Cladistics **13**, 285–312 (1997)
WWW http://www.apnet.com

Higher Level Phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on Larval Characters, with Special Reference to Broad-Nosed Weevils

Adriana E. Marvaldi

Instituto Argentino de Investigaciones de las Zonas Aridas (IADIZA), Casilla de Correo 507, 5500 Mendoza, Argentina

Accepted 6 August 1997

A cladistic analysis of Curculionidae was performed using 49 characters (41 from larvae, three from pupae, and five from adults). Illustrations of characters of immatures are provided. The analysis involved 19 terminal units and a hypothetical ancestor determined by the outgroup comparison method used to root the tree. One most parsimonious cladogram was obtained based on the complete data set and the following phylogenetic hypothesis is proposed: Ithycerinae, Microcerinae, and Brachycrinae *sensu stricto* are broad-nosed weevils placed sequentially at the base of the cladogram. The remaining weevil subfamilies form two major natural groups: one constituted by the sister taxa Rhynchophorinae—Platypodinae; the other with Erirhininae at the base, as sister taxon of the "Curculionidae *sensu stricto*" which show an unresolved trichotomy involving Curculioninae, Cossoninae—Scolytinae, and the clade including the Entiminae and allied subfamilies. This latter clade of broad-nosed weevils has Thecesterninae at the base; the next branch is Amycterinae, the sister taxon of the clade comprising two groups: one constituted by Aterpinae, Rhytirrhininae, and Gonipterinae; the other is Entiminae whose units form two main clades: one constituted by the sister tribes Pachyrhynchini—Ectemnorhinini, and the other by Alophini, Sitonini, and Entimini. When the analysis was done using only immature characters, results congruent with those based on the complete data set were obtained, except for the placement of Erirhininae. According to the results the hypothesis of monophyly of broad-nosed weevils is not accepted; the Entiminae are justified as monophyletic and their natural classification into tribes is proposed and the phylogenetic position and relationships of higher taxa of Curculionidae are discussed. This paper shows the importance of immature characters in recognition of natural groups and relationships in Curculionidae.

INTRODUCTION

Weevils (Coleoptera: Curculionidae), with about 48,000 valid species, are the largest family of known organisms (Anderson, 1993, 1995). Higher-level classification of weevils is difficult, and the subject of debate and disagreement among specialists (Morimoto, 1962; Crowson, 1967; Thompson, 1992; Kuschel, 1995). Because knowledge of immature stages is relatively poor, most of these studies are focused on adults. There is increasing interest in reconstructing phylogenies and discovering natural groups, and the use of characters from immature stages may prove helpful to reach this goal.

0748-3007/97/040285+28/$25.00/0/cl970049

One such difficulty concerns the monophyly of "broad-nosed" weevils, that group of curculionids which have a relatively short and stout rostrum not used to prepare oviposition sites. Taxa sharing this feature include Ithycerinae, Microcerinae, Brachycerinae *sensu stricto*, Thecesterninae, Amycterinae, Aterpinae, Rhytirrhininae, Gonipterinae, and Entiminae. Kuschel (1990, 1995) merged the broad-nosed weevils into the subfamily Brachycerinae, which he treated as a single terminal unit in his phylogenetic analysis of families and subfamilies of Curculionidae. Thompson (1992), however, questioned the monophyly of Brachycerinae *sensu* Kuschel because the subfamily contains taxa with both the orthocerous and gonatocerous type of male genitalia, and the latter character is deemed as the synapomorphy defining Curculionidae *senus stricto*. On the other hand, my own research (Marvaldi, 1995) on immature stages representative of several family groups of broad-nosed weevils led me to suspect that they probably do not constitute a monophyletic group. Kuschel (1995) admitted that the classification of Curculionidae into six subfamilies was far from satisfactory. Thus I decided not to assume a priori the monophyly of Brachycerinae *sensu* Kuschel, but to test this hypothesis using cladistic methodology and by including other weevil subfamilies as terminal units in the analysis.

My main objective was to use evidence from the immature stages to conduct a phylogenetic analysis of the higher taxa placed within Curculionidae, in order to test the monophyly of broad-nosed weevils. I was also interested in analysing the phylogenetic position and relationships of this group of weevils, as well as of other Curculionidae, with the goal of explaining some aspects of their evolutionary history. Finally, I also wanted to test the monophyly of Entiminae, the largest subfamily of broad-nosed weevils, and to propose a natural tribal classification.

MATERIALS AND METHODS

Taxa

The cladistic analysis involves 20 terminal taxa, including a hypothetical ancestor constructed by outgroup comparison. Nine of these terminal taxa are broad-nosed weevils belonging to Brachycerinae *sensu* Kuschel (1995): Ithycerinae, Microcerinae, Brachycerinae *sensu stricto*, Thecesterninae, Amycterinae, Aterpinae, Rhytirrhininae, Gonipterinae, and Entiminae. For the last I considered there to be five tribes: Pachyrhynchini, Ectemnorhinini, Alophini, Sitonini, and Entimini. All these taxa, except for Microcerinae, were defined on the basis of larval descriptions (Marvaldi, 1995, in press). Mature larvae, and sometimes first-instar larvae if available, of about 95 species of broad-nosed weevils were studied (Appendix I). Pupae were examined for some of these species. Information on larvae of Microcerinae was taken from Louw (1995).

The terminal taxa that do not correspond to broad-nosed weevils are: Rhynchophorinae, Platypodinae, Erirhininae, Curculioninae, Cossoninae, and Scolytinae. These taxa were defined on the basis of published information and on larval material (and also pupae if available) of about 35 species examined (Appendix I). Erirhininae (in the restricted sense of Kuschel, 1971, 1987) are treated as a separate subfamily (Kuschel, 1985, 1988), not as a tribe within Curculioninae (Kuschel, 1995). On the other hand Hyperini, though considered as a tribe of the enlarged Brachycerinae (May, 1993), are excluded as a terminal unit in the present analysis because their larval and adult characters correspond to Curculioninae, probably close to Cionini (Marvaldi, pers. obs.). The subfamily Curculioninae, in the broad sense of Kuschel (1995) and as here defined, comprise nearly 50% of the species of Curculionidae.

Characters, Polarity and Coding

Forty-nine characters were selected (Table 1). Most of them (84%) are taken from larval morphology (characters 1–41), three from the pupa (characters 42–44), and five from the adult, including the type of oviposition (characters 45–49).

Larval and Pupal Characters

The selection of immature characters was based on a previous morphological study of broad-nosed weevils (Marvaldi, 1995). The information on larvae and pupae

of non-broad-nosed weevils and the outgroup was taken from the material examined and from several bibliographical sources, mainly Böving and Craighead (1931), Gardner (1932, 1934a, b, 1938), Kuschel (1943), Scherf (1964), Costa et al. (1988), Anderson (1991) and May (1993, 1994). Information about the larval Malpighian tubules (character 41 in Table 1) was obtained from Sanborne (1981), Louw (1990), and May (1993, 1994). These papers were also used to compile data on the pupal stage.

The larval characters 1, 3, 7, 15 and 33 (Table 1) were also used by Kuschel (1995) and correspond to his characters 39, 40, 126, 32, and 81 respectively. However, the assignment of the character states is different, except for character 1.

Table 1. Character List Used in the Cladistic Analysis of Curculionidae (Plesiomorphic State=0; Apomorphic States=1–3)

Larva

1. Frontal lines [0] complete, reaching articulating membrane of mandibles (see Emden, 1938: figures 2, 3); [1] incomplete, not extending to mandibles (Fig. 1; see Emden, 1938: figures 1, 4).
2. Epicranial areas [0] without longitudinal furrows (Fig. 3); [1] with a longitudinal furrow coincident with dorsoepicranial seta 2; [2] with three longitudinal furrows coincident with dorsoepicranial setae 1, 2 and 5 (Fig. 4).
3. Postoccipital margin of head [0] simple (Fig. 5); [1] with condyle or sclerotized subtriangular flange on each side (Fig. 6); [2] with postoccipital condyles inconspicuous and represented by thickened ridge along margin (Fig. 7).
4. Head [0] lacking posterior lamina with two attachment points or apodemes (Figs 5-7); [1] bearing posterior lamina with two attachment points or apodemes (Figs 8, 9).
5. Frontal seta 5 [0] well developed (Figs 2-4); [1] very reduced or vestigial.
6. Dorsoepicranial seta 2 [0] well developed (Fig. 2-4); [1] very reduced or vestigial.
7. Dorsoepicranial seta 3 [0] on epicranium; [1] in frontal line or on frons (Figs 2-4).
8. Epicranial sensillum next to dorsoepicranial seta 2 [0] present (Fig. 2); [1] absent (Figs 3, 4).
9. Antennal sensorium [0] circular in apical view (Fig. 10B); [1] elliptical in apical view (Fig. 13B).
10. Antennal position on anterior margin of head [0] oblique (Figs 2, 4, 10, 11, 14); [1] transverse (Figs 3, 12, 13).
11. Antennal sensorium [0] longer than wide, ogival or conical (Fig. 10A); [1] flat, almost depressed (Fig. 11; see Louw, 1995: figure 4); [2] wider than long, dorsoventrally compressed, cushion-like (Figs 12, 13A); [3] about as long as wide, hardly compressed dorsoventrally, slightly pointed at apex (Fig. 14).
12. Antennal sensorium of larva I [0] symmetrical; [1] asymmetrical, projected outwards (see Marvaldi and Loiácono, 1994: figure 1).
13. Antennal sensorium of mature larva [0] symmetrical; [1] asymmetrical, projected outwards (Fig. 13A).
14. Clypeus [0] with three pairs of setae (Fig. 15); [1] with two pairs of setae (Fig. 16).
15. Labrum [0] with four pairs of setae (Fig. 15); [1] with three pairs of setae (Fig. 16).
16. Lateral labral seta [0] well developed (Figs 15, 16); [1] very reduced or vestigial (Fig. 17).
17. Labrum [0] uniformly pigmented (Figs 15, 17); [1] pigmented on two subtriangular areas (Fig. 16).
18. Epipharynx with anteromedian setae 1 [0] subequal or of smaller size than anterolateral setae (Fig. 18); [1] very conspicuous, of greater size than anterolateral setae (Fig. 19).
19. Epipharynx with sensillum clusters [0] between median epipharyngeal setae 1 and 2 (Fig. 18); [1] between median epipharyngeal setae 2 and 3.
20. Mandibular apex [0] bidentate (Figs 20, 21); [1] unidentate (Fig. 22); [2] tridentate (Fig. 23).
21. Mandibular cutting-edge [0] with accessory teeth on its intermediate part (Figs 20, 22); [1] without accessory teeth on its intermediate part (Figs 21, 23).
22. Mandibular scrobe [0] sclerotized as the rest of the mandible (Figs 20, 22, 23); [1] weakly sclerotized, pale (Fig. 21).
23. Maxillary mala [0] with five ventral setae (Figs 24, 25A-29A); [1] with four ventral setae (Figs 30A-34A).

