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Cladistics of the New World Genera of Listroderina (Coleoptera: Curculionidae: Rhytirrhinini)

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The weevil subtribe Listroderina belongs in the tribe Rhytirrhinini (subfamily Cyclominae), and has 25 genera and 300 species in the Americas. A cladistic analysis of the American genera was undertaken, using 53 characters from the external morphology, mouthparts, body vestiture, and male and female genitalia, and considering *Rhigopsidius* Heller (subtribe Rhytirrhinina) as the outgroup. The analysis yielded 20 equally parsimonious cladograms (108 steps, CI=0.42, RI=0.64), which after successive weighting resulted in three minimum-length cladograms (256 steps, CI=0.67, RI=0.82). In the strict consensus cladogram, which has the same topology as one of the original cladograms, the genera follow the sequence (*Philippius*, (*Trachodema*, (*Lamiarhinus*, (*Acrorius*, (*Acroriellus*, ((*Rupanius*, (*Adioristidius*, *Amathynetoides*, (*Puranius*, (*Macrostyphlus*, *Andesianellus*)))), (*Hyperoides*, (*Germainiellus*, (*Antarctobius*, *Nacodius*)), ((*Haversiella*, (*Listronotus*, *Neopachytychius*)), (*Listroderes*, *Acrostomus*), (*Falklandiellus*, (*Falklandiopsis*, (*Telurus*, (*Falklandius*, *Lanteriella*))))))))))). A phylogenetic classification for the genera of American Listroderina is proposed, where the five principal lineages are recognized as generic groups: *Macrostyphlus* group (*Rupanius*, *Adioristidius*, *Amathynetoides*, *Puranius*, *Macrostyphlus*, and *Andesianellus*), *Antarctobius* group (*Germainiellus*, *Antarctobius*, and *Nacodius*), *Listronotus* group (*Haversiella*, *Listronotus*, and *Neopachytychius*), *Listroderes* group (*Listroderes* and *Acrostomus*), and *Falklandius* group (*Falklandiellus*, *Falklandiopsis*, *Telurus*, *Falklandius*, and *Lanteriella*). © 1997 The Willi Hennig Society

INTRODUCTION

The tribe Rhytirrhinini (Coleoptera: Curculionidae: Cyclominae) comprises the subtribes Gronopina, Eupagina, Rhyparosomina, and Rhytirrhinina, basically distributed in the Old World, and Listroderina, widely ranged in the Americas, Australia, New Zealand, and the Tristan da Cunha-Gough islands. Listroderina are extraordinarily diversified in the Andean subregion of South America, specially in the Subantarctic province of southern Chile and Argentina, and in the Paramo province of the northern Andes (Morrone and Roig-Juñent, 1995; Anderson and Morrone, 1996). Although the systematics of the species currently assigned to the American genera has been extensively studied, the generic interrelationships are much less well established. I previously hypothesized that *Listroderes* Schoenherr, the type-genus of this subtribe, did not represent a natural taxon (Morrone, 1992a, c, 1993a, b, 1994a; Morrone et al., 1992), and restricted it to 38

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species, revalidating four former synonyms (*Acrorius* Kirsch, *Antarctobius* Fairmaire, *Hyperoides* Marshall, and *Trachodema* Blanchard) and describing three further new genera (*Germainiellus*, *Lamiarhinus*, and *Nacodius*) for some species excluded from it (Morrone, 1994e). As a result of these and other revisions, the American Listroderina comprise 25 genera and 300 species (Table 1).

It is almost certain that the American Listroderina represent a paraphyletic group, because the genera from Australia, New Zealand, and the Tristan da Cunha-Gough islands are probably closely related to some of the American genera. Their cladistic analysis, however, could lay the foundation for subsequent work, and provide a framework for further studies. My objective is to present a cladistic analysis of these genera, using characters from the external morphology, mouthparts, body vestiture, and male and female genitalia. This analysis will allow me to test my previous hypotheses concerning non-monophyly of *Listroderes*, provide a cladistic classification of the subtribe, and advance the construction of a phylogenetic system for the Rhytirrhinini.

MATERIALS AND METHODS

The terminal taxa of this study are the 25 genera of American Listroderina (Table 1, Fig. 1). For the valid species assigned to these genera see Appendix 1.

The following 53 characters were derived from the external morphology (40), mouthparts (four), body vestiture (two), and male and female genitalia (seven). Apomorphic character states were identified by outgroup comparison with *Rhigopsidius* Heller (Loiácono and Morrone, 1991; Morrone and Loiácono, 1992), which belongs to the subtribe Rhytirrhinina:

1. Eye shape: (0) transverse; (1) subcircular. The eyes of Listroderina are typically transverse, which is the plesiomorphic state. The apomorphic subcircular eyes

TABLE 1
Genera of New World Listroderina

Genera	No. of species	Distribution	References
Acroriellus	6	PAR and PUN	Morrone and Ocampo (1995)
Acrorius	10	PAR and PUN	Morrone (1994a), Ocampo and Morrone (1996)
Acrostomus	7	PAT and SUB	Morrone (1994b)
Adioristidius	24	CEN, PUN, and SUB	Morrone (1994c)
Amathynetoides	10	NEO and PUN	Morrone (1994c)
Andesianellus	9	PAR and PUN	Anderson and Morrone (1996)
Antarctobius	9	SUB	Morrone (1992a)
Falklandiellus	1	SUB	Morrone (1995a)
Falklandiopsis	1	SUB	Morrone and Anderson (1995)
Falklandius	6	SUB	Morrone (1992b), Morrone and Anderson (1995)
Germainiellus	12	CEN and SUB	Morrone (1993a, 1994e)
Haversiella	1	SUB	Morrone (1994d)
Hyperoides	5	CEN, NEO, PAT, and SUB	Morrone (1993b)
Lamiarhinus	2	CEN and SUB	Morrone (1992c)
Lanteriella	1	SUB	Morrone (1992b)
Listroderes	38	CEN, NEO, PAT, PUN, and SUB	Morrone (1993c, d, e, f, 1995b)
Listronotus	117	CEN, NEA, NEO, and SUB	O'Brien (1977, 1979), Morrone et al. (1995)
Macrostyphlus	10	PAR and PUN	Morrone (1994c)
Nacodius	4	PAR and PUN	Morrone (1994e)
Neopachytychius	1	CEN, NEO, and SUB	Marvaldi (1994)
Philippius	1	SUB	Morrone (1990)
Puranius	20	CEN, PUN, and SUB	Morrone (1994c)
Rupanius	1	PAR	Morrone (1995c)
Telurus	2	SUB	Morrone and Anderson (1995)
Trachodema	2	CEN and SUB	Morrone (1992c)

Distribution according to Morrone (1996): CEN=Central Chilean province; NEA=Nearctic subregion; NEO=Neotropical subregion; PAR=Paramo province; PAT=Patagonian province; PUN=Puna province; SUB=Subantarctic province. For species assigned to each genus see Appendix 1.

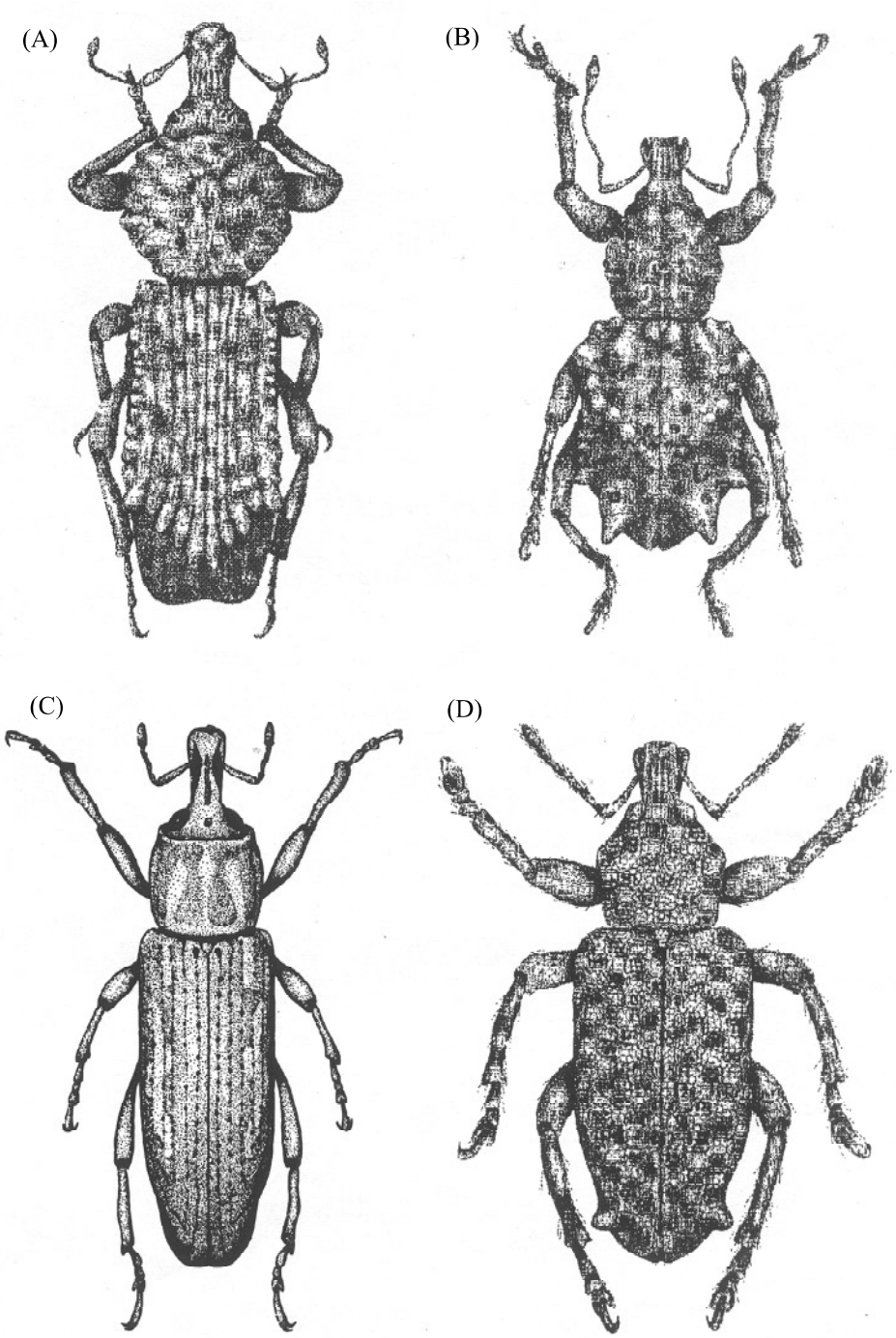

FIG. 1. Habitus of representative Listroderina. (A) *Philippius superbus*; (B) *Lamiarhinus aelficus*; (C) *Listronotus bosqi*; (D) *Listroderes annulipes*.

occur in *Andesianellus*, *Lanteriella*, and *Telurus*. This character is polymorphic for *Falklandius*, but according to Morrone and Anderson (1995), the transverse eyes are considered as a reversal, and thus the subcircular eyes are interpreted as the groundplan of the genus.

