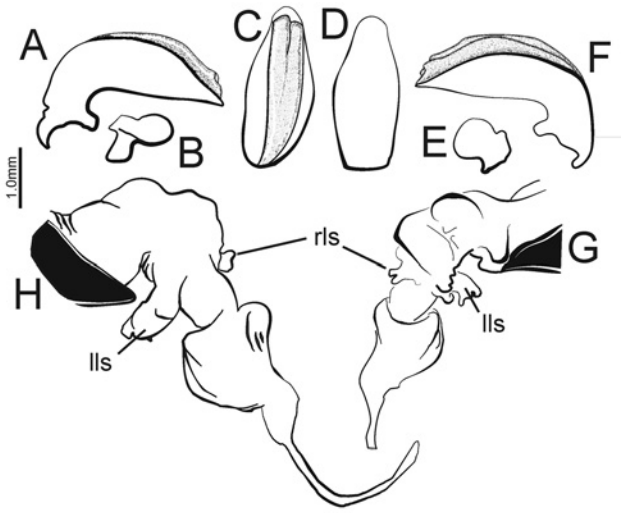

Fig. 6.—Male genitalia of *Loxandrus semperfidelis*. **A**, median lobe, left lateral view; **B**, right paramere, left lateral view; **C**, median lobe, dorsal view; **D**, median lobe, ventral view; **E**, left paramere, right lateral view; **F**, median lobe, right lateral view; **G**, everted endophallus, right lateral view; **H**, everted endophallus, left lateral view. Abbreviations: **lls**, left lateral sac; **rls**, right lateral sac.

(Fig. 5A); female metatrochanter not modified as in male, elongate, apex conical (Fig. 5B); metafemur anterior face with basal and medial (near ventral edge) setae, dorsal face with four to six near apex, femur otherwise glabrous; metatibia slightly arcuate, three rows of stout spines, two apical spurs, well developed ctenidium, dorsal surface with inner sulcus; metatarsomeres elongate, 1 equal to length of 2+3, 1–3 with internal and external sulci, two rows ventral setae, 5 glabrous.

Abdomen.—Ventral surface shiny, glabrous except one pair paramedial setae on sterna IV–VI; in male with one pair and female with two pairs paramedial setae on sternum VII; sternum II with irregular row of coarse punctures along base; male sternum III with posteriorly curving, keel–like medial intercoxal process extended ventrally beyond coxae (Fig. 2A), length of process beyond coxae approximately equal to distance from abdominal sternum II to ventral surface of coxae in lateral view, female sternum III unmodified (Fig. 2B); male sternum VII apex emarginate medially, slightly sinuate laterally, with thick marginal bead; female with sternum VII apical margin smoothly rounded at apex, narrower lateral bead.

Male Genitalia.—(Fig. 6). Aedeagal median lobe heavily sclerotized, relatively short and thick, broadly rounded at apex, ostium dorsal; parameres heavily sclerotized; endophallus uniformly covered in microtrichia, prominent left–lateral and right–lateral sac.

Female Genitalia and Reproductive Tract.—(Fig. 7A). Laterotergite IX large, broad, apically setose; gonocoxite 1 with row of 6–9 longer setae at apex; gonocoxite 2 with three minute ensiform setae and one pair of subapical nematiform setae in furrow; spermatheca large, broadly connected to common oviduct, shallowly annulated; appended gland connected dorsobasally to spermatheca; defensive gland (Fig. 7B) reservoir irregularly cordiform; collecting canal 5–8 times length of reservoir plus efferent duct and ended in an undetermined number of secretory cells; efferent duct with prominent basal lobe.

Allomones.—Chemical compounds from defensive glands include formic acid, senecioic acid, tiglic acid, hexanoic acid, decane, undecane, and 2–pentadecanone (*Loxandrus* sample EC199802L in Will et al. 2000, 2001).

Life History Data.—Specimens were collected at night by headlamp searching along remote trails in primary terra firme tropical forest at the crest or near the crest of small ridges adjacent to lower, swampy ground. Individuals were found either out walking and relatively exposed, or by raking leaf litter.

Description of 1st Instar Larva.—(Fig. 8). With same characteristics as pterostichine larvae as described by Bousquet (1985).

Microsculpture.—None visible on frontale and parietal; pronotum at apex and base, mesonotum and metanotum at base with region of microserrulate microsculpture. Tergites smooth.

