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Listroderes abditus or *Antarctobius abditus*? A simultaneous analysis of larval and adult characters (Coleoptera: Curculionidae)

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Abstract. The weevil species *Listroderes abditus* Enderlein belongs in the subtribe Listroderina. This species had been previously transferred to *Antarctobius*, based on characters from the adult morphology. However, larval characters suggest that it was placed correctly in *Listroderes*. A cladistic analysis of this species and nine other rhytirrhinines for which larvae are known was performed, based on 56 morphological characters (32 from larvae and 24 from adults). According to the single cladogram obtained (78 steps, CI = 0.65, and RI = 0.72), *L. abditus* should be included in *Listroderes* rather than in *Antarctobius*. Larval and adult characters were also analysed separately, leading to poorer resolution in comparison with the simultaneous analysis, and suggesting that a stable classification requires the analysis of data from both life stages.

INTRODUCTION

This paper began as a friendly exchange between the present authors concerning the systematic placement of *L. abditus* (Enderlein) (Curculionidae: Rhytirrhinini). This weevil species was described in *Listroderes* Schoenherr by Enderlein (1907). As part of revisionary studies that restricted the concept of *Listroderes*, Morrone (1992) revalidated its former synonym *Antarctobius* Fairmaire, based on characters from the adult morphology, and assigned *L. abditus* to it. In a cladistic analysis of the New World genera of Listroderina, *Listroderes* and *Antarctobius* proved to be only related distantly, belonging to different generic groups (Morrone, 1997a). However, analysis of larval characters prompted Marvaldi (1998) to reconsider the placement of *L. abditus* in *Listroderes*, although treating *Antarctobius* as a distinct genus. Thus a case of supposed incongruence between different data sets exists, so establishing the correct placement of *L. abditus* requires the analysis of both larval and adult characters.

There has been much discussion in recent cladistic literature over whether different data sets should be analysed separately or combined and analysed simultaneously (Kluge, 1989; Kluge & Wolf, 1993; Chippindale & Wiens, 1994; De Queiroz et al., 1995; Nixon & Carpenter, 1996; Page, 1996). Nixon & Carpenter (1996) have argued convincingly that simultaneous analyses maximize cladistic parsimony and, thus, should be preferred, although separate analyses could be useful to understand the incongruence between data sets.

The present objective is to analyse the cladistic placement of *L. abditus*, based on the simultaneous analysis of both adult and larval characters, and to investigate these characters separately.

MATERIAL AND METHODS

Ten rhytirrhinine taxa (seven genera and three species) for which both adult and larval information was available (Table 1) were chosen as terminal units for the study. The 56 characters (Table 2) were derived from larvae (32) and adults (24). The cladogram was rooted with the genus *Aegorhinus* Erichson, which belongs to the tribe Aterpini, closely related to Rhytirrhinini (Marvaldi, 1997; Morrone, 1997b). Multistate characters 14, 24, 41, 47, and 54 were treated as non-additive. Table 2 contains the data matrix used.

TABLE 1. Units of the analysis, with references to larvae and adults.

Taxa	References	
	Larvae	Adults
Antarctobius	Marvaldi (1998)	Morrone (1992)
Gromilus	May (1977, 1981, 1993)	Kuschel (1964)
Listroderes abditus	Marvaldi (1998)	Morrone (1992)
L. bruchi	Marvaldi (1998)	Morrone (1993a, b)
L. costirostris	Marvaldi (1998)	Morrone (1993a, b)
Listronotus	May (1977, 1993), Marvaldi (1998)	O'Brien (1977), Morrone et al. (1995)
Nestrius	May (1977, 1993)	Kuschel (1964)
Rhigopsidius	Loiácono & Morrone (1991)	Morrone & Loiácono (1992)
Steriphus	May (1977, 1993, 1994)	
Tristanodes	Kuschel (1962)	

TABLE 2. Data matrix and characters used in the analysis, with *Aegorhinus* as root. Multistate characters 14, 24, 41, 47, and 54 – non-additive. ? – polymorphic.