24. Maxillae and epipharynx [0] with simple setae (Figs 18, 27B); [1] with some branched setae (Fig. 26B).
25. Dorsal malar setae [0] regularly aligned in one file (Figs 26B-34B); [1] irregularly distributed (Fig. 25).
26. Postmentum [0] not pigmented (Figs 28, 32-34); [1] pigmented (Fig. 29).
27. Labium with posterior extension of premental sclerite [0] subtriangular, with convergent sides and acute apex (Figs 28, 29, 32); [1] subrectangular, with subparallel sides and truncate or expanded apex (Figs 33, 34).
28. Legs [0] present and bisegmented (see Sanborne, 1981: figures 33, 42, 136); [1] vestigial with faint segmentation; [2] absent (Fig. 35).
29. Pedal areas [0] not sclerotized; [1] sclerotized (see May, 1970: figure 9).
30. Pronotum [0] simple (Fig. 35); [1] projected as a hood over head (see May, 1993: figure 569).
31. Pronotal setae 2 and 6 [0] not conspicuously longer and thicker than the others (Fig. 35); [1] markedly longer and thicker than all others (see Chown and Scholtz, 1989: figure 1).
32. Prodorsum of thoracic and abdominal segment [0] with one to two setae (Fig. 35); [1] with four or more setae (see Louw, 1990: figure 11).
33. Abdominal segments [0] with two dorsal folds (see Sanborne, 1981; figures 33, 61; Louw, 1995: figures 1-3); [1] with three to four dorsal folds (Fig. 35).
34. Prodorsal seta on abdominal segment VIII [0] present (Fig. 35); [1] absent (Fig. 37).
35. Postdorsal seta 5 on abdominal segment VIII [0] present (Figs 35, 37); [1] absent (Fig. 36).
36. Spiracular airtubes on abdominal segments I-VII [0] dorsoposteriorly directed (Fig. 35); [1] posteriorly directed (Fig. 36); [2] dorsally directed (Fig. 37).
37. Spiracle of abdominal segment VIII [0] lateral (Fig. 35); [1] laterodorsal or dorsal (Figs 36, 37).
38. Spiracular airtubes on abdominal segment VIII [0] dorsoposteriorly directed; [1] posteriorly directed; [2] dorsally directed.
39. Abdominal pleura [0] entire (Fig. 35); [1] subdivided into two or more superimposed lobes (see Anderson, 1991: figures 34.883a, 34.897a; May, 1994: figure L925).
40. Intersegmental pockets between epipleura and pleura [0] absent (Fig. 35); [1] present (see May, 1994: figure L829).
41. Malpighian tubules [0] four in number; [1] six in number.

Pupa

42. Mandibular theca [0] lacking setae (Fig. 38); [1] with one to two setae (Fig. 39).
43. Femoral apex [0] with three or more setae (see Sanborne, 1981; figures 86, 87; Costa et al., 1988: figures 2, 3; Louw, 1990: figure 16; May, 1994: figure P1190); [1] with one to two setae (Figs 38, 39).
44. Last pair of legs [0] covered by pterothecae (Figs 38, 39; May, 1994: figures P585, P1065); [1] not covered by pterothecae (May, 1994: figures P924, P936).

Adult

45. Antennae [0] straight (Kissinger, 1964: figure 6); [1] geniculate (Kissinger, 1964: figure 1).
46. Mouthparts [0] phanerognathous, with maxillae exposed at the sides of the prementum (Crowson, 1967: figure 204); [1] adelognathous, with maxillae covered by enlarged prementum (Crowson, 1967: figure 205).
47. Deciduous mandibular processes [0] absent; [1] present (Kissinger, 1964: figures 2, 3; Thompson, 1992: figures 120-166).
48. Male genitalia [0] of the orthocerous type, with aedeagal tectum or dorsal plate present (Morimoto, 1962; Figs. XVII5-7, XVIII12, 13, XIX13; see Thompson, 1992: 879); [1] of the gonatocerous type, lacking aedeagal tectum or dorsal plate (Morimoto, 1962: figure 8; see Thompson, 1992: 880).
49. Oviposition [0] endophytic in a site prepared with rostrum; [1] ectophytic without participation of rostrum.

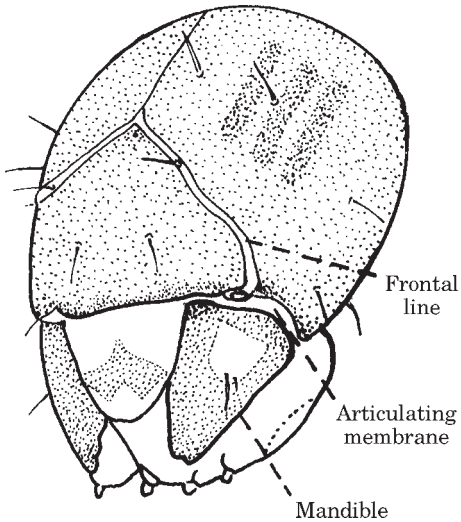

FIG. 1. Larval head in frontolateral view (Entiminae-Entimini: *Otiorhyncus sulcatus*).

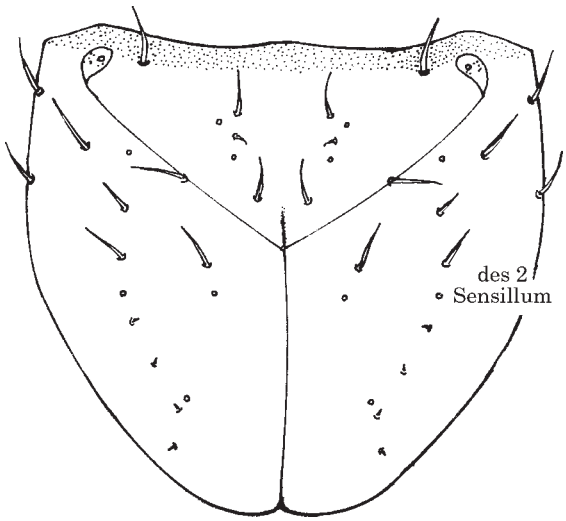

FIG. 2. Larval head in dorsal view (Brachycerinae *sensu stricto*: *Brachycerus albidentatus*). des: dorsoepicranial seta.

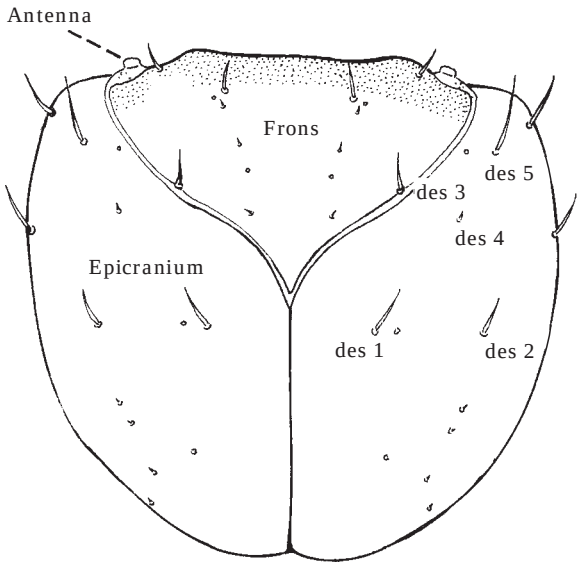

FIG. 3. Larval head in dorsal view (Entiminae-Entimini: *Malvinius compressiventris*). des: dorsoepicranial seta; frons: frontal seta.

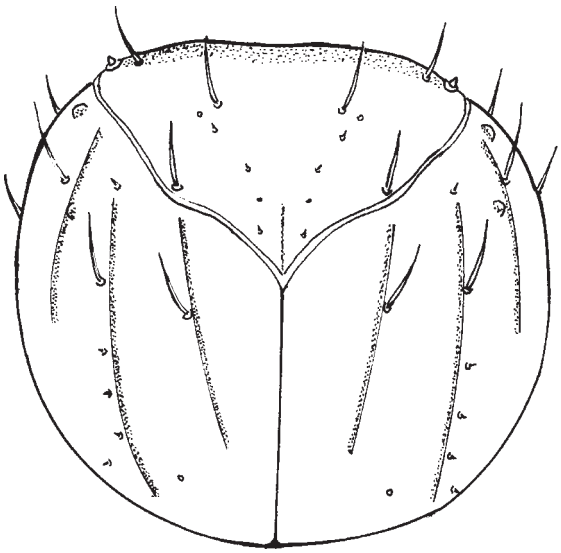

FIG. 4. Larval head in dorsal view (Amycterinae: *Cubicorhyncus crenicollis*).