Chaetotaxy.—Adnasale without additional setae. Prementum without additional setae. Femur with five setae. Frontale (FR), FR2 short, FR4 at level of FRc. Parietal (PA), PA4 one half length of PA7, PA5 of equal length to PA1–3, PA6 one half length of PA7, PAb laterad PA4. Maxilla (MX), MX5 much longer than MX6 (MX5 about 5x length of MX6), MX6 minute and on a large prominence, setal group gMX with about 40 setae. Pronotum (PR) PR3 and PR11 distinct, PR12 distinct and one half length PR11. Mesonotum (ME), ME12 and ME13 distinct, ME12 of equal length to PR11, ME12 0.75x length of ME13. Metanotum (MT), MT12, MT13 distinct and of equal length. Tergites (TE), TE1, TE6, TE7 on tergites I–VII of subequal lengths or TE7 slightly shorter, TE10 distinct and equal to length of TE9.

Head.—(Fig. 8E). Width 0.68mm. Nasale form straight, irregularly serrate. Ovirupters ended at level of FR2, consisting of around 12 microspinulae. Frontal sutures oblique. Coronal suture present. Parietal without stemmata (Fig. 8F). Cervical groove extended dorsally to level of PAa and laterally ended short of PA15. Antennomere I without membranous area near base. Mandible moderately curved, retinaculum moderately wide, medial margin of terebra smooth. Stipes length 2.5x width, with lateral membranous region. Maxillary palpomere II one half length of palpomere III. Ligula larger and robustly developed.

Legs.—Claws of equal length.

DISCUSSION

Individuals of *L. semperfidelis* have many autapomorphic characteristics in adult morphology that have not been noted in any other *Loxandrus*, e.g. unequal width of elytral intervals (Fig. 1), sexually dimorphic metatrochanter form (Fig. 5), and ventral keel (Fig. 2A). Other character-

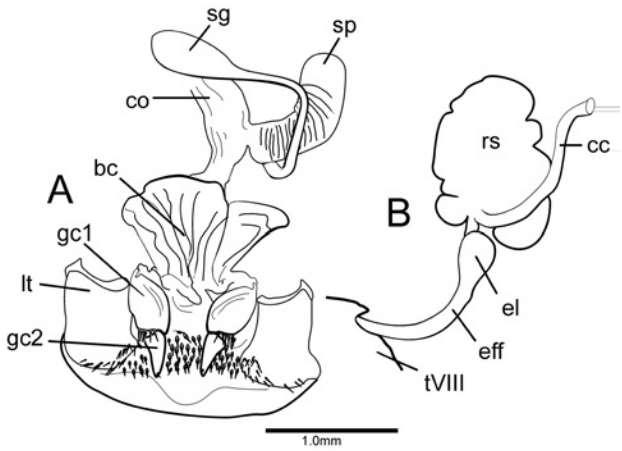

Fig. 7.—*Loxandrus semperfidelis*. **A,** ventral view of female genitalia and reproductive tract; **B,** ventral view of cuticular portions of left pygidial gland. Abbreviations: **bc**, bursa copulatrix; **cc**, collecting canal; **co**, common oviduct; **eff**, efferent duct; **el**, efferent duct basal lobe; **gc1**, gonocoxite–1; **gc2**, gonocoxite–2; **lt**, laterotergite IX; **rs**, reservoir; **sg**, spermathecal gland; **sp**, spermatheca; **tVIII**, tergite VIII.