2. Eye length: (0) large to medium-sized; (1) small to very small. Reduction in the length of the eyes of *Amathynetoides*, *Andesianellus*, *Falklandius*, *Lanteriella*, and *Philippius* (Fig. 1A), which vary from as long as to shorter than rostrum height, is considered as the

apomorphic condition. *Adioristidius*, *Macrostyphlus*, and *Puranius* also have some species with small eyes, but according to previous analyses (Morrone, 1994c) the large to medium-sized eyes are plesiomorphic and interpreted as the groundplan of these genera.

3. Eye convexity: (0) flat; (1) slightly convex. Slightly convex eyes are hypothesized as autapomorphic for *Telurus*, although a similar condition was described in *Amathynetoides ebeninus* (Morrone, 1994c).

4. Eye position: (0) lateral; (1) dorsal. The eyes of Listroderina are usually lateral (Fig. 1A–D). The apomorphic dorsal eyes occur in *Falklandius* and *Lanteriella*.

5. Rostrum shape: (0) medium-sized and slender; (1) long and slender; (2) very short and broad. Although the shape of the rostrum is considerably variable within Listroderina, three character states were defined. A medium-sized (as short as half of pronotum) and slender rostrum (Fig. 1A, B) in the majority of the genera is considered plesiomorphic, whereas a long and slender rostrum (in *Listronotus* and *Neopachythchius*; Fig. 1C) and very short (shorter than half of pronotum) and broad rostrum (in *Falklandiellus*, *Falklandiopsis*, *Falklandius*, and *Lanteriella*) are treated as non-additive apomorphic conditions.

6. Rostral dorsal carinae: (0) present, strongly developed; (1) present, slightly developed; (2) absent. Strongly developed rostral dorsal carinae are plesiomorphic within Listroderina. There are two apomorphic conditions, treated as additive: slightly developed carinae (*Andesianellus*) and absent carinae (*Falklandiellus*, *Falklandiopsis*, *Falklandius*, *Haversiella*, *Lanteriella*, and *Telurus*). Although internal variation exists within *Adioristidius*, *Amathynetoides*, and *Nacodius*, the plesiomorphic condition was considered as the groundplan, based on previous analyses (Morrone, 1994c, e).

7. Scrobe shape: (0) deep, extends to eyes; (1) shallow, directed towards but not extending to eyes. Scrobes deep and extending to the eyes in *Adioristidius*, *Amathynetoides*, *Andesianellus*, *Haversiella*, *Listronotus*, *Macrostyphlus*, *Neopachytychius*, *Puranius*, and *Trachodema* are plesiomorphic, whereas scrobes shallow and directed towards but not extending to eyes in the remainder genera is the apomorphic condition.

8. Scrobes position: (0) lateral; (1) dorsal. Dorsal scrobes in *Falklandius* and *Lanteriella* are considered apomorphic.

9. Scrobal ventral teeth: (0) absent; (1) present. The presence of teeth in the scrobal ventral carinae is considered as an autapomorphy of *Acrostomus*. The presence of these teeth in several species of the *Listroderes costirostris* species group is not considered as the groundplan of this genus (Morrone, 1993f), so the character in *Listroderes* was scored as plesiomorphic.

10. Suprascrobal keel: (0) absent; (1) present. The presence of a relatively conspicuous keel above the scrobe in *Adioristidius*, *Amathynetoides*, *Andesianellus*, *Macrostyphlus*, and *Puranius* is considered an apomorphic condition.

11. Pterygia: (0) well-developed, protruding; (1) poorly developed, non-protruding. *Haversiella*, *Listronotus*, and *Neopachytychius* have poorly developed and non-protruding pterygia (Fig. 1C), which is considered apomorphic.

12. Epistome: (0) not protruding; (1) protruding. The protruding epistome is hypothesized to be an autapomorphy of *Acrostomus* (Morrone, 1994b).

13. Number of mandibular setae; (0) two; (1) three to four. Mandibles in Listroderina typically have two setae, the presence of three to four setae in the mandibles of *Philippius* (Fig. 2A) is autapomorphic.

14. Pharyngeal process: (0) short; (1) very long. The very long pharyngeal process of *Neopachytychius* (Fig. 2B) is hypothesized to be autapomorphic.

15. Maxillary mala: (0) with lacinial teeth; (1) lacking lacinial teeth. The maxillary mala in Listroderina usually have four to nine lacinial teeth (Morrone et al., 1992; Fig. 2C), their absence in *Haversiella* (Fig. 2D) is hypothesized to be autapomorphic (Morrone, 1994d).

16. Ligula of prementum: (0) membranous; (1) sclerotized. The ligula of the prementum in Listroderina is usually membranous (Fig. 2E), whereas the sclerotized ligula of *Philippius* (Fig. 2F) is hypothesized to be an autapomorphy.

17. Relative length of funicular articles 1 and 2: (0) 1 longer than 2; (1) 1 subequal or shorter than 2. Funicular article 1 is longer than 2 in the majority of the genera of Listroderina (Fig. 2G, H), where it is considered plesiomorphic; a funicular article 1 subequal or shorter than 2 is an autapomorphy of *Listronotus* (Morrone et al., 1995).

18. Shape of funicular article 2: (0) elongate; (1) monilliform. An elongate funicular article 2 (Fig. 2G) is plesiomorphic, whereas a monilliform funicular

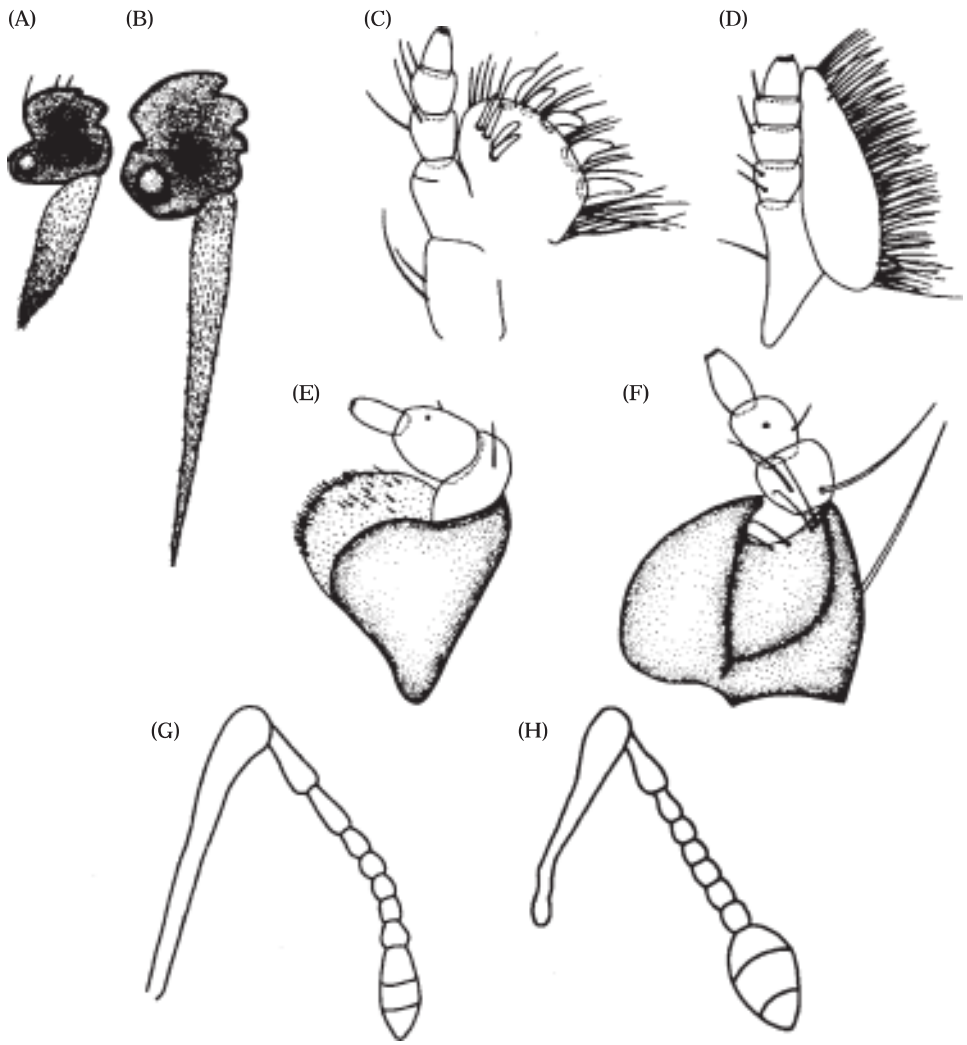

FIG. 2. Mouthparts and antennae of representative Listroderina. (A, B) mandibles; (C, D) maxillae; (E, F) prementa; (G, H) antennae, (A, F, G) *Philippius superbus*; (B) *Neopachytychius squamosus*; (C) *Lamiarhinus aelficus*; (D) *Haversiella albolimbata*; (E) *Listroderes lugens*; (H) *Falklandius turbificatus*.

article 2 (Fig. 2H) in *Falklandiellus*, *Falklandiopsis*, and *Lanteriella* is apomorphic. Although *Falklandius goliath* and *F. kuscheli* have an elongate article, the cladistic analysis revealed it to be a reversal to the plesiomorphic state and the monilliform article is considered as the groundplan of *Falklandius* (Morrone and Anderson, 1995).

19. Shape of funicular articles 4–6: (0) monilliform to transverse; (1) elongate. There exists some variation in the shape of funicular articles 4–6 in Listroderina, but an elongate article can be regarded as an autapomorphy of *Lamiarhinus*.

20. Club shape: (0) ovate; (1) inflated. The antennal club in Listroderina is typically ovate (Fig. 2G); the inflated club (Fig. 2H) of *Andesianellus*, *Falklandiopsis*, *Falklandius*, *Macrostyphlus*, *Puranius*, and *Rupanius* is apomorphic.