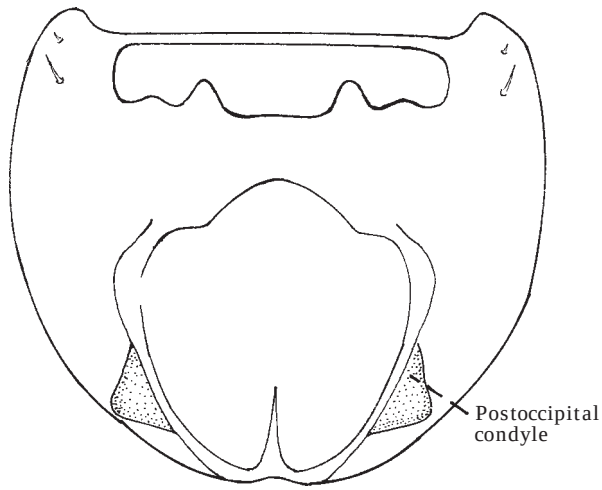

FIG. 5. Larval head in ventral view (Ictycerinae: *Ithycerus noveboracensis*).

FIG. 6. Larval head in ventral view (Entiminae-Entimini: *Malvinius compressiventris*).

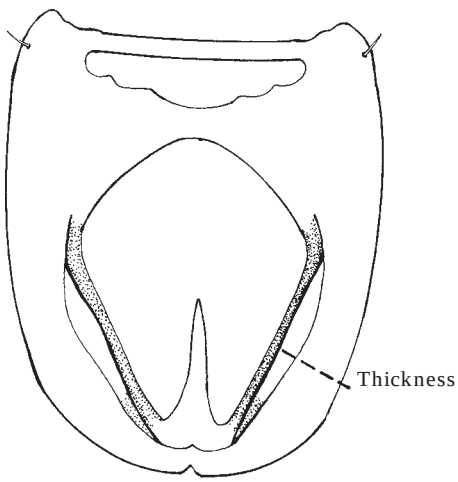

FIG. 7. Larval head in ventral view (Scolytinae: *Scolytus scolytus*).

FIG. 8. Larval head in ventral view (Rhychophorinae: *Cosmopolites sordidus*).

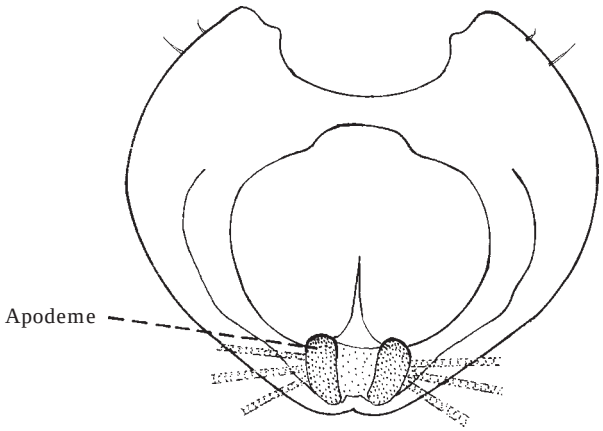

FIG. 9. Larval head in ventral view (Platypodinae: *Platypus* sp.).

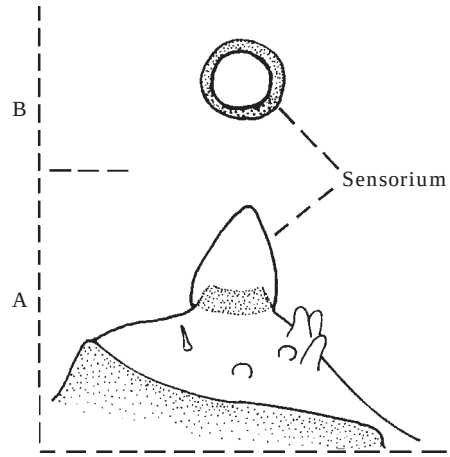

FIG. 10. Larval antennae of Amycterinae: *Sosytelus pubescens*. A: lateral view, B: apical view of sensorium.

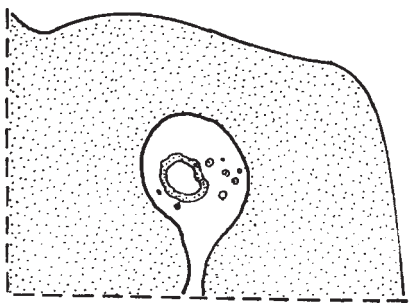

FIG. 11. Larval antennae of Brachycerinae: *Brachycerus albidentatus*.

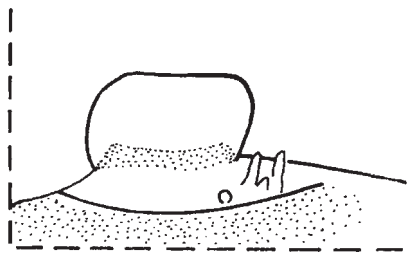

FIG. 12. Larval antennae of Entiminae-Entimini: *Trachyphloeus bifoveolatus*.

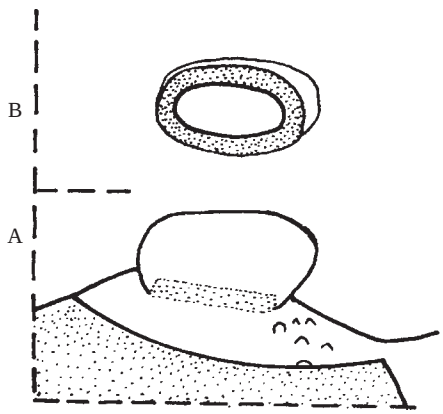

FIG. 13. Larval antennae of Entiminae-Sitonini: *Sitona cylindricollis*. A: lateral view, B: apical view of sensorium.

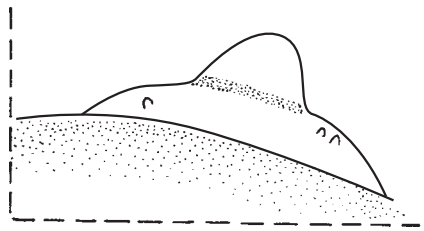

FIG. 14. Larval antennae of Entiminae-Alophini: *Trichalophus didymus*.

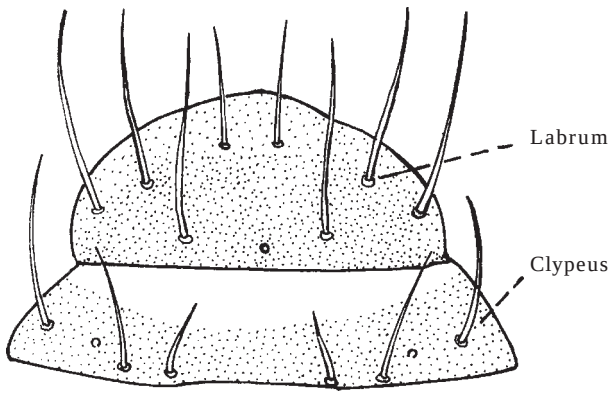

FIG. 15. Larval clypeus and labrum of Ithycerinae: *Ithycerus noveboracensis.*

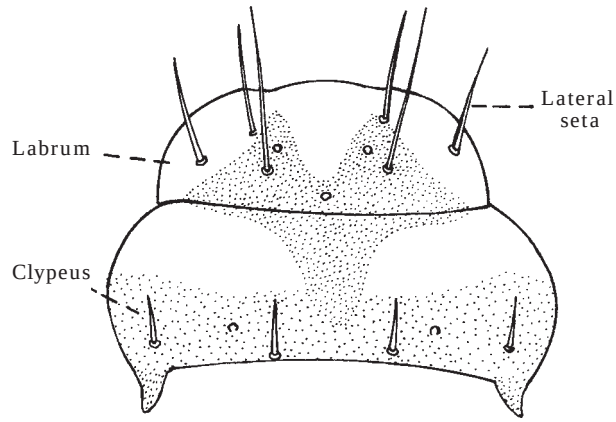

FIG. 16. Larval clypeus and labrum of Entiminae-Entimini: *Baryotus obscurus.*

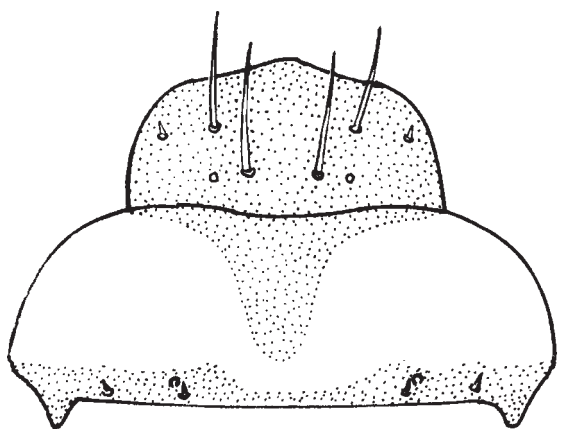

FIG. 17. Larval clypeus and labrum of Rhytirrhininae: *Listronotus bonariensis.*

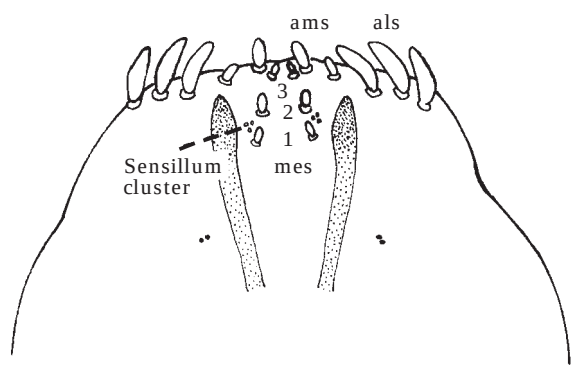

FIG. 18. Larval epipharynx of Entiminae-Entimini: *Barynotus obscurus.* ams: anteromedian setae; als: anterolateral setae; mes: median epipharyngeal setae.