Root	0000000000	0000000000	0000?00000	0000000000	00000000?0	000000
Antarctobius	0000010000	0002010000	0102000000	0000101000	1000102011	000?00
Gromilus	00110?00?0	0001000000	0110001100	201010?001	10000?2010	000201
Listroderes abditus	1110100111	1113011110	1011100011	1000101000	1000102011	000200
L. bruchi	1110100101	1113111011	1010100011	1100111000	2101002011	001000
L. costirostris	1110100111	1113011111	1010100011	1100111000	2000002011	001010
Listronotus	0001000010	0001011000	0110000010	2011001010	0000002011	000001
Nestrius	00110?0010	0000000000	0110001100	2010101100	1000112010	000201
Rhigopsidius	0001011000	0000000000	0000000000	0000000000	2110001100	110101
Steriphus	00100000?0	0002000000	011?010100	?011101000	0000002010	000201
Tristanodes	0011010011	0002000000	0110000000	2011001000	1000002010	000000

Data were analysed with two computer programmes: Hennig86 1.5 (Farris, 1988) and Pee-Wee 2.5.1 (Goloboff, 1996). Hennig86 was used to find the shortest cladograms under equal weights, applying the implicit enumeration option (ie*) and the successive weighting procedure. Pee-Wee was used to find the most parsimonious weighted cladograms, using options search and mswap*3. Consistency and retention indices were calculated with Hennig86 excluding autapomorphies. The test of incongruence between larval and adult characters was performed calculating Mickevich & Farris's (1981) index for separate larval and adult matrices and 10,000 partitions selected randomly into matrices of the two original sizes (see details in Farris et al., 1995), using Random Cladistics (Siddall, 1995).

Separate analyses were performed breaking the original matrix into two separate data matrices, one based on the 32 larval characters and the other based on the 24 adult characters. Each data set was then analysed separately with Hennig86 and Pee-Wee under the same conditions as the simultaneous analysis.

Larval characters

1. Head color: (0) uniformly pigmented; (1) with maculate pattern.
2. Head shape: (0) subcircular; (1) wider than long.
3. Endocarina: (0) conspicuous; (1) absent or vestigial.
4. Hypopharyngeal bracon: (0) lacking maculae; (1) with maculae.
5. Tentorial bridge: (0) of modal form, clear; (1) thin medially, pigmented on each side.
6. Frontal setae 5 (fs 5): (0) reduced or vestigial; (1) well-developed.
7. Dorsal setae 3 (des 3): (0) on frons or contiguous to frons; (1) contiguous to epicranium.
8. Posterior epicranial setae (pes): (0) equisdistant; (1) pes 4 separated distinctly from the others.
9. Ventral cranial setae 1, 2 (vcs 1, 2): (0) subequal; (1) unequal.
10. Stemmata: (0) inconspicuous or as pigmented spots; (1) with convex cornea.
11. Antennal sensorial structures: (0) moderate size; (1) about as long as sensorium.
12. Anterior margin of labrum: (0) trilobed or convex; (1) emarginate.
13. Lateral labral sensilla: (0) present; (1) absent.
14. Labral rods: (0) subparallel; (1) convergent toward base; (2) joined at base; (3) reduced to distal tips.
15. Epipharyngeal clusters of sensilla: (0) with 3 and 2 sensilla, respectively; (1) with 4 and 1 sensilla, respectively.
16. Dorsal malar setae (dms) in maxillae: (0) 7–8; (1) 6.
17. Ventral malar setae (vms) close to sensillum: (0) well-developed; (1) minute.
18. Proximal vms of maxillary mala: (0) similar to distal vms; (1) wider than distal vms.
19. Premental sclerite: (0) trident-shaped; (1) reduced to lateral extensions.
20. Lateral extensions of premental sclerite: (0) united medially; (1) separated medially.
21. Postmental setae: (0) distinct; (1) translucid, indistinct.
22. Alar area: (0) with 2 setae; (1) with 1 seta.
23. Pedal area: (0) with sensilla and microseta between setae v and w; (1) without such sensilla and microseta.
24. Airtubes of thoracic spiracles: (0) 7–8 annulated; (1) 10–12 annulated; (2) 4–5 annulated.
25. Spiracles: (0) not surrounded by pigmented band; (1) surrounded by pigmented band.
26. Spiracular airtubes: (0) internal; (1) external, modified for plant piercing.
27. Postodorsal setae (pds) on abdominal segment VI: (0) 5; (1) 4, lacking homologous pds 2 of preceding segments.
28. Postodorsal setae (pds) on abdominal segment VII: (0) 5; (1) 4, lacking homologous pds 2 of preceding segments.
29. Abdominal segment X: (0) not modified; (1) projecting into a pygopod.
30. Cuticular asperities: (0) spiniform; (1) tuberculiform.
31. Body setae: (0) well-developed, of moderate length; (1) very reduced or vestigial; (2) some of them reduced, but those larger conspicuously long.
32. Body setae: (0) pointed; (1) blunt.