21. Pronotum shape: (0) transverse; (1) subcircular; (2) subcylindrical to subquadrate. Although the shape of the prothorax within Listroderina is considerably variable and its interpretation is not straightforward, I distinguished three additive character states: the transverse pronotum (Fig. 1D), subcircular pronotum (Fig. 1A), and subcylindrical to subquadrate pronotum (Fig. 1C).

22. Pronotum width: (0) not wider than elytra; (1) wider than elytra. The pronotum wider than elytra represents an autapomorphy of *Philippius* (Fig. 1A).

23. Pronotal disc integument: (0) punctured and rugose; (1) smooth and polished. The integument of the pronotal disc in Listroderina is typically punctured and rugose, and this is the plesiomorphic character state. Species of *Amathynetoides*, *Lanteriella*, and *Nacodius* have smooth and polished discs, herein treated as the apomorphic character state.

24. Pronotum disc: (0) tuberculate; (1) non-tuberculate. The non-tuberculate disc of the pronotum of the majority of the Listroderina is apomorphic with respect to the plesiomorphic tuberculate disc (Fig. 1A) of *Lamiarhinus*, *Philippius*, *Rupanius*, and *Trachodema*.

25. Postocular lobes: (0) present, well developed; (1) present, slightly developed; (2) absent. Within the American Listroderina, I distinguished an additive sequence of three character states dealing with the relative development of the postocular lobes of the prothorax: the plesiomorphic present and well-developed lobes, and two apomorphic ones: present and slightly developed, and absent lobes. In *Acroriellus*, slightly developed lobes are the groundplan condition, although some species lack them (Morrone and Ocampo, 1995), and in *Puranius* well-developed lobes is the groundplan, with some species having slightly developed lobes (Morrone, 1994c).

26. Scutellum: (0) visible; (1) not visible. The scutellum is usually visible in Listroderina; *Philippius* (Fig. 1A) presents the autapomorphic state not visible.

27. Metepisternal suture: (0) present; (1) absent. The metepisternial suture is usually present in Listroderina, and its absence is treated as apomorphic. Within *Acrorius*, *Adioristidius*, *Amathynetoides*, and *Puranius* this character is polymorphic, but according to previous analyses (Morrone, 1994c; Ocampo and Morrone, 1996), the present suture is the groundplan.

28. Elytral shape: (0) subquadrangular to subrectangular; (1) ovate. Within Listroderina, the majority of the genera have the apomorphic ovate elytra (Fig. 1B–D), whereas *Lamiarhinus*, *Philippius*, and *Rupanius* have the plesiomorphic subquadrate to subrectangular elytra (Fig. 1A).

29. Elytra: (0) not fused; (1) fused. Elytra fused along the interelytral suture are autapomorphic for *Philippius* (Fig. 1A).

30. Elytral stridulatory files on males: (0) absent; (1) present. Males of *Listroderes* and *Acrostomus* have stridulatory files. Lyal and King (1996) have reported the presence of these files in several curculionid taxa, postulating that they represent a synapomorphy, whereas the absence represents a loss. At this level of analysis, however, and based on the absence in *Rhigopsidius*, I prefer to treat the presence as apomorphic.

31. Elytral disc (0) flat; (1) convex. *Philippius* and *Rupanius* are the only genera with plesiomorphic flat elytra.

32. Basal elytral margin: (0) not raised; (1) raised. The raised margin at the base of the elytra of *Andesianellus* (Anderson and Morrone, 1996) is autapomorphic.

33. Humeri: (0) subquadrate; (1) rounded. In general, the elytra of Listroderina have rounded humeri (Fig. 1D), whereas the plesiomorphic subquadrate humeri occur only in *Lamiarhinus*, *Philippius*, and *Trachodema* (Fig. 1A).

34. Humeral tubercles: (0) absent; (1) present. The development of tubercles in the humeri of *Falklandiopsis* and *Trachodema* is apomorphic.

35. Elytral apical declivity: (0) non-carinate; (1) carinate. The presence of a carina at the elytral apical declivity is an autapomorphy of *Rupanius*.

36. Female elytral apex: (0) not produced; (1) slightly produced; (2) strongly produced. The elytral apex of female Listroderina is usually not produced, and this is the plesiomorphic condition. The slightly produced apex of *Lanteriella* and the strongly produced apex of *Telurus* are treated as two additive apomorphic states.

37. Tubercles on elytral disc: (0) present, strong; (1) present, small, rounded; (2) absent. In order to account for the development of tubercles on the elytral disc in the American Listroderina, an additive sequence of three character states is hypothesized: from present and strong tubercles (Fig. 1B), passing through present, small and rounded tubercles, to absent (Fig. 1C).

38. Anteapical elytral tubercles: (0) present; (1) absent. The absence of anteapical elytral tubercles in 15 genera is apomorphic. Some species of *Acrorius*, *Antarctobius*, *Germainiellus*, and *Nacodius* lack these tubercles, but according to previous analyses (Morrone, 1992a, 1993a, 1994a, e) the groundplan is the presence of such tubercles.

39. Series of declivital tubercles on elytral intervals 1–5: (0) present; (1) absent. A series of tubercles in the elytral intervals 1–5 in *Falklandiellus*, *Falklandiopsis*, and *Philippius* (Fig. 1A) is considered plesiomorphic, whereas its absence in the remaining genera is apomorphic. In the *Listroderes nodifer* species group and in

Germainiellus planipennis these tubercles are also present (Morrone, 1993a, e), but the phylogenetic analyses revealed them to be further apomorphies and not the groundplan of *Listroderes* and *Germainiellus*.

40. Declivital tubercle on interval 2: (0) present; (1) absent. The presence of a declivital tubercle on interval 2 in the elytra of *Acroriellus*, *Acrorius*, and *Lamiarhinus* (Fig. 1B) is plesiomorphic.

41. Declivital tubercles on interval 5: (0) absent; (1) present. The presence of a declivital tubercle on interval 5 in the elytra of *Acroriellus*, *Acrorius*, and *Lamiarhinus* (Fig. 1B) is apomorphic.

42. Femora shape: (0) subcylindrical, slightly clavate; (1) subcylindrical, markedly clavate; (2) dorsoventrally compressed. The femora of Listroderina are usually subcylindrical (Fig. 3A), which is the plesiomorphic condition. The markedly clavate femora of *Falklandiopsis* (Fig. 3B) and the dorsoventrally compressed femora of *Lanteriella* (Fig. 3C) are independent autapomorphies.

43. Tibiae shape: (0) subcylindrical; (1) with expanded apex. Tibiae with an expanded apex represent an autapomorphy of *Lanteriella* (Fig. 3C).

44. Tarsomeres 3 shape: (0) bilobed; (1) subcylindrical. Tarsomeres 3 are commonly bilobed in Listroderina, which is the plesiomorphic character state; the subcylindrical tarsomere 3 of *Philippius* is autapomorphic.

45. Scales: (0) subpolygonal; (1) subcircular; (2) seta-like; (3) absent. There is considerable variation in the scales of the body vestiture of Listroderina. Within the taxa analysed, four non-additive character states are recognized: subpolygonal, subcircular, seta-like, and absent. Five genera are polymorphic for this

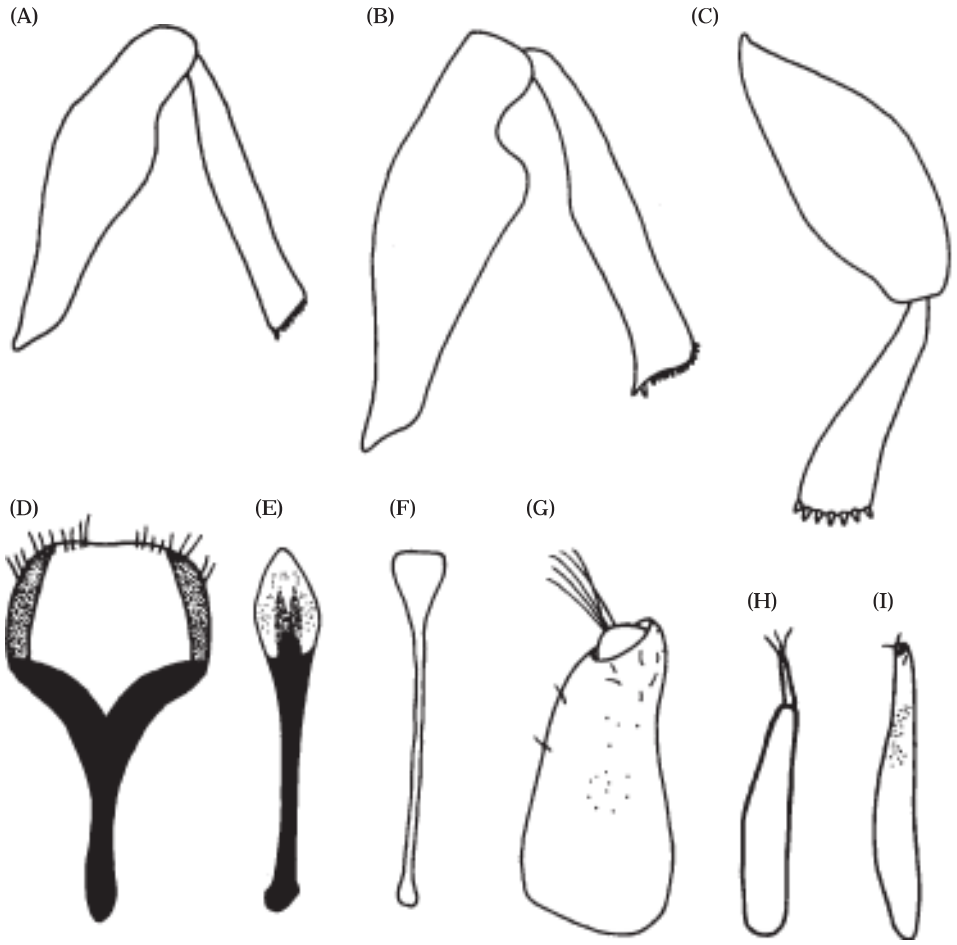

FIG. 3. Legs and female genitalia of representative Listroderina. (A–C) legs; (D–F) sternum 8; (G–I) oviscapt. (A) *Falklandius antarcticus*; (B, E, I) *Falklandiopsis magellanica*; (C) *Lanteriella microphthalma*; (D) *Germainiellus angulipennis*; (F) *Telurus caudicalatus*; (G) *Antarctobius abditus*; (H) *Puranius pusillus*.

character: in *Acrostomus* the more basal species has subcircular scales and the remaining species, seta-like scales (Morrone, 1994b), so the groundplan could not be inferred, and I scored it as missing. In the remaining four genera, the groundplan condition was deduced from previous analyses: seta-like scales for *Antarctobius* (Morrone, 1992a), subcircular scales for *Macrostyphlus* and *Puranius*, and seta-like scales for *Amathynetoides* (Morrone, 1994c).