FIG. 19. Larval epipharynx of Entiminae-Sitonini: *Sitona gressorius.*

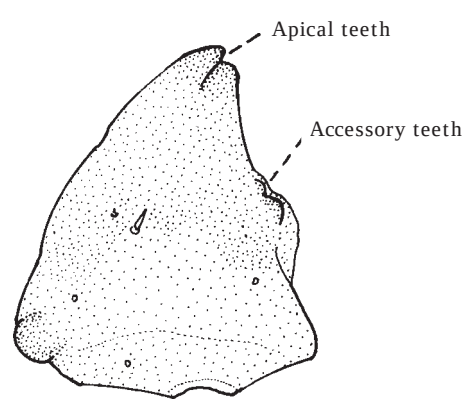

FIG. 20. Larval mandibles of Rhytirrhininae: *Rhigopsidius piercei.*

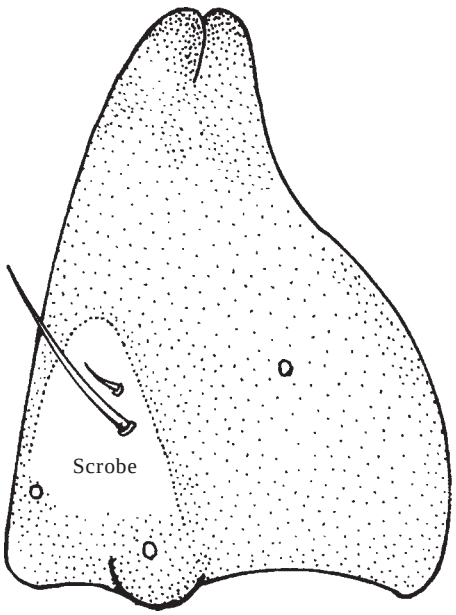

FIG. 21. Larval mandibles of Entiminae-Entimini: *Barypeithes mollicomus*.

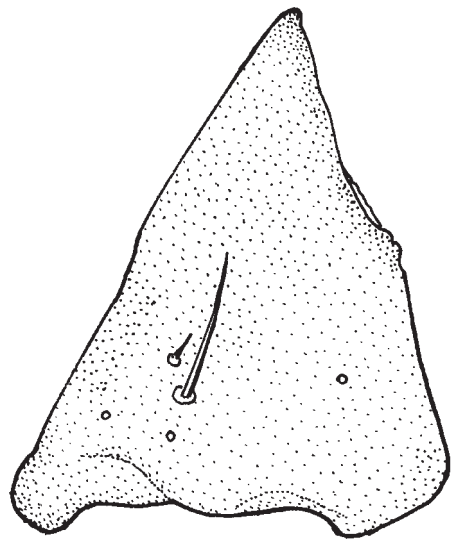

FIG. 22. Larval mandibles of Entiminae-Pachyrhynchini: *Pantorhytes biplagiatus*.

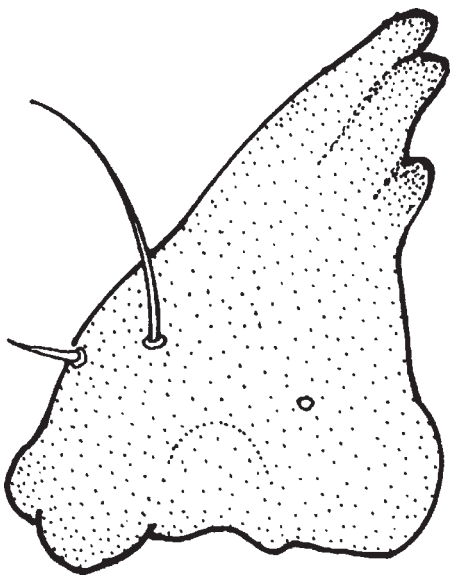

FIG. 23. Larval mandibles of Entiminae-Sitonini: *Sitona gressorius*.

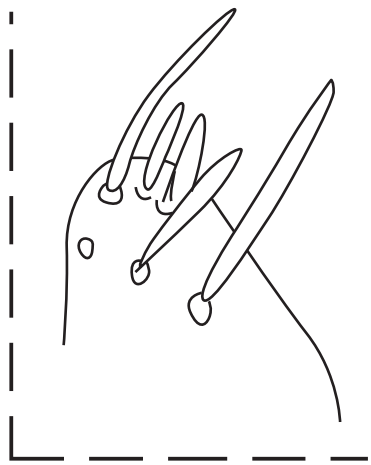

FIG. 24. Larval maxilliary mala of Ithycerinae: *Ithycerus noveboracensis*. A: ventral setae; B: dorsal setae.

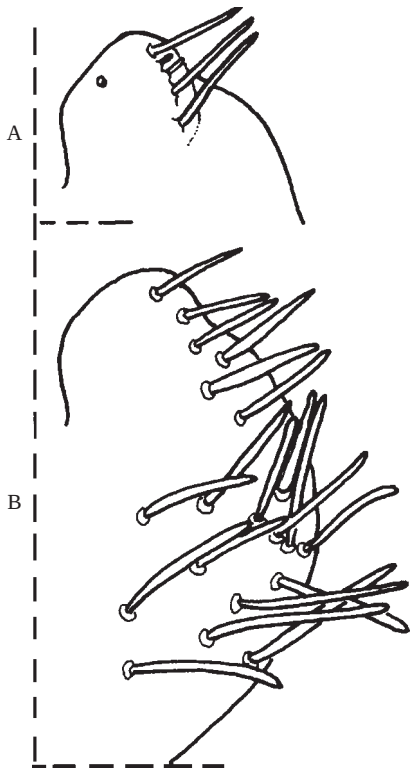

FIG. 25. Larval maxilliary mala of Brachycerinae *sensu stricto*: *Brachycerus albidentatus*. A: ventral setae, B: dorsal setae.

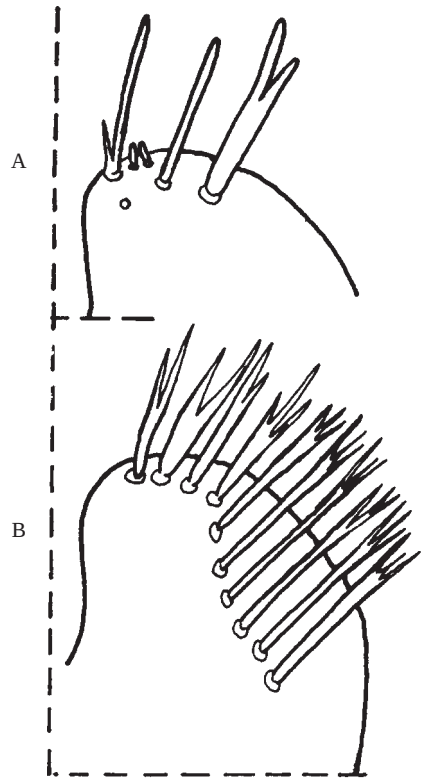

FIG. 26. Larval maxilliary mala of Rhynchophoridae: *Cosmopolites sordidus*. A: ventral setae; B: dorsal setae.

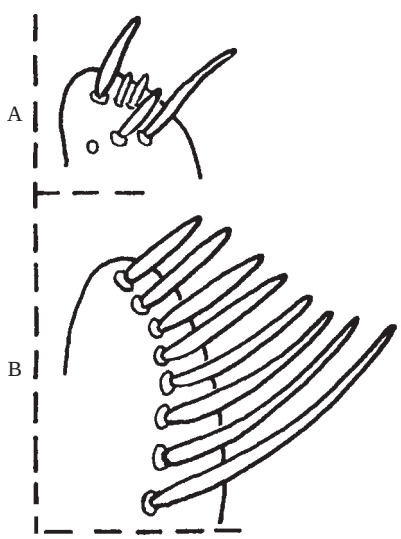

FIG. 27. Larval maxilliary mala of Amycterinae: *Cubicorhynchus crenicollis*. A: ventral setae; B: dorsal setae.

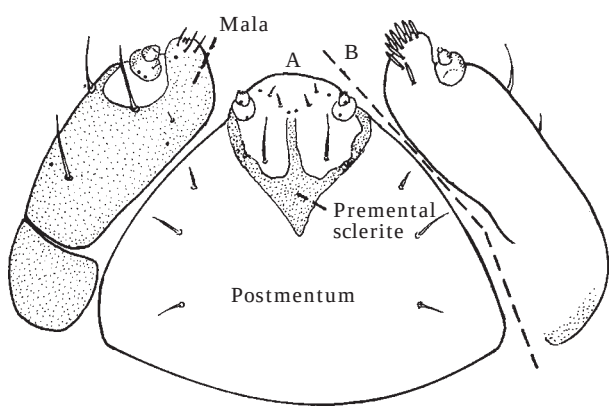

FIG. 28. A: larval maxilla and labium, ventral view; and B: larval maxilla, dorsal view, of Rhytirrhininae: *Rhigopsidius piercei*.