Adult characters

33. Shape of rostrum: (0) medium-sized and broad; (1) relatively long and slender.
34. Pterygia: (0) well-developed, protruding; (1) poorly developed, not protruding.
35. Scrobes: (0) deep, reaching the eyes; (1) shallow, not reaching the eyes.
36. Scrobal ventral teeth: (0) absent; (1) present.
37. Epistome: (0) protruding; (1) not protruding.
38. Eye length: (0) medium to large; (1) small.
39. Relative length of funicular articles 1 and 2: (0) 1 longer than 2; (1) 1 subequal or shorter than 2.
40. Number of mandibular setae: (0) 2; (1) 1.
41. Shape of pronotum: (0) subcylindrical; (1) subcircular; (2) transverse.

42. Pronotal dorsum: (0) convex; (1) flat.
43. Pronotal disc: (0) not tuberculate; (1) tuberculate.
44. Pronotal median keel: (0) absent; (1) present.
45. Postocular lobes: (0) present, well-developed; (1) absent.
46. Scutellum: (0) visible; (1) not visible.
47. Elytral shape: (0) subcylindrical; (1) subrectangular; (2) ovate.
48. Elytral disc: (0) convex; (1) flat.
49. Humeri: (0) subquadrate; (1) rounded.
50. Tubercles on elytral disc: (0) absent; (1) present.
51. Series of declivital tubercles on elytral intervals 1–5: (0) absent; (1) present.
52. Declivital tubercle on interval 2: (0) absent; (1) present.
53. Elytral stridulatory files: (0) absent; (1) present.
54. Scales: (0) subcircular; (1) subpolygonal; (2) seta-like.
55. Aedeagus: (0) symmetrical; (1) asymmetrical.
56. Degree of sclerotization of the aedeagus: (0) strongly sclerotized; (1) slightly sclerotized.

RESULTS AND DISCUSSION

The simultaneous analysis with Hennig86 using equal weights yielded a single cladogram (78 steps, CI = 0.65, RI = 0.72), stable to successive weighting. Pee-Wee produced the same cladogram, which has a fit of 341.0 (66%). The cladogram is presented in Fig. 1, and synapomorphies and homoplastic changes defining the different clades are presented in Table 3. The placement of *L. abditus* within *Listroderes* (clade 4) is supported strongly by 12 synapomorphies (all from larvae) and five homoplastic changes (four from larvae and one from adults). In general, all clades are supported by both larval and adult characters, only clade 3 being supported exclusively by larval characters. The significance of the incongruence between larval and adult characters gave a p-value of 0.119400, showing that disagreement between characters is smaller than disagreement within each data set, i.e., larval and adult characters are relatively congruent.