46. Finger-like processes on scales: (0) present; (1) absent. The finger-like processes in the scales of *Philippius* and *Trachodema* are plesiomorphic.

47. Degree of sclerotization of the aedeagus: (0) slightly sclerotized; (1) strongly sclerotized. The aedeagus of the American Listroderina is usually strongly sclerotized, which is the apomorphic condition. *Listronotus* and *Neopachytychius* are the only genera with the plesiomorphic character state slightly sclerotized aedeagus.

48. Apodeme of female sternum 8: (0) long; (1) short. The length of female sternum 8 in Listroderina is considerably variable. I distinguished two character states: the plesiomorphic long apodemes (>twice longer than plate; Fig. 3E, F) and the apomorphic short apodemes (slightly longer than to shorter than plate; Fig. 3D).

49. Apical setae on plate of female sternum 8: (0) present; (1) absent. The plate of female sternum 8 in Listroderina usually has a series of apical setae (Fig. 3D), considered plesiomorphic. Its absence in *Falklandiopsis*, *Falklandius*, and *Telurus* (Fig. 3F) is apomorphic.

50. Sclerotized arms of female sternum 8: (0) present; (1) absent. Female sternum 8 of Listroderina usually has a pair of sclerotized arms (Fig. 3D), considered plesiomorphic, whereas its absence in *Falklandiopsis*, *Falklandius*, and *Telurus* (Fig. 3F) is apomorphic.

51. Oviscapt length: (0) short; (1) long. The long oviscapt (Fig. 3I) of *Adioristidius*, *Falklandiopsis*, and *Falklandius* is apomorphic.

52. Oviscapt styli: (0) present; (1) absent. Listroderina usually have styli in the oviscapt (Fig. 3G), the absence of which (Fig. 3I) is herein treated as apomorphic. Although some species of *Antarctobius*, *Falklandius*, *Germainiellus*, *Listroderes*, *Listronotus*, and *Hyperoides* lack styli, their presence is interpreted as the groundplan of these genera.

53. Oviscapt baculi: (0) absent; (1) present. *Adioristidius*, *Andesianellus*, *Falklandiellus*, and *Rupanius* have baculi in the oviscapt, considered apomorphic. Although some species of *Amathynetoides* and *Puranius* also have baculi, their absence is the groundplan condition (Morrone, 1994c).

Table 2 contains the data matrix used, which was analysed with Hennig86 1.5 (Farris, 1988), applying the mhennig* and bb* options for calculating trees. Consistency and retention indices were calculated excluding autapomorphies. I applied the successive weighting procedure implemented in Hennig86. CLADOS 1.1 (Nixon, 1992) was used for examination of character distributions.

RESULTS

The analysis using equal weights yielded 20 equally parsimonious cladograms, each with 108 steps, a CI of 0.42, and a RI of 0.64. When successive weighting was applied, three minimum-length cladograms resulted, with length 256, a CI of 0.67, and a RI of 0.82. The strict consensus cladogram (Fig. 4) has the same topology as one of the original cladograms, showing that the extra branches in the remaining two cladograms are unnecessary to account for the characters. Synapomorphies and homoplastic changes for all nodes and terminal taxa are listed in Table 3.

In the cladogram, the genera follow the sequence *Philippius*, *Trachodema*, *Lamiarhinus*, *Acrorius*, *Acroriellus*, and the remaining genera, arranged in two clades. The former comprises the genera *Rupanius*, *Adioristidius*, *Amathynetoides*, *Puranius*, *Macrostyphlus*, and *Andesianellus*. The latter has a trichotomy for *Hyperoides*, the clade comprising *Germainiellus*, *Antarctobius*, and *Nacodius*, and the clade including the remaining genera. These latter are arranged in three clades: one including *Haversiella*, *Listronotus*, and *Neopachytychius*; the second including *Listroderes* and *Acrostomus*; and the third including *Falklandiellus*, *Falklandiopsis*, *Telurus*, *Falklandius*, and *Lanteriella*.

Based on the relationships depicted in the cladogram, the following phylogenetic classification for the American genera of Listroderina is proposed, combining subordination with phylogenetic sequencing (Nelson, 1972, 1974).

1.0 *Philippius* Germain
2.0 *Trachodema* Blanchard
3.0 *Lamiarhinus* Morrone
4.0 *Acrorius* Kirsch
5.0 Acroriellus Morrone and Ocampo
6.0 *Macrostyphlus* generic group
  6.1 *Rupanius* Morrone
  6.2 *Adioristidius* Morrone
  6.3 *Amathynetoides* Morrone
  6.4 *Puranius* Germain
  6.5 *Macrostyphlus* Kirsch
  6.6 *Andesianellus* Anderson and Morrone
7.0 *Hyperoides* Marshall, *sedis mutabilis*
8.0 *Antarctobius* generic group, *sedis mutabilis*
  8.1 *Germainiellus* Morrone
  8.2 *Antarctobius* Fairmaire
  8.3 *Nacodius* Morrone
9.0 *Listronotus* generic group, *sedis mutabilis*
  9.1 *Haversiella* Schweiger
  9.2 *Neopachytychius* Hustache
  9.3 *Listronotus* Jekel
10.0 *Listroderes* generic group, *sedis mutabilis*
  10.1 *Listroderes* Schoenherr
  10.2 *Acrostomus* Kuschel
11.0 *Falklandius* generic group, *sedis mutabilis*
  11.1 *Falklandiellus* Kuschel
  11.2 *Falklandiopsis* Morrone and Anderson
  11.3 *Telurus* Kuschel
  11.4 *Falklandius* Enderlein
  11.5 *Lanteriella* Morrone

DISCUSSION

The cladistic analysis of the American Listroderina allowed me to identity five principal lineages (herein considered generic groups) for 19 out of 25 of the genera analysed. This analysis helped to clarify some previous statements concerning the relationships of Listroderina. For example, some of the unusual characters of *Philippius* cast doubt on its placement in

TABLE 2
Data Matrix Used in the Cladistic Analysis of Listroderina, with *Rhigopsidius* as Outgroup

Rhigopsidius	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0
Acroriellus	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 1 0 0 1 0 0	1 0 1 0 0 0 0 1 1 0	1 0 0 0 2 1 1 1 0 0	0 0 0
Acrorius	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 1 0 0 1 0 0	1 0 1 0 0 0 1 0 1 0	1 0 0 0 2 1 1 1 0 0	0 0 0
Acrostomus	0 0 0 0 0 1 1 0 1 0	0 1 0 0 0 0 0 0 0 0	2 0 0 1 0 0 0 1 0 1	1 0 1 0 0 0 0 1 1 1	0 0 0 0 ? 1 1 1 0 0	0 0 0
Adioristidius	0 1 0 0 0 1 0 0 0 1	0 0 0 0 0 0 0 0 0 1	1 0 0 1 1 0 0 1 0 0	1 0 1 0 0 0 0 1 1 1	0 0 0 0 2 1 1 0 0 0	1 0 1
Amathynetoides	0 1 0 0 0 1 0 0 0 1	0 0 0 0 0 0 0 0 0 1	2 0 1 1 1 0 0 1 0 0	1 0 1 0 0 0 0 1 1 1	0 0 0 0 2 1 1 0 0 0	0 0 0
Andesianellus	1 1 0 0 0 0 0 0 0 1	0 0 0 0 0 0 0 0 0 1	2 0 0 1 2 0 1 1 0 0	1 1 1 0 0 0 2 1 1 1	0 0 0 0 3 1 1 0 0 0	0 0 1
Antarctobius	0 0 0 0 0 ? 1 0 0 0	0 0 0 0 0 0 0 0 0 0	1 0 0 1 2 0 0 1 0 0	1 0 1 0 0 0 2 0 1 1	0 0 0 0 2 1 1 1 0 0	0 0 0
Falklandiellus	0 0 0 0 2 2 1 0 0 0	0 0 0 0 0 0 0 0 1 0 0	0 0 0 1 2 0 1 1 0 0	1 0 1 0 0 0 2 1 0 1	0 0 0 0 1 1 1 1 0 0	0 0 1
Falklandiopsis	0 0 0 0 2 2 1 0 0 0	0 0 0 0 0 0 0 0 1 0 1	1 0 0 1 1 0 0 1 0 0	1 0 1 1 0 0 2 1 0 1	0 1 0 0 3 1 1 0 1 1	1 1 0
Falklandius	1 1 0 1 2 2 1 1 0 0	0 0 0 0 0 0 0 0 1 0 1	1 0 0 1 2 0 1 1 0 0	1 0 1 0 0 0 2 1 1 1	0 0 0 0 3 1 1 0 1 1	1 0 0
Germainiellus	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 1 0 0 1 0 0	1 0 1 0 0 0 2 0 1 1	0 0 0 0 2 1 1 1 0 0	0 0 0
Haversiella	0 0 0 0 1 2 0 0 0 0	1 0 0 0 1 0 0 0 0 0	1 0 0 1 2 0 0 1 0 0	1 0 1 0 0 0 2 1 1 1	0 0 0 0 1 1 1 1 0 0	0 0 0
Hyperoides	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 1 0 0 1 0 0	1 0 1 0 0 0 2 1 1 1	0 0 0 0 2 1 1 1 0 0	0 0 0
Lamiarhinus	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 0 0 0 1 0	0 0 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 1 0	1 0 0 0 2 1 1 1 0 0	0 0 0
Lanteriella	1 1 0 1 2 2 1 1 0 0	0 0 0 0 0 0 0 1 0 0	1 0 1 1 2 0 1 1 0 0	1 0 1 0 0 1 2 1 1 1	0 2 1 0 3 1 ? ? ? ?	0 1 0
Listroderes	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 0 1 0 1	1 0 1 0 0 0 2 0 1 1	0 0 0 0 1 1 1 1 0 0	0 0 0
Listronotus	0 0 0 0 1 1 0 0 0 0	1 0 0 0 0 0 1 0 0 0	2 0 0 1 0 0 0 1 0 0	1 0 1 0 0 0 2 0 1 1	0 0 0 0 1 1 0 1 0 0	0 0 0
Macrostyphlus	0 1 0 0 0 1 0 0 0 1	0 0 0 0 0 0 0 0 0 1	2 0 0 1 2 0 1 1 0 0	1 0 1 0 0 0 0 1 1 1	0 0 0 0 1 1 1 0 0 0	0 0 0
Nacodius	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 1 2 0 0 1 0 0	1 0 1 0 0 0 2 0 1 1	0 0 0 0 2 1 1 1 0 0	0 0 0
Neopachytychius	0 0 0 0 1 1 0 0 0 0	1 0 0 1 0 0 0 0 0 0	1 0 0 1 0 0 0 1 0 0	1 0 1 0 0 0 2 0 1 1	0 0 0 0 1 1 0 1 0 0	0 0 0
Philippius	0 1 0 0 0 1 1 0 0 0	0 0 1 0 0 1 0 0 0 0	1 1 0 1 1 1 0 0 1 0	0 0 0 0 0 0 0 0 0 1	0 0 0 1 0 0 1 1 0 0	0 0 0
Puranius	0 1 0 0 0 ? 0 0 0 1	0 0 0 0 0 0 0 0 0 1	0 0 0 1 1 0 0 1 0 0	1 0 1 0 0 0 0 1 1 1	0 0 0 0 1 1 1 0 0 0	0 0 0
Rupanius	0 0 0 0 0 1 1 0 0 0	0 0 0 0 0 0 0 0 0 1	0 0 0 0 1 0 0 0 0 0	0 0 1 0 1 0 0 1 1 1	0 0 0 0 2 1 1 0 0 0	0 1 1
Telurus	1 0 1 0 0 2 1 0 0 0	0 0 0 0 0 0 0 0 0 0	1 0 0 1 2 0 1 1 0 0	1 0 1 0 0 2 2 1 1 1	0 0 0 0 3 1 1 0 1 1	0 1 0
Trachodema	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 0	1 0 0 1 0 0 0 0 1 1	0 0 0 0 0 0 1 1 0 0	0 0 0