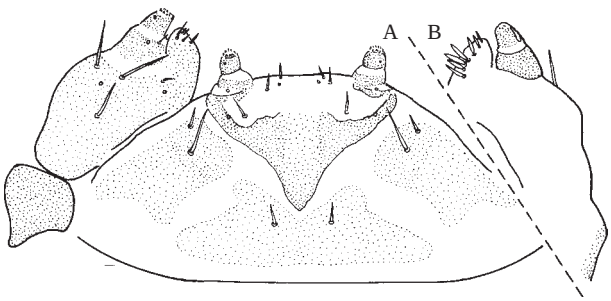

FIG. 29. A: larval maxilla and labium, ventral view; and B: larval maxilla, dorsal view, of Gonipterinae: *Gonipterus gibberus*.

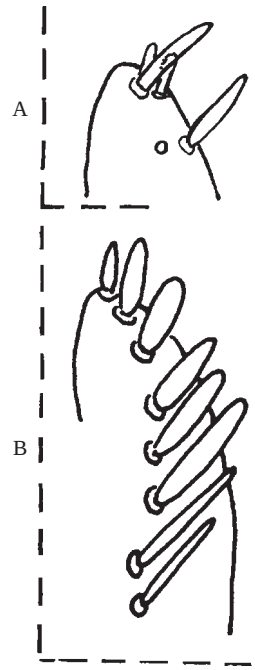

FIG. 30. Larval maxilliary mala of Entiminae-Pachyrhynchini: *Pantorytes biplagiatus*. A: ventral setae; B: dorsal setae.

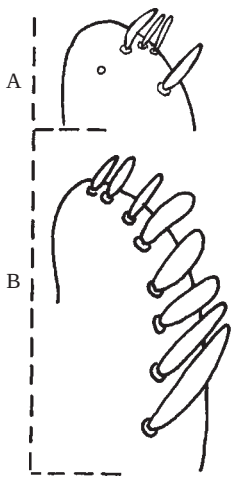

FIG. 31. Larval maxilliary mala of Entiminae-Alophini: *Trichalophus didymus*. A: ventral setae; B: dorsal setae.

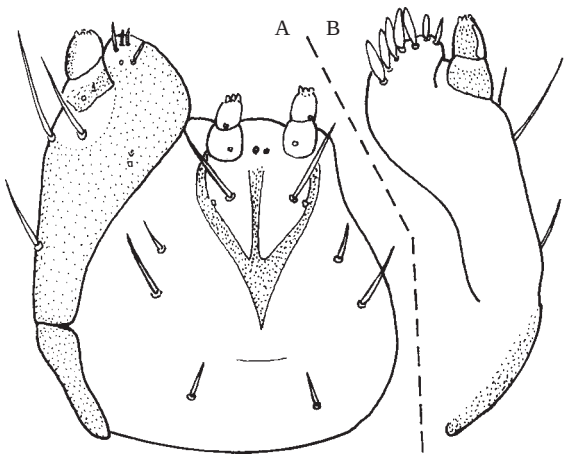

FIG. 32. A: larval maxilla and labium, ventral view; and B: larval maxilla, dorsal view, of Entiminae-Sitonini: *Sitona gressorius*.

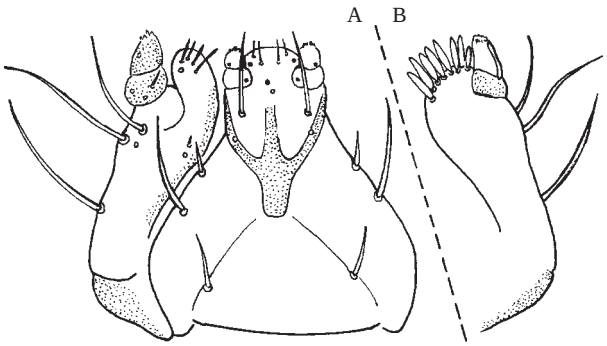

FIG. 33. A: larval maxilla and labium, ventral view; and B: larval maxilla, dorsal view, of Entiminae-Entimini: *Barynotus obscurus.*

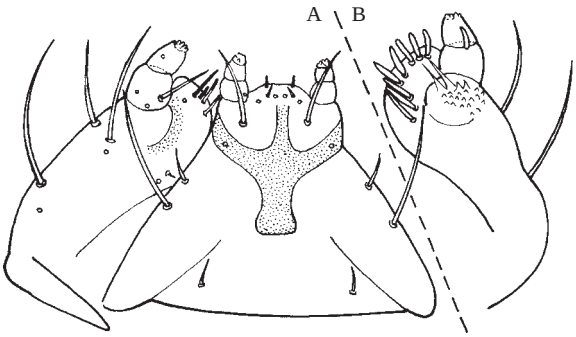

FIG. 34. A: larval maxilla and labium, ventral view; and B: larval maxilla, dorsal view, of Entiminae-Entimini: *Asynonychus cervinus.*

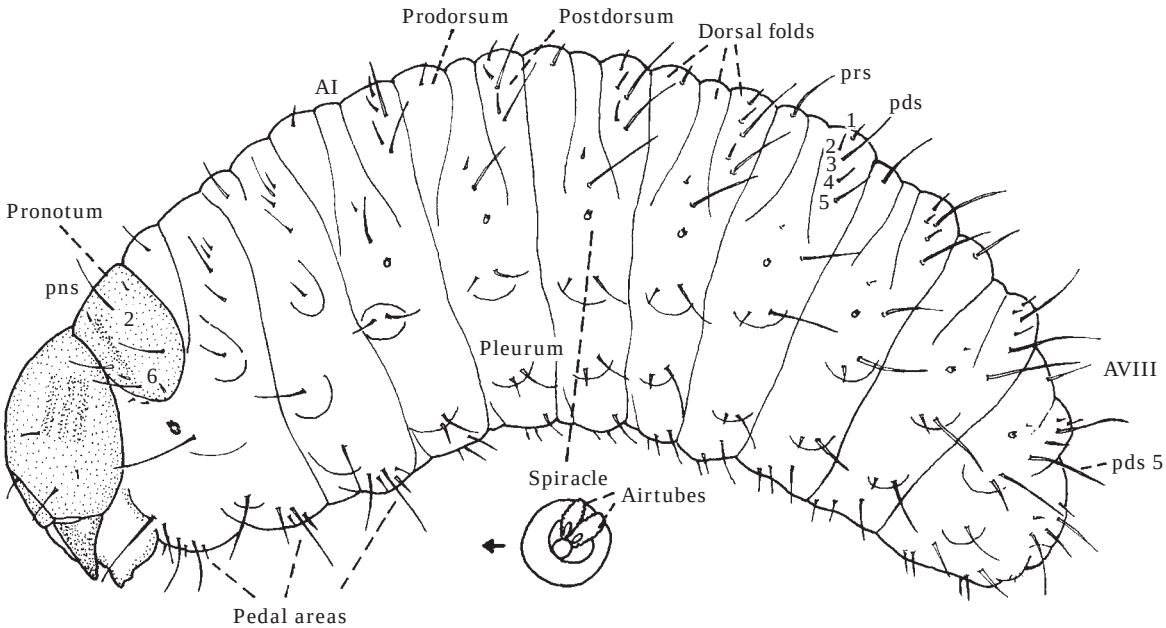

FIG. 35. Larva in lateral view of Entiminae-Entimini: *Otiorhyncus sulcatus.* pns: pronotal seta; prs: prodorsal seta; pds: postdorsal seta; A: abdominal segment.

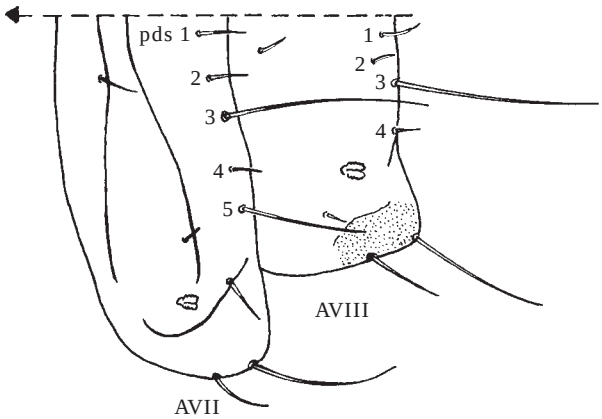

FIG. 36. Larval abdominal segments VII and VIII of Rhytirrhininae: *Tristanodes* sp. in dorsal view. pds: postdorsal seta; A: abdominal segment.

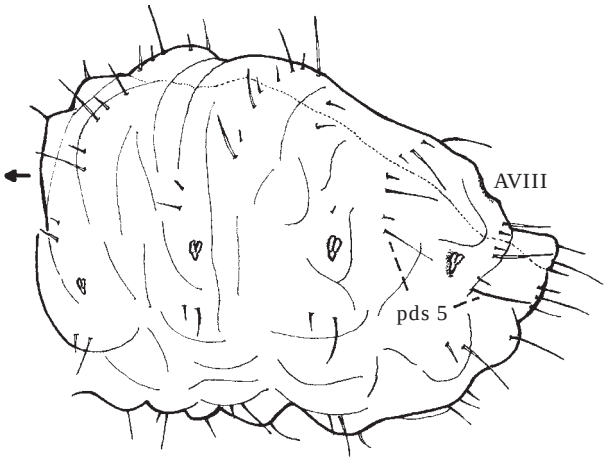

FIG. 37. Larval abdominal segments V-VIII of Entiminae-Pachyrhynchini: *Pantorhytes biplagiatus*. pds: postdorsal seta; A: abdominal segment.