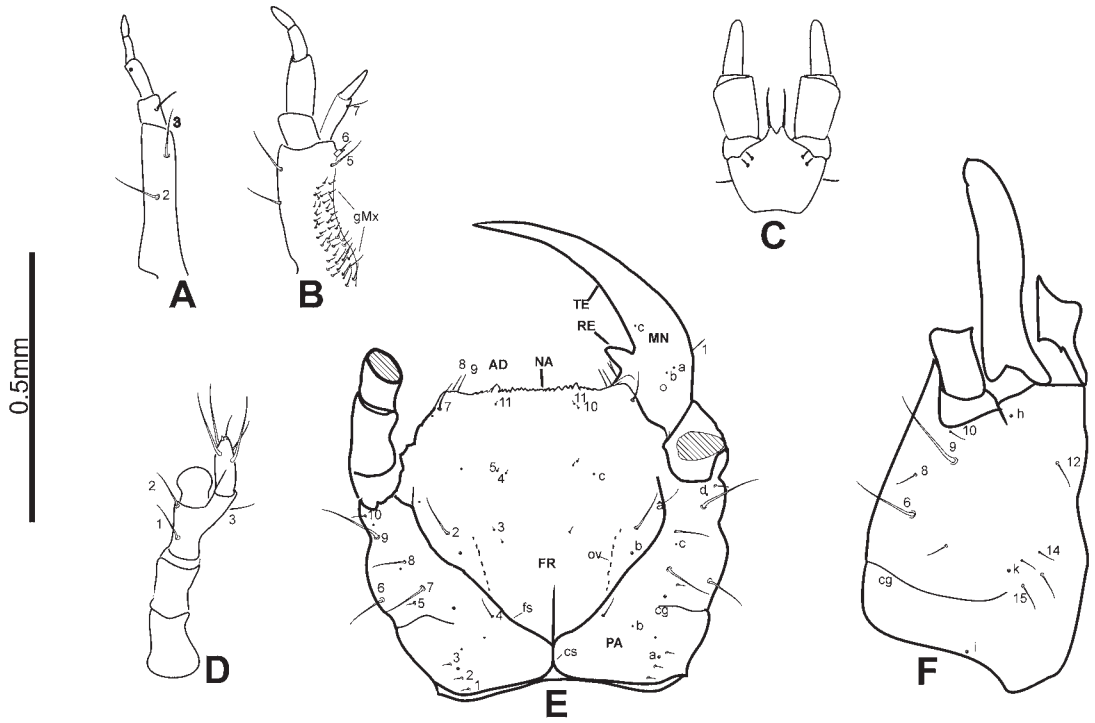

Fig. 8.—First instar larva, *Loxandrus semperfidelis*. **A,** left maxilla, left lateral; **B**, left maxilla, dorsal; **C**, labium, dorsal; **D**, left antenna, dorsal; **E**, head capsule and right mandible, dorsal; **F**, head capsule, right lateral. Abbreviations: **cs**, coronal suture; **cg**, cervical groove; **D**, adnasale; **FR**, frontale; **fs**, frontal suture; **gMX**, setal group of the maxilla; **MN**, mandible; **NA**, nasale; **ov**, ovirupter; **PA**, parietal; **RE**, retinaculum; **TE**, terebra. Note that the left/right asymmetry in the head capsule is apparently due to problems in larval development. Numbers and unbolded small letters refer to the notation of primary setae and pores in Bousquet and Goulet (1984).

istics seem to be plesiomorphic, e.g. presence of a well–developed spermatheca (Fig. 7A) (absent in many taxa) and fully sclerotized ventral surface of the male median lobe (Fig. 6) (membranous in various South American taxa). This species is sister to *Loxandrus castanipes* Straneo in my unpublished analysis of DNA sequence data. *Loxandrus semperfidelis* is superficially similar to *L. castanipes* and *L. punctatissimus* Straneo (both group–3 taxa) in regard to relatively large size, dark legs, pronotal form and distinctly punctate elytral striae. Punctation of the pronotal base and form of the pronotal submarginal sulcus, which separates these species in Straneo's key (1991) into groups 1–3, are variable for these and other *Loxandrus* species. As Straneo clearly stated (1991:5), the groups "are only conveniences for identification of the species" not intended to connote phylogenetic relationships. They do, however, give us a starting point to look for similarity and potentially find natural groups of species.

Larval characters are not known for many loxandrines or related taxa. Only *Loxandrus velocipes* Casey has been described for Loxandrini (Bousquet 1985). Arndt (1988) described the larva of *Abacetus villiersianus* Straneo. It was noted that these taxa have five pigmented stemmata, reduced from the normal complement of six. I have reared larvae of *L. icarus* Will and Liebherr from North America, eight South American *Loxandrus* species, two *Stolonis* species and *Abacetus perrieri* Tschitschérine from Madagascar. While *A. perrieri* and both *Stolonis* species I have reared have six pigmented stemmata in their 1st instar larvae, the *Loxandrus* species vary. Many of the *Loxandrus* larvae recently eclosed from their eggs generally lack any visible pigmented stemmata, but may show six poorly defined pigmented spots later in the instar. The anterior three typically are better defined but even these lack any evident lenses on the head capsule. In later instars there are typically six pigmented stemmata but often the rear three stemmata do not have evident lenses. It is possible that the first instar larva of *L. semperfidelis* would have matured to have pigmented stemmata. However, there is no indication of lenses on the head capsule. I have not yet made an adequate study of the chaetotaxy of all of these species but a cursory inspection suggests that they differ very little from each other. The character of stemmata number, however, appears to be more complex than simply loss or partial reduction, and changes in stemmata configuration probably occurred multiple times and by different modes, in the Abacetini + Loxandrini lineage.

Despite their highly divergent characteristics, individuals of *L. semperfidelis* are not known to have any peculiar life history traits. Even the incredible ventral keel, which would seem to strongly imply some unusual behavior in males, was never seen being put to any "use" during observations in the laboratory. Feeding and individual interaction of both sexes were casually observed. Beetles

were never seen copulating nor can any behavior observed be readily interpreted as courtship or mating behaviors. No doubt much remains to be learned about this and other *Loxandrus* species.

ACKNOWLEDGMENTS

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