Multistate characters 6, 21, 25, 36, and 37=additive, and 5, 42, and 45=non-additive.

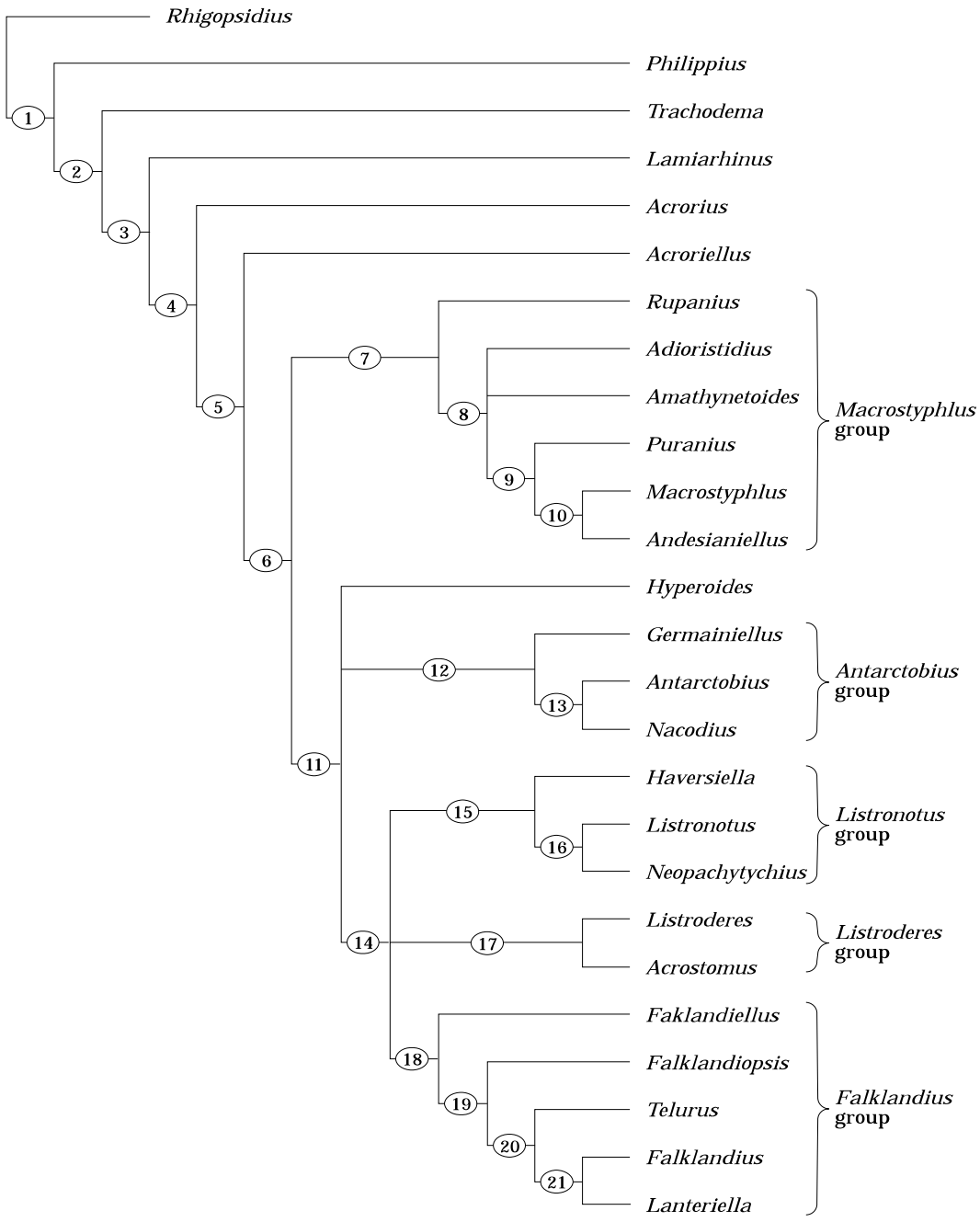

FIG. 4. Cladogram of the 25 genera of American Listroderina. Synapomorphies and homoplastic changes of nodes and terminal taxa are listed in Table 3.

TABLE 3
Synapomorphies and Homoplastic Changes Listed by Nodes and Terminal Taxa of Fig. 2

Nodes and terminal taxa		Synapomorphies	Homoplastic changes
1		6.1, 7.1, 47.1, 48.1	—
2		31.1, 39.1	—
3		41.1, 45.2, 46.1	—
4		33.1	24.1, 25.1, 28.1
5		38.1	—
6		—	40.1, 41.0
7	(*Macrostyphlus* group)	—	20.1, 48.0
8		10.1	2.1, 7.0, 21.1
9		—	45.1
10		—	21.2, 25.2, 27.1
11		—	37.2
12	(*Antarctobius* group)	—	38.0
13		—	25.2
14		—	45.1
15	(*Listronotus* group)	5.1, 11.1	7.0, 21.1
16		—	25.0, 38.0, 47.0
17	(*Listroderes* group)	30.1	25.0
18	(*Falklandius* group)	5.2, 18.1	6.2
19		49.1, 50.1	21.1, 45.3, 48.0, 52.1
20		—	1.1, 25.2, 27.1
21		4.1, 8.1	2.1
	Philippius	13.1, 16.1, 22.1, 26.1, 29.1, 44.1	2.1, 21.1, 24.1, 25.1, 40.1
	Trachodema	—	7.0, 28.1, 34.1, 40.1
	Lamiarhinus	19.1	—
	Acrorius	37.1	—
	Acroriellus	—	—
	Rupanius	35.1	24.0, 28.0, 31.0, 52.1, 53.1
	Adioristidius	—	51.1, 53.1
	Amathynetoides	—	21.2, 23.1
	Puranius	—	21.0
	Macrostyphlus	—	—
	Andesianellus	32.1	1.1, 6.0, 37.2, 45.3, 53.1
	Hyperoides	—	—
	Germainiellus	—	—
	Antarctobius	—	21.1
	Nacodius	—	23.1
	Haversiella	15.1	6.2
	Neopachytychius	14.1	—
	Listronotus	17.1	21.2
	Listroderes	—	38.0
	Acrostomus	9.1, 12.1	21.2, 37.0
	Falklandiellus	—	25.2, 27.1, 39.0, 53.1
	Falklandiopsis	42.1	20.1, 34.1, 39.0, 51.1
	Telurus	3.1, 36.2	5.0, 18.0
	Falklandius	—	20.1, 51.1, 52.0
	Lanteriella	36.1, 42.2, 43.1	23.1

Listroderina (Kuschel, 1958; Morrone, 1990), but this analysis shows that it represents the most primitive taxon of the group, being the sister genus to the remaining genera analysed. According to the cladogram, *Listroderes sensu lato* (Kuschel in Wibmer and O'Brien, 1986), namely, including also *Trachodema*, *Lamiarhinus*, *Acrorius*, *Hyperoides*, *Germainiellus*, *Antarctobius*, and *Nacodius*, is paraphyletic, being all the other American Listroderina (except *Philippius*) closely related to the genera formerly treated as its synonyms or based on species excluded from it. I previously believed that *Trachodema*, *Lamiarhinus*, *Acrorius*, and *Acroriellus* were closely related (Morrone, 1992c, 1994a; Morrone and Ocampo, 1995), but according to this analysis, they constitute a paraphyletic group.

Future analyses will corroborate this hypothesis, as well as incorporating the extra-American listroderines. For example, Kuschel (1964) considered *Nestrius* and *Gromilus* from New Zealand to be related to *Falklandius*; May (1994) considered the Australian *Ethemaia* and *Ophryota* related to *Listroderes*; and Morrone (1994d) commented on the close relationship of *Haversiella*, *Listronotus*, and *Neopachytychius* with *Palaechtus* and related genera from Tristan da Cunha-Gough islands. Further studies will determine if these extra-American taxa are assigned, respectively, to the *Falklandius*, *Listroderes*, and *Listronotus* generic groups.

It should be noted that the rooting of the cladogram with *Rhigopsidius* rests on the assumption that Listroderina are more closely related to Rhytirrhinina than to the other subtribes. Elucidation of the proper cladistic relationship among the subtribes of Rhytirrhinini as a whole could lead to the choice of another outgroup, and thus change this hypothesis. Ongoing revisionary studies by S. Louw (pers. comm.) on the Old World Rhytirrhinini and E. Zimmerman on the Australian taxa may help clarify Rhytirrhinini relationships.