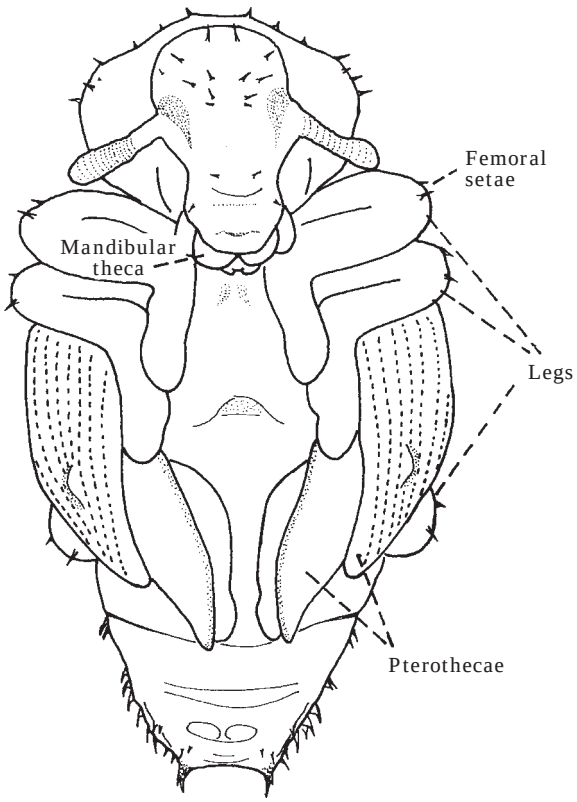

FIG. 38. Pupae in ventral view of Rhytirrhininae: *Listroderes costirostris*.

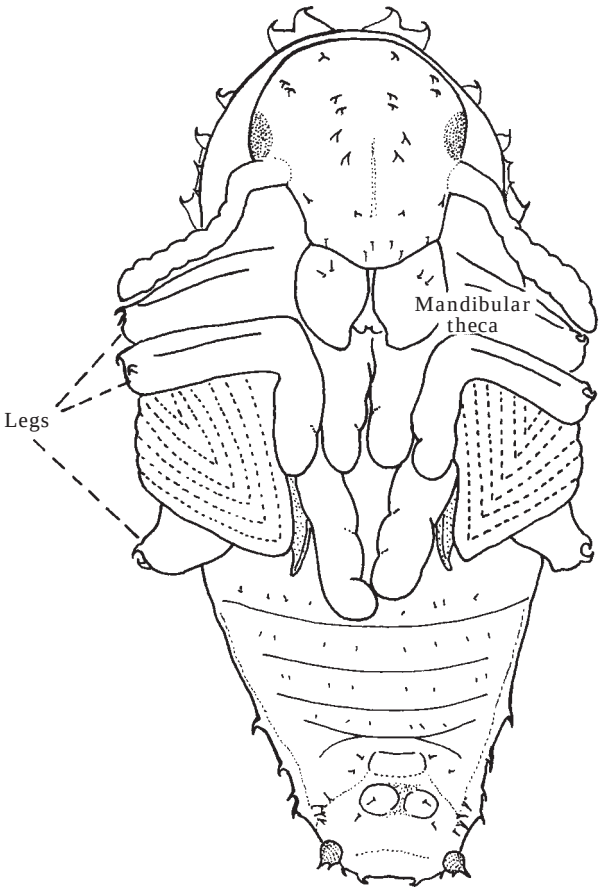

FIG. 39. Pupae in ventral view of Entiminae-Entimini: *Eurymetopus oblongus*.

Adult Characters

Although I was mainly concerned with using evidence from the immature stages, five adult characters (45-49 in Table 1) were also included in the final analysis in order to obtain a phylogenetic hypothesis based on more evidence and because combining data, i.e. immature plus adult characters, can allow the discovery of relationships that would have been missed by analysing different data sets separately (Chippindale and Wiens, 1994: 281). Characters 45-48 have been used previously by authors in forming primary divisions of weevils (Schoenherr, 1826; Lacordaire, 1863, 1866; Kuschel, 1985; Thompson, 1992), and they are well documented and illustrated, especially by Morimoto (1962), Kissinger (1964), Crowson (1967), Thompson (1992), and Zimmerman (1993, 1994), among others. I also included the oviposition type (character 49 in Table 1), on which the proposal to combine all the broad-nosed weevils into a single subfamily is mainly based (May, 1993). Although the oviposition habits of weevils are highly diverse (see Howden, 1995, for examples), two main types can be recognized depending on whether or not the rostrum is used in oviposition site preparation (character 49 in Table 1). Adult synapomorphies of Curculionidae and adult autapomorphies of the terminal taxa were not included in the present data set (Table 2).

Polarity of characters was determined by the outgroup comparison method (Watrous and Wheeler, 1981; Maddison et al., 1984; Nixon and Carpenter, 1993). Brentidae, the sister family of Curculionidae (according to Kuschel, 1995), was used as the outgroup. The larvae of Curculionidae and Brentidae share the antenna reduced to a single article, the maxillary palp lacking seta on the distal segment, and more or less standard numbers of setae on the body areas (May, 1993). Outgroup comparison in its simplest form (Watrous and Wheeler, 1981:5) was difficult to apply for characters 14, 15, 28, 33, 41, 43, 45 because the outgroup is heterogeneous, so the method of Maddison et al. (1984) was used to assign the character state of the outgroup node. Although the outgroup interrelationships proposed by Kuschel (1995) (for subfamilies of Brentidae and other families of Curculionidae) were accepted, the larval and pupal characters of *Car*, recently described by May (1994), suggest two other possible outgroup resolutions: Caridae standing alone either before Brentidae-Curculionidae, or before Curculionidae. Finally, when such an assignment had more than one equally parsimonious alternative state ("equivocal"), the plesiomorphic state (for characters 14, 41, 43) was estimated by using the "functional ingroup / outgroup" technique (Watrous and Wheeler, 1981). *Ithycerus*, the only genus included in Ithycerinae, was used as a functional outgroup. As a final result of polarity determination, a hypothetical ancestor was constructed using all plesiomorphic states (scored zero) to root the tree.

A missing data code, "?", was used when the character state was unknown or when the terminal taxon was polymorphic for the character. Multistate characters 3 and 28 were treated as additive and multistate characters 2, 11, 36, and 38 as non-additive.

A data matrix of 20 terminal units, including the outgroup, by 49 characters was constructed (Table 2).

Analysis

The data were analysed using Hennig86 version 1.5 (Farris, 1988), applying the implicit enumeration option (Farris, 1988; Platnick, 1989). Tree length and consistency (Kluge and Farris, 1969) and retention (Farris, 1989) indices were calculated excluding autapomorphies and the synapomorphy of Curculionidae to avoid artificially increasing these indices. The successive weighting procedure was applied if more thanone tree was initially obtained. When the analysis yielded more than one cladogram, a strict consensus tree was calculated with the nelsen option of Hennig86.

Two analyses were performed:

1. analysis based only on characters from the immature stages. The data matrix (Table 2) was analysed including the larval and pupal characters (1-44) and excluding the adult characters (45-49);
2. analysis based on characters from both the immature and adult stages. The complete data matrix (Table 2) was analysed.

Table 2. Data Matrix Used in the Cladistic Analysis of Curculionidae. Refer to Table 1 for Characters

	–	–	–	–	–	–	–	–	–	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Outgroup	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
Ithycerinae	1	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	1	0	0	0	1	0	0	1
Microcerinae	1	?	?	?	?	?	?	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	?	0	?	?	?	?	?	0	?	?	?	?	?	0	1	1	0	1
Brachycerinae	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	?	0	0	0	0	0	1	0	0	2	0	0	0	1	1	0	0	?	0	?	0	0	1	0	0	0	0	1	1	0	1
Rhynchophorinae	1	0	?	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	?	2	1	1	1	0	1	0	1	1	1	0	0	0	0
Platypodinae	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	?	?	0	0	0	1	0	0	?	2	0	0	0	0	1	0	?	2	0	2	1	0	1	0	1	1	1	0	0	?	0
Erirhininae	1	0	1	0	?	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	?	?	?	0	0	1	0	1	0	1	0	0	0	0
Curculioninae	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	?	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	?	?	?	?	0	0	1	0	1	0	1	0	0	1	0
Cossoninae	1	0	2	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0
Scolytinae	1	0	2	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0
Thecesterninae	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	?	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1
Amycterinae	1	2	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1
Gonipterinae	1	0	1	0	1	0	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	0	1	0	?	1	1	1	0	1	1	0	1	0	1	0	0	1	1
Rhytirrhininae	1	0	1	0	?	0	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	1	1	1	0	0	1	0	1	0	1	0	0	1	1
Aterpinae	1	1	1	0	?	0	1	1	0	0	0	0	0	1	1	0	0	0	0	?	0	0	0	0	0	0	0	2	0	0	0	0	1	0	?	1	1	1	0	0	1	0	1	0	1	0	0	1	1
Pachyrhynchini	1	0	1	0	1	0	1	1	0	0	2	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	2	0	0	0	0	1	1	0	2	1	2	0	0	1	1	1	0	1	1	0	1	1
Ectemnorhinini	1	0	1	0	1	1	1	1	0	0	2	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	2	1	0	1	0	1	1	0	2	0	2	0	0	1	1	1	0	1	0	?	1	1
Alophini	1	0	1	0	0	0	1	1	0	0	3	0	0	1	1	0	1	0	?	0	1	0	1	0	0	0	0	2	0	0	0	0	1	0	0	1	0	1	0	0	1	?	1	0	1	0	1	1	1
Sitonini	1	0	1	0	0	0	1	1	1	1	2	1	1	1	1	0	1	1	0	2	1	0	1	0	0	0	0	2	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	1	0	1	1	1
Entimini	1	0	1	0	0	0	1	1	1	1	2	1	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1

RESULTS

Cladogram Based on Characters from the Immature Stages (Fig. 40)

The analysis of the data matrix including only characters from the immature stages yielded three most parsimonious cladograms of 51 steps, a CI of 0.72 and a RI of 0.80. The successive weighting procedure did not reduce the number of minimum-length cladograms. The cladogram shown in Fig. 40 coincides with the strict consensus tree. The other two cladograms differ from the chosen one in that the relationships between Erirhininae, Aterpinae and Rhytirrhininae-Gonipterinae are resolved, with Erirhininae and Aterpinae being the basal taxon of the clade respectively. The distribution of the immature characters corresponds to the cladogram in Fig. 41.