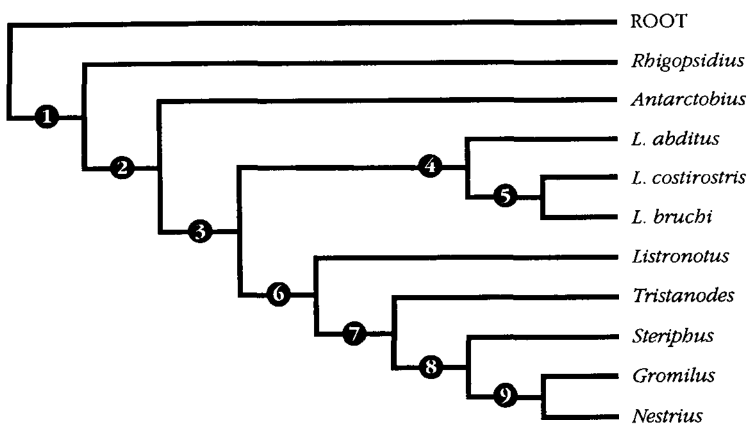
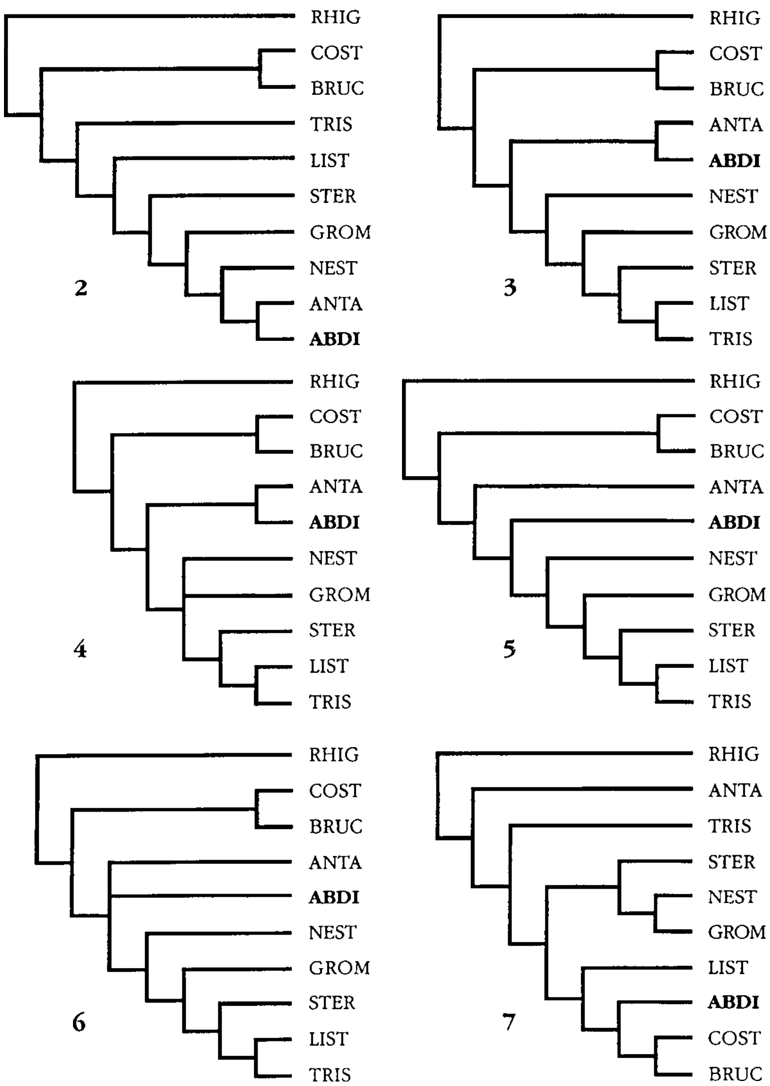


Fig. 1. Cladogram obtained for the data matrix of Table 2. Synapomorphies and homoplastic changes of nodes and terminal taxa listed in Table 3.



Figs 2–7: Cladograms obtained for the separate analyses. 2–6 – adult characters; 7 – larval characters. ABDI – *L. abditus*; ANTA – *Antarctobius*; BRUC – *L. bruchi*; COST – *L. costirostris*; GROM – *Gromilus*; LIST – *Listronotus*; NEST – *Nestrius*; RHIG – *Rhigopsidius*; STER – *Steriphus*; TRIS – *Tristanodes*.