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APPENDIX 1

List of Valid Names of the American Listroderina, with Indication of Country Records and Collections where Specimens Examined by the Author are Deposited

Acroriellus *Morrone and Ocampo, 1995*

1. *A. bobi* Morrone and Ocampo, 1995. Ecuador. AMNH and CMN.
2. *A. carinatus* Morrone and Ocampo, 1995. Ecuador. CMN.
3. *A. similaris* Morrone and Ocampo, 1995. Ecuador. CMN.
4. *A. tuberculosus* Morrone and Ocampo, 1995. Ecuador. CMN.
5. *A. viridisquamosus* Morrone and Ocampo, 1995. Peru. CMN and FMNH.
6. *A. vittetae* Morrone and Ocampo, 1995. Colombia. AMNH and USNM.

Acrorius *Kirsch, 1889*

7. *A. andersoni* Morrone, 1994a. Ecuador. CMN.
8. *A. bolivianus* Ocampo and Morrone, 1996. Bolivia. HAHC and MLP.
9. *A. cuprinus* Morrone, 1994a. Ecuador. CMN.
10. *A. nymphalis* Morrone, 1994a. Ecuador. CMN.
11. *A. otramas* Ocampo and Morrone, 1996. Ecuador. HAHC.
12. *A. puncticollis* Kirsch, 1889. Colombia.
13. *A. papallacta* Morrone, 1994a. Ecuador. CMN and HAHC.
14. *A. pillahuata* Morrone, 1994a. Peru. CMN and FMNH.
15. *A. plicatifrons* Morrone, 1994a. Peru. FMNH.
16. *A. sisyphus* Morrone, 1994a. Colombia. CNCI and HAHC.

Acrostomus *Kuschel, 1955*

17. *A. bruchi* (Hustache, 1926). Argentina. CWOB, IPCN, MACN, and MLP.
18. *A. cruralis* Kuschel, 1958. Argentina. MACN and USNM.
19. *A. foveicollis* Kuschel, 1958. Argentina. CBPC, CWOB, and MHNS.
20. *A. griseus* (Guérin, 1839). Argentina and Chile. CWOB, FIML, IPUM, MHNS, and MLP.
21. *A. magellanicus* Kuschel, 1958. Chile. BMNH, MHNS, and USNM.
22. *A. mordor* Morrone, 1994b. Argentina. AMNH, MACN, and MLP.
23. *A. vianai* Kuschel, 1958. Argentina and Chile. BMNH and MHNS.

Adioristidius *Morrone, 1994c*

24. *A. anchonoideus* (Hustache, 1938). Bolivia. DEI, HAHC, and MLP.
25. *A. carinicollis* (Voss, 1954). Peru.
26. *A. chilensis* Morrone, 1994c. Chile. MHNS.
27. *A. costulatus* (Hustache, 1938). Bolivia. DEI.
28. *A. crassirostris* (Hustache, 1938). Bolivia. DEI.
29. *A. cuprisquameus* (Voss, 1954). Peru.
30. *A. granulatus* (Hustache, 1938). Bolivia. DEI.
31. *A. hirsutus* Morrone, 1994c. Chile. MHNS and MLP.
32. *A. hydanius* Morrone, 1994c. Bolivia. DEI.
33. *A. jorgei* Morrone, 1994c. Chile. MHNS and MLP.
34. *A. lidiae* Morrone, 1994c. Bolivia. HAHC.
35. *A. manu* Morrone, 1994c. Peru. CMN and FMNH.
36. *A. morio* (Voss, 1954). Peru. CWOB and MLP.
37. *A. nivalis* (Kuschel, 1949). Chile. MHNS and NZAC.
38. *A. pampaensis* (Voss, 1954). Peru.
39. *A. peruvianus* (Voss, 1954). Peru.
40. *A. puncticollis* (Hustache, 1938). Bolivia. DEI.
41. *A. scrobicollis* (Voss, 1954). Peru.
42. *A. similaris* (Voss, 1954). Peru. DEI.
43. *A. subimpressus* (Voss, 1954). Peru.
44. *A. subtuberculatus* (Voss, 1954). Peru.
45. *A. sulcicollis* (Hustache, 1938). Bolivia. DEI.
46. *A. tuberculatus* (Voss, 1954). Bolivia and Peru. CWOB and USNM.
47. *A. variegatus* (Voss, 1954). Bolivia. DEI.

Amathynetoides *Morrone, 1994c*

48. *A. appendiculatus* (Kuschel, 1949). Bolivia, Chile, and Peru. CWOB, HAHC, MHNS, NZAC, and USNM.
49. *A. ebeninus* (Hustache, 1938). Peru. BPBM, CWOB, and DEI.
50. *A. intemperatus* Morrone, 1994c. Peru. AMNH, CWOB, and MLP.
51. *A. longulus* (Kuschel, 1949). Chile and Peru. CWOB, MHNS, NZAC, and USNM.
52. *A. morbeamus* Morrone, 1994c. Peru. FIML.
53. *A. nitidiventris* (Hustache, 1938). Bolivia. DEI.
54. *A. normae* Morrone, 1994c. Bolivia. HAHC and MLP.
55. *A. palustris* (Kuschel, 1949). Bolivia, Chile, and Peru. CWOB, FIML, MHNS, NZAC, and USNM.
56. *A. sparsesetosus* (Hustache, 1938). Bolivia and Peru. CWOB, DEI, and HAHC.
57. *A. sundrianus* Morrone, 1994c. Peru. BMNH, CWOB, FIML, and MLP.

Andesianellus *Anderson and Morrone, 1996*

58. *A. carltoni* Anderson and Morrone 1996. Ecuador. CMN.
59. *A. cotopaxi* Anderson and Morrone 1996. Ecuador. AMNH.
60. *A. fulgidus* Anderson and Morrone 1996. Ecuador. CMN.
61. *A. hermani* Anderson and Morrone 1996. Colombia. AMNH.
62. *A. masneri* Anderson and Morrone 1996. Ecuador. CMN.
63. *A. microphthalmicus* Anderson and Morrone 1996. Ecuador. CMN and MLP.
64. *A. minutus* Anderson and Morrone 1996. Peru. CMN and FMNH.
65. *A. planirostris* Anderson and Morrone 1996. Peru. AMNH, BMNH, CMN, CWOB, FMNH, HAHC, MLP, and USNM.
66. *A. tricarinatus* Anderson and Morrone 1996. Peru. CMN and FMNH.

Antarctobius *Fairmaire, 1885*

67. *A. abditus* (Enderlein, 1907). Argentina. BMNH.
68. *A. bidentatus* (Champion, 1918). Argentina. BMNH.
69. *A. falklandicus* (Enderlein, 1907). Argentina. AMPC and BMNH.
70. *A. germaini* (Kolbe, 1907). Argentina and Chile. AMNH, BMNH, CADIC, CMN, CWOB, IPUM, MHNS, and MLP.
71. *A. hyadesii* Fairmaire, 1885. Argentina and Chile. BPBM, CMN, MHNS.
72. *A. lacunosus* Fairmaire, 1885. Argentina and Chile. BPBM, MCZ, MHNS.
73. *A. rugirostris* Champion, 1918. Chile. BMNH.
74. *A. vulsus* (Enderlein, 1907). Argentina. BMNH and USNM.
75. *A. yefacel* Morrone, 1992a. Chile. AMNH.

Falklandiellus *Kuschel, 1950*

76. *F. suffodens* (Enderlein, 1907). Argentina and Chile. BMNH, CADIC, MACN, MLP, USNM, and ZMHU.

Falklandiopsis *Morrone and Anderson, 1995*

77. *F. magellanica* (Morrone, 1992b). Chile. MLP, NZAC, and ZMHU.

Falklandius *Enderlein, 1907*

78. *F. antarcticus* (Stierlin, 1903). Argentina and Chile. AMPC, BMNH, CADIC, CMN, CWOB, MACN, MHNS, and USNM.
79. *F. chilensis* Morrone and Anderson, 1995. Chile. AMNH, BMNH, CMN, CWOB, FMNH, HAHC, MLP, and USNM.
80. *F. goliath* Morrone, 1992b. Argentina. BMNH.
81. *F. kuscheli* Morrone, 1992b. Argentina. BMNH.
82. *F. peckorum* Morrone and Anderson, 1995. Chile. AMNH, BMNH, CMN, CWOB, FMNH, HAHC, MLP, and USNM.
83. *F. turbificatus* Enderlein, 1907. Argentina. BMNH.

Germainiellus *Morrone, 1993a*

84. *G. angulipennis* (Germain, 1895). Chile. MHNS.

85. *G. attenuatus* (Germain, 1895). Chile. ARPC and MHNS.

86. *G. dentipennis* (Germain, 1895). Argentina and Chile. CBPC, CWOB, HAHC, MHNS, and USNM.

87. *G. fulvicornis* (Germain, 1895). Argentina and Chile. AMNH, BPBM, CBCP, CMN, CWOB, FIML, MCZ, MHNS, MLP, and USNM.

88. *G. laevirostris* (Germain, 1895). Argentina and Chile. BPBM, IPUM, MCZ, MHNS, MLP, and USNM.

89. *G. lugens* (Germain, 1895). Argentina and Chile. CMN, CWOB, IPUM, MACN, MCZ, and MHNS.

90. *G. ovatus* (Boheman, 1842). Chile. BMNH, MHNS, and USNM.

91. *G. philippi* (Germain, 1896). Chile. CMN, DEI, HAHC, and MHNS.

92. *G. planipennis* (Blanchard, 1851). Chile. BMNH, CWOB, and MHNS.

93. *G. punctiventris* (Germain, 1895). Chile. MHNS.

94. *G. rugipennis* (Blanchard, 1851). Argentina and Chile. AMNH, BPBM, CADIC, CBCP, CMN, MHNS, MLP, and USNM.

95. *G. salebrosus* (Enderlein, 1907). Argentina. BMNH.

Haversiella *Schweiger, 1958*

96. *H. albolimbata* (Champion, 1918). Argentina and Chile. BMNH, MHNS, and USNM.

Hyperoides *Marshall, 1914*

97. *H. balfourbrownei* (Kuschel, 1952). Argentina. MLP.

98. *H. fragariae* Marshall, 1914. Argentina and Uruguay. BMNH, CBPC, and MNHN.

99. *H. murinus* (Germain, 1896). Chile. BMNH, CWOB, and MHNS.

100. *H. subcinctus* (Boheman, 1842). Argentina and Chile. AMNH, BMNH, CBPC, CWOB, HAHC, IADIZA, MACN, MHNS, and MNHN.

101. *H. victus* (Germain, 1896). Chile. BMNH, CWOB, HAHC, and MHNS.

Lamiarhinus *Morrone, 1992c*

102. *L. aelficus* Morrone, 1992c. Chile. CMN, CWOB, HAHC, and MLP.