Cladogram Based on Characters from Immature and Adult Stages (Fig. 41)

The analysis of the complete data matrix yielded one most parsimonious cladogram of 64 steps, a CI of 0.65 and a RI of 0.76 (Fig. 41). This tree has almost the same topology as the one in Fig. 40, both trees being highly congruent and differing only in the placement of Erirhininae. The inclusion of adult characters allowed a clearer resolution, since a single tree with less polytomies was obtained (Fig. 41).

The cladogram in Fig. 41 depicts the distribution of the characters and represents the phylogenetic hypothesis discussed in the next section.

DISCUSSION

On the Monophyly of the Broad-Nosed Weevils

The broad-nosed weevils (marked * in Fig. 41) present an ecological strategy different from that of the majority of weevils (Zwölfer, 1975) because they do not use the rostrum to prepare the oviposition site inside plant tissues (May, 1993; Howden, 1995). Not having an "ovipositor function", their rostrum is relatively short, broad, and without sexual dimorphism (Anderson, 1995).

According to the results of the cladistic analysis (Fig. 41), the hypothesis of monophyly of broad-nosed weevils is not accepted, because they constitute at least four monophyletic groups: Ithycerinae, Microcerinae, Brachycerinae *sensu stricto*, and the clade comprising Thecesterninae, Amycterinae, Aterpinae—Rhytirrhininae—Gonipterinae, and Entiminae (hereafter informally called "Entiminae and allied subfamilies"). The change toward an ectophytic oviposition mode without rostrum participation has occurred more than once in the evolutionary history of Curculionidae. This mode probably appeared early, in the ancestor of Curculionidae, remaining in that state in Ithycerinae, Microcerinae, and Brachycerinae *sensu stricto*, reverting to the use of the rostrum in oviposition site preparation, and appearing again at the base of the clade formed by Entiminae and allied subfamilies. I do not discard the hypothesis that, at least in the past, the basal taxa Ithycerinae, Microcerinae, and Brachycerinae *sensu stricto* may have been members of greater groups also including long-nosed weevils that used the rostrum for oviposition site preparation. It is precisely the oviposition and larval development in soil that must have allowed them to tolerate extreme climate changes and other adverse factors to survive until present times. Furthermore, the Entiminae and allied subfamilies include the species that make up the bulk of the weevil faunas in deserts, mountains, and cold climates (Kuschel, 1995).

The present cladogram (Fig. 41), which does not support the hypothesis of monophyly of the broad-nosed weevils, contrasts with Kuschel's cladogram (1995). It is worth noting, however, that Kuschel considered all the broad-nosed weevils as a single terminal unit (Brachycerinae *sensu lacto*) in his analysis, while in the present study, 13 broad-nosed weevil taxa were treated as terminal units, enabling me to test such a hypothesis. On the other hand, it seems that in Kuschel's paper several polymorphic character states were assigned to Brachycerinae *sensu lacto* according to the predominant state. This is because I note that states present in large groups (e.g. Entiminae) included in his enlarged Brachycerinae are considered as defining the whole last subfamily, even though such states are different in smaller included groups, such as Ithycerinae, Microcerinae or Brachycerinae *sensu stricto*.

Results of the cladistic analysis suggest that there are certain characters present in all or a majority of the broad-nosed weevils that have arisen as a common adaptive response to similar selective pressures. Certain environmental, climatic (e.g. aridification, colder temperatures) and/or biotic (e.g. parasitoids) conditions probably favoured the fixation of characters associated with the ectophytic oviposition and subterranean life of immature stages. Such characters are adelognathous mouthparts, presence of mandibular processes in the teneral adult, and pupal mandibular theca with setae. The expanded prementum covering the maxillae is frequent among broad-nosed species, and the mandibular processes are deemed to assist the adult in emerging to the surface from its pupal cell in the soil.

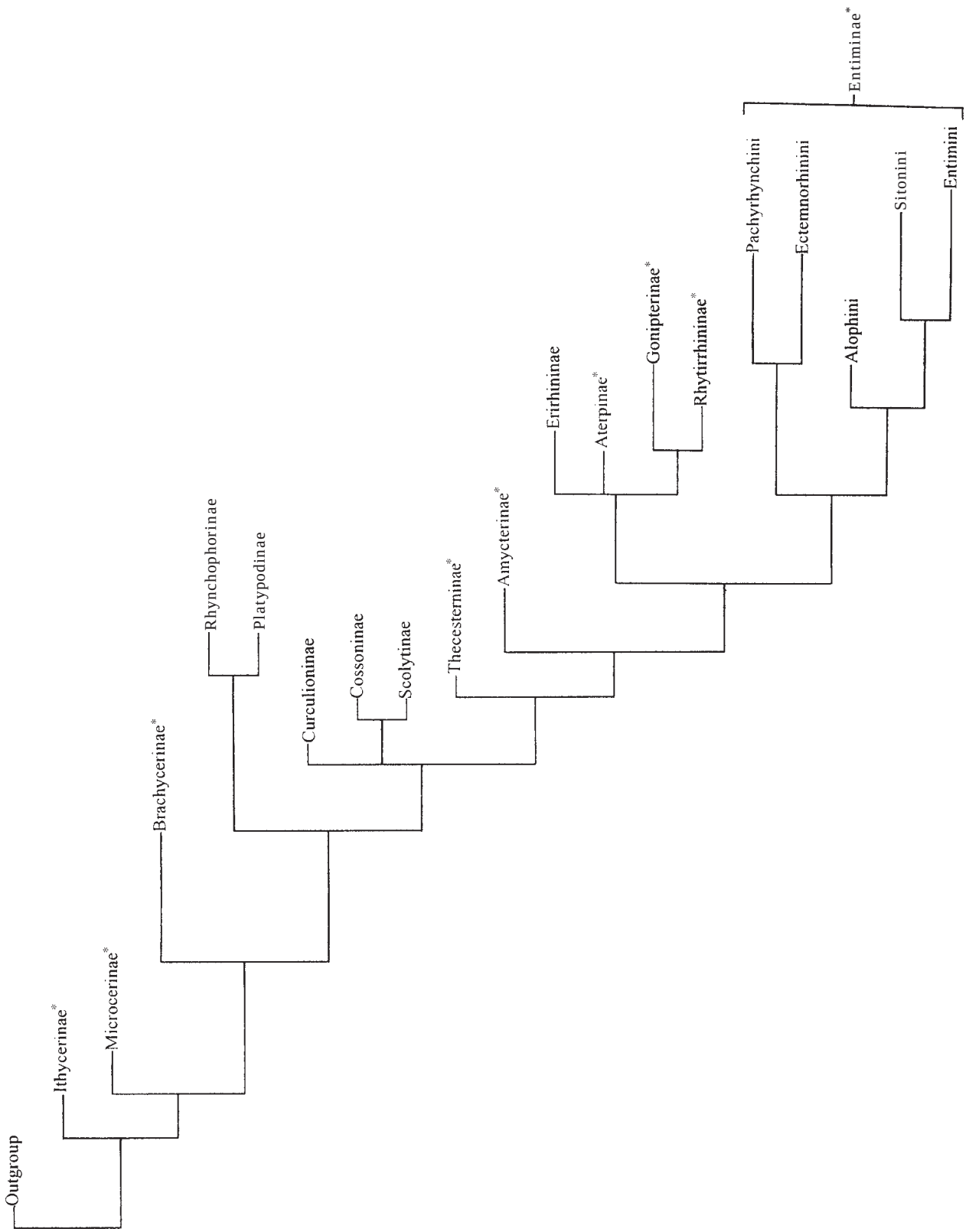

FIG. 40. Cladogram based on immature characters. *Broad-nosed weevils.