Analysis of adult characters produced 20 cladograms (28 steps, CI = 0.64, and RI = 0.66) which, after successive weighting, resulted in five cladograms (160 steps, CI = 0.80, and RI = 0.81). Pee-Wee replicated these five cladograms, which have a fit of 98.0 (58%). Cladogram topologies are presented in Figs 2–6. *Listroderes abditus* is included in

Antarctobius in three cladograms (Figs 2–4), whilst they both constitute a paraphyletic group in cladogram 5 and their relationship is unresolved in cladogram 6. In all these cladograms, *Rhigopsidius* is the most basal taxon, and the pair *L. costirostris – L. abditus* is the sister taxon of the remainder taxa. Relationships of *Tristanodes, Listronotus, Steriphus, Gromilus, Nestrius, Antarctobius,* and *L. abditus* differ in the cladograms. Knowledge of rhytirrhinine larvae is extremely poor, with larvae known for less than 4% of the described species, and a better knowledge of immature stages may change or confirm the hypothesis that *L. abditus* belongs in *Listroderes*.

TABLE 3. Synapomorphies and homoplastic changes of the cladogram of Fig. 1, listed by nodes and terminal taxa.

Nodes and terminal taxa	Larval characters		Adult characters	
	Synapomorphies	Homoplastic changes	Synapomorphies	Homoplastic changes
1	–	6.1	41.7, 47.1	–
2	14.2, 16.1	–	37.1, 47.2, 49.1, 50.1	–
3	9.1, 23.1, 31.1	6.0	–	–
4	1.1, 2.1, 5.1, 8.1, 11.1, 12.1, 13.1, 14.3, 19.1, 21.1, 25.1, 30.1	3.1, 10.1, 17.1, 29.1	–	35.1
5	20.1, 32.1	–	36.1, 53.1	41.2
6	31.2	4.1, 22.1, 33.1, 34.1	–	–
7	–	3.1, 16.0	–	50.0
8	28.1	–	–	35.1, 54.2, 56.1
9	27.1	14.1	–	34.0
Rhigopsidius	7.1	4.1	43.1, 48.1, 51.1, 52.1, 56.1	41.2, 42.1, 54.1
Antarctobius	24.2	22.1	–	35.1, 45.1
L. abditus	24.1	18.1	–	45.1, 54.2
L. costirostris	–	18.1	55.1	–
L. bruchi	15.1	9.0	44.1	42.1
Listronotus	–	14.1, 17.1, 29.1	39.1	41.0, 56.1
Tristanodes	–	6.1, 10.1	–	–
Steriphus	26.1	4.0	–	41.0
Gromilus	40.1	–	–	–
Nestrius	–	14.0	38.1, 46.1	45.1

Analysis of larval characters produced a different result. Four cladograms were obtained (47 steps, CI = 0.72, and RI = 0.81) which, after successive weighting, resulted in one cladogram (274 steps, CI = 0.89, and RI = 0.93), coincident with that produced by the Pee-Wee analysis, which has a fit of 251.0 (77%). The topology of this cladogram (Fig. 7) is in relative accordance with the simultaneous analysis, and in contrast to the analysis based on adult characters, *L. abditus* is the sister taxon of the pair *L. costirostris – L. bruchi.*

The results of the simultaneous analysis and the separate analysis of the larval data set both confirm the separation of *Antarctobius* and *Listroderes,* although *L. abditus* is placed in the former instead of the latter as was proposed by Morrone (1992), thus confirming Marvaldi's (1998) conclusions. It is worth noting that inclusion of *L. abditus* within *Listroderes* and the more basal position of *Antarctobius* in the cladogram, are both due almost exclusively to larval characters.

These results coincide with previous analyses, e.g., Alexander (1990) on Hymenoptera, and Miller (1991) on Lepidoptera, where larval data showed less homoplasy and better resolution than adult data. Alexander (1990) has hypothesized that larval characters are less complex and evolve more slowly so, when evolutionary novelties arise, they are subsequently conserved, whereas adult characters evolve more rapidly, and lead to higher levels of homoplasy. The most basal nodes of our cladogram are particularly well supported by larval characters, which indicates the conservative nature of most of them.

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