103. *L. horridus* (Germain, 1896). Chile. MHNS.

Lanteriella *Morrone, 1992b*

104. *L. microphtalma* Morrone, 1992b. Argentina. BMNH.

Listroderes *Schoenherr, 1826*

105. *L. affinis* Hustache, 1926. Argentina and Chile. CBPC, IPCN, IPUM, MACN, and MNHN.

106. *L. angusticeps* Blanchard, 1851. Chile. MHNS and MNHN.

107. *L. annulipes* Blanchard, 1851. Chile. CBPC, CWOB, MHNS, and MNHN.

108. *L. apicalis* Waterhouse, 1841. Argentina, Brazil, Chile, Paraguay, and Uruguay. AMNH, BMNH, HAHC, MACN, MHNS, and MLP.

109. *L. bimaculatus* Boheman, 1842. Argentina and Chile. AMNH, BMNH, CWOB, HAHC, MACN, and MHNS.

110. *L. brevirostris* Germain, 1895. Chile. MHNS.

111. *L. brevisetis* Hustache, 1926. Argentina. CBCP, DZUP, IPCN, MACN, MLP, and MNHN.

112. *L. bruchi* Hustache, 1926. Argentina. DZUP, FIML, HAHC, IADIZA, MACN, and MLP.

113. *L. charybdis* Morrone, 1993d. Argentina. MACN and MLP.

114. *L. cinerarius* Blanchard, 1851. Chile. BMNH, CWOB, HAHC, IADIZA, MHNS, and MNHN.

115. *L. confusus* Hustache, 1926. Argentina and Brazil. DZUP, FIML, MACN, MLP, and MNHN.

116. *L. costirostris* Schoenherr, 1826. Argentina, Brazil, Paraguay, and Uruguay. AMNH, BMNH, CBPC, CMN, CWOB, DZUP, FIML, GJWC, HAHC, MACN, MHNS, MLP, MNHN, MZSP, and USNM.

117. *L. curvipes* Germain, 1895. Chile. BMNH, CWOB, and MHNS.

118. *L. delaiguei* Germain, 1895. Argentina, Chile, and Uruguay. BMNH, CADIC, CWOB, IPUM, and MHNS.

119. *L. desertorum* Germain, 1895. Chile. BMNH, CWOB, HAHC, and MHNS.

120. *L. difficilis* Germain, 1895. Argentina, Chile, and Uruguay. CWOB and MHNS.

121. *L. elegans* Hustache, 1926. Argentina and Uruguay. GJWC, MACN, MLP, and MNHN.

122. *L. erinaceus* Germain, 1895. Chile. MHNS.

123. *L. fallax* Germain, 1895. Chile. CWOB and MHNS.

124. *L. foveatus* (Lea, 1928). Argentina, Brazil, Chile, and Uruguay. BMNH, DZUP, FIML, GJWC, HAHC, MACN, and MZSP.

125. *L. hoffmanni* Germain, 1895. Chile. BMNH, CWOB, and MHNS.

126. *L. howdenae* Morrone, 1993d. Chile. HAHC and MLP.

127. *L. leviculus* Kuschel, 1952. Argentina. BMNH.

128. *L. montanus* Germain, 1895. Chile. MHNS.

129. *L. nodifer* Boheman, 1842. Chile and Peru. BMNH, CWOB, MACN, and MHNS.

130. *L. obliquus* Klug, 1829. Argentina, Brazil, and Uruguay. CWOB and MHNS.

131. *L. obrieni* Morrone, 1993d. Chile. MHNS and MLP.

132. *L. paranensis* Hustache, 1926. Argentina. DZUP and MNHN.

133. *L. punicola* Kuschel, 1949. Bolivia, Chile, and Peru. HAHC and MHNS.

134. *L. pusillus* Hustache, 1926. Argentina. CBPC, MLP, and MNHN.

135. *L. robustior* Schenkling and Marshall, 1931. Chile. BMNH, CMN, CWOB, MHNS, and MLP.

136. *L. robustus* Waterhouse, 1841. Chile. CWOB, HAHC, and MHNS.

137. *L. scylla* Morrone, 1993d. Argentina. FIML and MLP.

138. *L. trivialis* Germain, 1895. Chile. MHNS.

139. *L. tuberculifer* Blanchard, 1851. Chile, HAHC and MHNS.

140. *L. uruguayensis* Kuschel, 1952. Brazil and Uruguay. BMNH and HAHC.

141. *L. wagneri* Hustache, 1926. Argentina and Uruguay. BMNH and MNHN.

142. *L. wittei* Hustache, 1926. Argentina. MACN and MNHN.

Listronotus *Jekel, 1865*

143. *L. alternatus* (Dietz, 1889). Canada and USA.

144. *L. americanus* LeConte, 1876. USA. BMNH.

145. *L. angustatus* (Champion, 1902). Belize, Honduras, Mexico, and Nicaragua.

146. *L. annulipes* (Blatchley, 1925). USA.

147. *L. anthracinus* (Dietz, 1889). USA.

148. *L. apicalis* (Hustache, 1926). Argentina and Chile. MLP.

149. *L. appendiculatus* (Boheman, 1842). Canada, Honduras, Mexico, and USA. AMNH and BMNH.

150. *L. argentinensis* (Hustache, 1926). Argentina, Paraguay, and Uruguay. AMNH, MACN, and MLP.

151. *L. arizonicus* O'Brien, 1981. USA.

152. *L. blandus* Henderson, 1940. Honduras and USA. AMNH and BMNH.

153. *L. blatchleyi* Henderson, 1940. USA.

154. *L. bonariensis* (Kuschel, 1955). Argentina, Bolivia, Chile, and Uruguay. BMNH and MHNS.

155. *L. borrichiae* O'Brien, 1981. Mexico and USA.

156. *L. bosqi* (Hustache, 1926). Argentina, Bolivia, and Uruguay. BMNH and MLP.

157. *L. breyeri* (Bréthes, 1910). Argentina and Uruguay. MACN.

158. *L. burkei* O'Brien, 1981. USA.

159. *L. californicus* (Dietz, 1889). Canada and USA. AMNH.

160. *L. callosus* LeConte, 1876. USA. BMNH and AMNH.

161. *L. carinatus* (Blatchley, 1928). USA.

162. *L. carinicollis* (Hustache, 1926). Argentina and Paraguay.

163. *L. caudatus* (Say, 1924). Canada and USA. BMNH and AMNH.

164. *L. cinnamoneus* (Hustache, 1926). Argentina and Uruguay. MLP.

165. *L. conabilis* O'Brien, 1981. USA.

166. *L. crypticus* O'Brien, 1981. USA.

167. *L. cryptops* (Dietz, 1889). Dominican Republic, Mexico, Nicaragua, and USA. BMNH and AMNH.

168. *L. cyrticus* (Desbrochers, 1898). Argentina, Bolivia, Chile, and Uruguay. AMNH, MACN, and MLP.

169. *L. dauci* (Bréthes, 1926). Argentina and Uruguay. MACN.

170. *L. debilis* Blatchley, 1916. USA. AMNH.

171. *L. deceptus* (Blatchley, 1916). USA.

172. *L. delumbis* (Gyllenhal, 1834). Canada and USA. BMNH and AMNH.

173. *L. dietrichi* (Stockton, 1963). Belize, Costa Rica, Honduras, Mexico, Nicaragua, and Panama.
174. *L. dietzi* O'Brien, 1981. USA. AMNH.
175. *L. distinctus* Henderson, 1940. USA. BMNH.
176. *L. dorsalis* (Dietz, 1889). USA.
177. *L. dorytomoides* (Hustache, 1926). Argentina and Uruguay.
178. *L. durangoensis* O'Brien, 1977. Mexico. AMNH and BMNH.
179. *L. echinatus* (Dietz, 1889). USA. AMNH.
180. *L. echinodori* O'Brien, 1977. Honduras, Mexico, and USA. AMNH and BMNH
181. *L. elegans* Van Dyke, 1929. USA.
182. *L. elegantulus* O'Brien, 1981. USA. CWOB.
183. *L. elongatus* (Hustache, 1939). Argentina, Brazil, Paraguay, and Uruguay. MLP.
184. *L. fasciatus* O'Brien, 1981. USA. CWOB.
185. *L. filiformis* (LeConte, 1876). Canada and USA. BMNH and AMNH.
186. *L. frontalis* LeConte, 1876. Canada and USA. AMNH and BMNH.
187. *L. geminatus* (Hustache, 1926). Argentina, Bolivia, Chile, and Uruguay. MACN and MLP.
188. *L. griseus* (Hustache, 1926). Argentina, Chile, Paraguay, and Uruguay. AMNH, MACN, and MLP.
189. *L. grypidioides* (Dietz, 1889). Mexico and USA. AMNH.
190. *L. haldemani* (Burke, 1963). USA. BMNH.
191. *L. hirtellus* (Dietz, 1889). Guatemala, Mexico, and USA.
192. *L. hoodi* (Stockton, 1963). USA.
193. *L. hornii* (Dietz, 1889). USA. AMNH.
194. *L. hubbardi* (LeConte, 1876). USA. BMNH.
195. *L. humilis* (Gyllenhal, 1834). Mexico and USA. AMNH.
196. *L. hyperodes* (Dietz, 1889). USA. AMNH.
197. *L. incompletus* (Hatch, 1971). USA. AMNH.
198. *L. ingens* Henderson, 1940. USA. AMNH.
199. *L. insignis* Henderson, 1940. USA.
200. *L. laevis* (Hustache, 1926). Argentina, Bolivia, and Paraguay.
201. *L. laramiensis* (Angell, 1898). USA.
202. *L. latinasus* (Blatchley, 1922). USA.
203. *L. lineolaticollis* (Blanchard, 1851). Argentina, Chile, and Uruguay. MLP.
204. *L. lodingi* (Blatchley, 1920). USA.
205. *L. lucens* (Hustache, 1926). Argentina and Paraguay.
206. *L. lutulentus* (Boheman, 1843). Mexico and USA. BMNH.
207. *L. maculatus* (Hatch, 1971). USA.
208. *L. maculicollis* (Kirby, 1837). Canada, Mexico, and USA. AMNH.
209. *L. manifestus* Henderson, 1940. Mexico and USA. AMNH and BMNH.
210. *L. marginalis* O'Brien, 1977. Mexico and Nicaragua. BMNH.
211. *L. marginicollis* (Hustache, 1926). Argentina and Uruguay. MACN and MLP.
212. *L. marshalli* O'Brien, 1981. USA.
213. *L. meridionalis* O'Brien, 1977. Costa Rica, Honduras, and Mexico. BMNH.
214. *L. minutus* (Blanchard, 1851). Argentina, Bolivia, and Chile. AMNH.
215. *L. montanus* (Dietz, 1889). Canada and USA.
216. *L. nebulosus* LeConte, 1876. USA. AMNH.
217. *L. neocallosus* O'Brien, 1981. USA.
218. *L. nevadicus* LeConte, 1876. USA.
219. *L. nigropunctatus* (Suffrian, 1870). Cuba.
220. *L. novellus* (Blatchley, 1916). USA. AMNH.
221. *L. obscurellus* (Dietz, 1889). USA.
222. *L. obtectus* (Dietz, 1889). Mexico and USA.
223. *L. oregonensis* (LeConte, 1876). Canada, Mexico, and USA. AMNH and BMNH.
224. *L. ornatipennis* (Blanchard, 1851). Chile. MHNS.
225. *L. pallidus* O'Brien, 1981. USA.
226. *L. palustris* Blatchley, 1916. USA. AMNH and BMNH.
227. *L. pampaensis* (Voss, 1954). Peru.
228. *L. peninsularis* (Blatchley, 1916). USA.
229. *L. plumosiventris* O'Brien, 1977. Mexico. BMNH.
230. *L. porcellus* (Say, 1881). USA. AMNH.
231. *L. poseyensis* (Blatchley, 1920). USA.
232. *L. pseudosetosus* O'Brien, 1981. USA.
233. *L. puncticollis* (Hustache, 1926). Argentina, Bolivia, and Paraguay. MLP.
234. *L. punctiger* LeConte, 1876. Canada, Mexico, and USA. AMNH and BMNH.
235. *L. pusillus* (Hustache, 1926). Argentina and Paraguay. MLP.
236. *L. rotundicollis* LeConte, 1876. Costa Rica, Mexico, and USA. AMNH and BMNH.
237. *L. rubtzoffi* O'Brien, 1981. USA. AMNH.
238. *L. rufomarginatus* (Hustache, 1939). Argentina. MLP.
239. *L. salicorniae* O'Brien, 1981. Mexico and USA.

240. *L. scapularis* Casey, 1895. USA. AMNH.
241. *L. setosipennis* (Hustache, 1926). Argentina, Brazil, and Uruguay. MLP.
242. *L. setosus* LeConte, 1876. USA. AMNH.
243. *L. similis* Henderson, 1940. USA. AMNH and BMNH.
244. *L. sondondoanus* (Voss, 1954). Peru.
245. *L. sordidus* (Gyllenhal, 1834). USA. AMNH and BMNH.
246. *L. sparsus* (Say, 1831). USA. AMNH and BMNH.
247. *L. squamiger* (Say, 1831). Canada and USA. AMNH and BMNH.
248. *L. sulcipennis* (Boheman, 1834). Brazil.
249. *L. suturalis* O'Brien, 1981. USA.
250. *L. teretirostris* (LeConte, 1857). USA. AMNH and BMNH.
251. *L. testaceipes* (Champion, 1902). Mexico.
252. *L. texanus* (Stockton, 1963). USA. AMNH.
253. *L. truncatus* (Hatch, 1971). Canada and USA. AMNH.
254. *L. tuberosus* LeConte, 1876. USA, AMNH and BMNH.
255. *L. turbatus* O'Brien, 1981. USA.
256. *L. vitticollis* (Kirby, 1837). USA. AMNH.
257. *L. vulgaris* (Hustache, 1926). Argentina, Bolivia, Paraguay, and Uruguay. MLP.
258. *L. wallacei* (Stockton, 1963). USA.
259. *L. weiseri* (Hustache, 1926). Argentina and Bolivia.

Macrostyphlus *Kirsch, 1889*

260. *M. bilbo* Morrone, 1994c. Ecuador. CNCI.
261. *M. coelorum* (Olliff, 1891). Ecuador. CWOB.
262. *M. frodo* Morrone, 1994c. Colombia. ICNB and USNM.
263. *M. gandalf* Morrone, 1994c. Colombia. CNCI, CMN, and MLP.
264. *M. gualcalae* Kirsch, 1889. Colombia. SMTD.
265. *M. howdenorum* Morrone, 1994c. Ecuador. HAHC.
266. *M. peruvianus* Morrone, 1994c. Peru. FMNH.
267. *M. sturmi* Morrone, 1994c. Colombia. ICNB.
268. *M. transatlanticus* (Kirsch, 1889). Ecuador. SMTD.
269. *M. venezolanus* Morrone, 1994c. Venezuela.

Nacodius *Morrone, 1994e*

270. *N. alectrus* Morrone, 1994e. Ecuador. CWOB.
271. *N. brevirostris* (Voss, 1954). Peru. SMTD.
272. *N. martitae* Morrone, 1994e. Peru. AMNH, CWOB, and MLP.
273. *N. omissus* (Kuschel, 1952). Ecuador. BMNH.

Neopachytychius *Hustache, 1939*

274. *N. squamosus* Hustache, 1939. Argentina, Bolivia, Chile, and Uruguay. FIML, IADIZA, MACN, MHNS, and MLP.

Philippius *Germain, 1895*

275. *P. superbus* (Reed, 1872). Argentina and Chile. IADIZA, MACN, MHNS, MLP, and USNM.

Puranius *Germain, 1896*

276. *P. argentinensis* Morrone, 1994c. Argentina. AMNH, BMNH, and MLP.
277. *P. australis* Germain, 1896. Argentina and Chile. AMNH, CWOB, MHNS, and NZAC.
278. *P. championi* (Kuschel, 1952). Argentina. BMNH, CWOB, and NZAC.
279. *P. dubius* (Germain, 1896). Chile. CWOB, MHNS, and NZAC.
280. *P. elguetai* Morrone, 1994c. Chile, AMNH, MHNS, and MLP.
281. *P. exsculpticollis* (Enderlein, 1907). Argentina. BMNH.
282. *P. fasciculiger* (Blanchard, 1851). Chile. CWOB, MHNS, NZAC, and USNM.
283. *P. hispidus* (Germain, 1896). Chile. CWOB, MHNS, and NZAC.
284. *P. inaequalis* Germain, 1896. Chile. CWOB, HAHC, MHNS, NZAC.
285. *P. midas* Morrone, 1994c. Chile. AMNH.
286. *P. nigrinus* (Fairmaire, 1884). Argentina and Chile. ARPC, BMNH, CADIC, CBPC, CMN, CNCI, CWOB, DEI, FIML, IPUM, MCZ, MHNS, NZAC, and USNM.
287. *P. obrienorum* Morrone, 1994c. Bolivia and Peru. AMNH, CWOB, HAHC, and MLP.

288. *P. pusillus* Morrone, 1994c. Chile. MHNS and MLP.

289. *P. scaber* (Enderlein, 1907). Argentina. AMPC, BMNH, CWOB, and NZAC.

290. *P. sylvanius* Morrone, 1994c. Chile. AMNH, BMNH, CMN, and MLP.

291. *P. torosus* Morrone, 1994c. Chile. MHNS and MLP.

292. *P. tothus* Morrone, 1994c. Chile. MHNS.

293. *P. tuberosus* Germain, 1896. Chile. CWOB, MHNS, and NZAC.

294. *P. verrucosus* (Germain, 1896). Chile. CWOB, HAHC, MHNS, and NZAC.

295. *P. vulgaris* Morrone, 1994c. Argentina and Chile. AMNH, BMNH, CMN, MHNS, and MLP.

Rupanius *Morrone, 1995c*

296. *R. carinatus* Morrone, 1995c. Colombia, CMN.

Telurus *Kuschel, 1955*

297. *T. caudiculatus* Morrone and Anderson, 1995. Argentina and Chile. AMNH, BMNH, CMN, CNCI, CWOB, HAHC, MCZ, MHNS, MLP, USNM, and ZMC.

298. *T. dissimilis* (Fairmaire, 1885). Chile, BMNH, IPUM, MHNS, and NZAC.

Trachodema *Blanchard, 1851*

299. *T. minuta* (Hustache, 1930). Chile.

300. *T. tuberculosa* Blanchard, 1851. Chile. CMN, CWOB, DZUP, FIML, MHNS, and USNM.

Collection Codes

AMNH American Museum of Natural History, New York, USA (L. H. Herman, Jr.)
AMPC Amyan MacFadyen, private collection, Coleraine, Northern Ireland
ARPC Alexander Riedel, private collection, Friedberg, Germany
BMNH The Natural History Museum, London, England (Christopher Lyal)
BPBM Bernice P. Bishop Museum, Honolulu, USA (G. A. Samuelson)
CADIC Centro Austral de Investigaciones Científicas, Ushuaia, Tierra del Fuego, Argentina (A. Sobral)
CBPC Carlos Bordón, private collection, Maracay, Venezuela
CMN Canadian Museum of Nature, Ottawa, Canada (R. S. Anderson)
CNCI Canadian National Collection of Insects, Center for Land and Biological Resources Research, Agriculture Canada, Ottawa, Canada (D. E. Bright)
CWOB Charles W. O'Brien, private collection, Talahassee, Florida, USA
DEI Deutsches Entomologisches Institut, Eberswalde-Finow, Germany (L. Zenche)
DZUP Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (G. Rosado-Neto)
FIML Fundación e Instituto Miguel Lillo, San Miguel de Tucumán, Argentina (A. L. Terán)
FMNH Field Museum of Natural History, Chicago, USA (A. F. Newton, Jr.)
GJWC Guillermo J. Wibmer, private collection, Talahassee, Florida, USA
HAHC Henry F. and Anne T. Howden, private collection, Ottawa, Canada
IADIZA Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (S. Roig-Juñent)
ICNB Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santafé de Bogotá, Colombia (G. Andrade)
IPUM Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile (J. Petersen)
MACN Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (A. O. Bachmann)
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, USA (D. G. Furth)
MHNS Museo Nacional de Historia Natural, Santiago, Chile (M. Elgueta)
MLP Museo de La Plata, La Plata, Argentina (J. Schnack)
MNHN Museum National d'Histoire Naturelle, Paris, France (H. Perrin)

NZAC New Zealand Arthropod Collection, Auckland, New Zealand (R. Craw)
SMTD Staatliches Museum für Tierkunde, Dresden, Germany (R. Krause)
USNM National Museum of Natural History, Washington D.C., USA (J. Pakaluk)
ZMC Zoologisk Museum, Copenhagen, Denmark (M. Hansen)
ZMHU Zoologische Museum der Humboldt Universität, Berlin, Germany (F. Hieke)