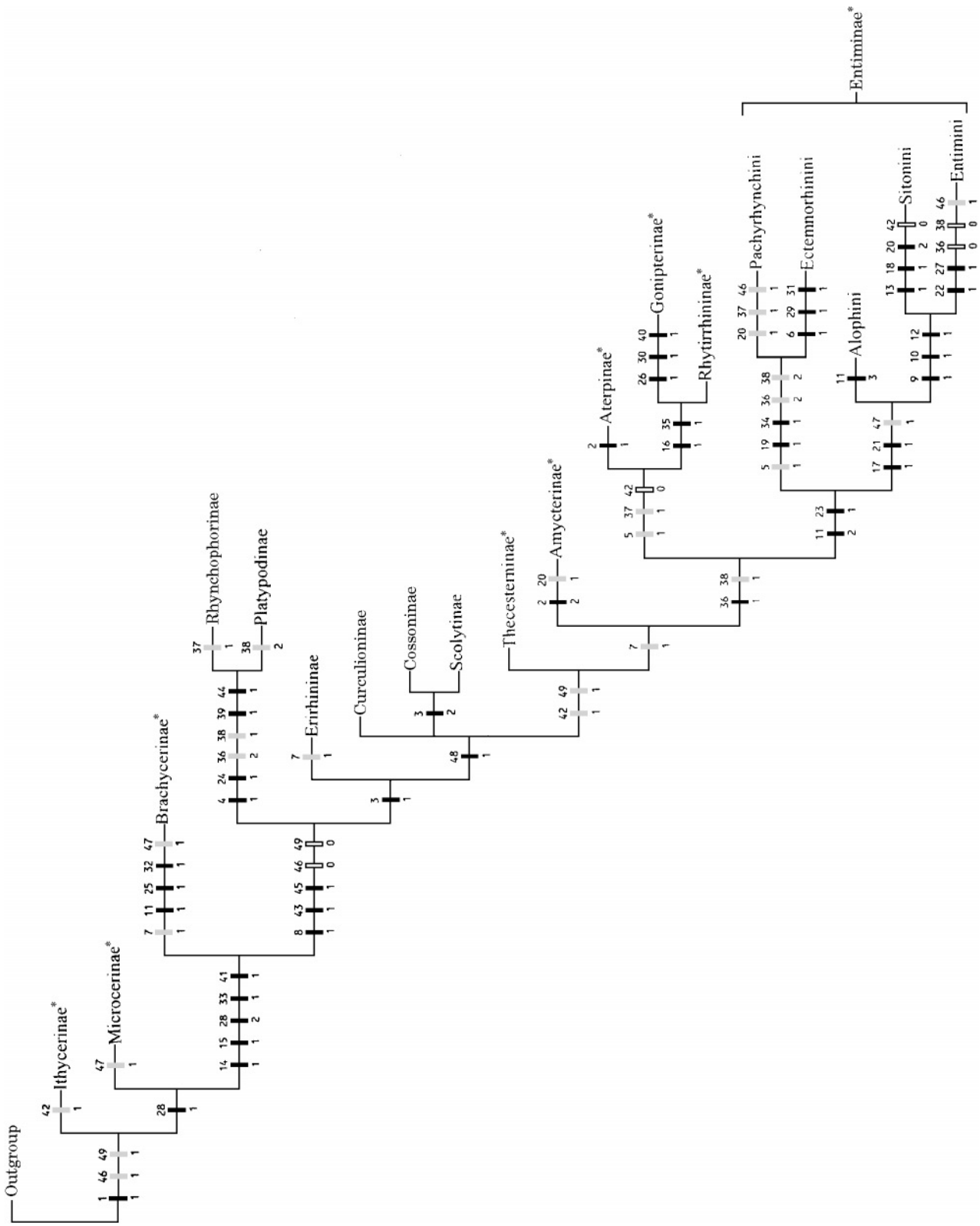

FIG. 41. Cladogram based on immature and adult characters. *Broad-nosed weevils; black bars: apomorphies; grey bars: parallelisms; white bars: reversals.

The presence of pupal mandibular setae is proposed by May (1970, 1978) as associated with the mandibular processes in the adult, and she interprets the presence of these pupal setae in species with adults lacking mandibular processes as evidence of secondary loss of such processes. Results of the cladistic analysis (Fig. 41) lead to consideration of an alternative hypothesis: that the pupal mandibular setae (42.1) and the adult mandibular processes (47.1) are independent features. I note, however, that they seem to be correlated with the increased overall mandibular size of shortened rostra. In addition, Anderson (1991) discusses the occurrence of pupal mandibular setae in some species of Lixini *sensu* Kuschel (Curculioninae), which have no mandibular processes in the adults, also suggesting that they are independent character states. It is worth noting that, outside Curculionidae, pupae with mandibular setae are also found in Nemonychidae (May, 1994: table 3, figure P74), but have not been reported for Brentidae or other curculionoids. Thus, by outgroup comparison, this feature was coded here as apomorphic in Curculionidae, contrasting with Anderson's (1991) proposal of its being plesiomorphic to explain that not all taxa having this feature share a common ancestor. This seems to be better explained by the homoplastic nature of the pupal mandibular setae, which suffered parallel evolution and reversals, as depicted in the cladogram (Fig. 41).

Some of the characters mentioned above, especially the adelognathous and phanerognathous conditions (maxillae covered versus not covered by the prementum) and the presence/absence of mandibular processes, have been used by authors in weevil classification; however, specialists (e.g. Thompson 1992; Zimmerman, 1994) consider that too much taxonomic importance has been given to such features. According to the present cladistic analysis, these characters are highly homoplastic. The adelognathous and phanerognathous conditions are two extremes of variation between which many intermediate states exist (Thompson, 1992). In fact, an intermediate state "Mesognatha" has been proposed by Kuschel (1985). Finally, the adelognathous condition is also displayed by some Brentidae (Zimmerman, 1993: 30).

The deciduous mandibular processes also show homoplasy, not only among Curculionidae but in other Curculionoidea, for instance in some Attelabidae—Rhynchitinae (Thompson, 1992). The examples of taxa with mandibular processes known to date have a biological feature in common: pupation in soil (though not all weevils that pupate in soil show such processes). In the tribe Pachyrhynchini of the Entiminae (Fig. 41) these processes are absent, though the setae in the mandibular theca are present. This lack of mandibular processes can be accounted for by the fact that larvae and pupae of Pachyrhynchini develop in aerial parts of plants rather than in the soil (May, 1978).

Position of Ithycerinae

The cladogram is consistent with the hypothesis that the Ithycerinae, represented by the single species *Ithycerus noveboracensis* in North America, is a relict taxon. They may be the only survivor of a group with a greater number of species and distribution in the past.

The total absence of legs in larvae of all Curculionidae, except for the most basal taxon Ithycerinae and, to a lesser extent, Microcerinae, suggests that the loss of legs occurred early and only once in the evolutionary history of Curculionidea. The weevil larva is preadapted to live inside the substratum and natural selection would act against the presence of legs. Although legless larvae occur in several other Curculionidae (in some members of Nemonychidae, certain Anthribidae, Attelabidae and Belidae, and some Brentidae (e.g. Apioninae) (Crowson, 1967)), the loss of legs in Curculionidae occurred independently of other Curculionidea. The last conclusion is based on the fact that there is a particular pattern of setae and sensilla on the pedal area of representatives of all curculionid legless terminal units that is not found in other legless Curculionoidea (Marvaldi, 1995).

Position of Microcerinae—Brachycerinae

Microcerinae, according to the present phylogenetic hypothesis (Fig. 41), have a basal placement, standing as one of the less advanced Curculionidae, after Ithycerinae but before Brachycerinae *sensu stricto.*

The results of the cladistic analysis (Fig. 41) suggest that Brachycerinae *sensu stricto* and Microcerinae form a grade or paraphyletic group at the base of the clade, and not a monophyletic group as proposed by

Thompson (1992). Although my results agree with Louw's (1995) taxonomic conclusion that Microcerinae and Brachycerinae *sensu stricto* do not together form a monophyletic group (since the latter taxon shares with the remaining Curculionidae the larval synapomorphies of absence of legs, and abdominal segments with 3-4 dorsal folds), they do not support Louw's proposal of a Microcerinae sister relationship with *Spartecerus* (Entiminae). According to my hypothesis (Fig. 41), Entiminae are phylogenetically closer to more advanced weevils, with which they share several apomorphic characters (see below), than to any of the basal Curculionidae (Ithycerinae, Microcerinae or Brachycerinae *sensu stricto*) that lack such apomorphies. Furthermore, I disagree with the larval character interpretation made by Louw to justify a Microcerinae—*Spartecerus* (Entiminae) sister relationship. This is because I note that the antenna of the *Spartecerus* larva (see Louw, 1995: figure 5) has the apomorphic shape of Entiminae (i.e. it is cushion-like and fairly dorsoventrally compressed; it is also elliptical in apical view), while in Microcerinae the antenna has the plesiomorphic shape (i.e. it is conical, longer than wide, and circular in apical view). The completely flat antenna of *Brachycerus* is here interpreted as a different apomorphic state. On the other hand, the intermediate abdominal fold narrower than the others is the usual condition in all taxa with three to four dorsal folds, and *Brachycerus* with the three folds equally broad is an exception.

There are some important taxa, covered by Thompson (1992), and included by Kuschel (1995) in his Brachycerinae *sensu lato* for which no immatures are available. They may predictably have a basal phylogenetic placement on account of their orthocerous type of male genitalia. One of these is the Desmidophorinae, linked by Thompson (1992) with Brachycerinae *sensu stricto* and Microcerinae due to their similar dorsal plate of tegmen, but Thomas also notes significant external differences. The oviposition mode is known for *Ocladius* spp (Desmidophorinae: Ocladiini), being endophytic in grass stems, as in *Notaris* spp (Erirhininae) (Howden, 1995), whereas in *Brachycerus* spp and *Microcerus* spp it is ectophytic in soil. Oviposition data suggest that Desmidophorinae may be placed near Erirhininae. Another odd taxon with unknown larvae and uncertain affinities is Cryptolarynginae, but Thompson (1992) notes that they share a similarly shaped male sternite 8 with some Brachycerinae *sensu stricto*, Microcerinae, and Desmidophorinae. Further information on the larvae and pupae of representatives of these problematical taxa would be valuable in resolving weevil higher relationships, especially at the base of the clade.

Position of the Entiminae and Allied Subfamilies

Thecesterninae, Amycterinae, Aterpinae, Rhytirrhininae, Gonipterinae, and Entiminae share with the "primitive" broad-nosed weevils treated above (Ithycerinae, Microcerinae and Brachycerinae *sensu stricto*) the oviposition mode without rostrum participation, a feature that shows homoplasy (Fig. 41). They have a phylogenetic placement more advanced than the latter, justified by their larvae with postoccipital placement more advanced than the latter, justified by their larvae with postoccipital condyles and lacking the sensilla next to dorsoepicranial seta 2, their pupae with only one or two setae on the femoral apex, and their adults with geniculate antennae and male genitalia of the gonatocerous type. This latter character, the derived type of male genitalia, supports their closer relationship with Curculioninae and Cossoninae—Scolytinae, and defines the Curculionidae *sensu stricto* or *sensu* Thompson (1992) and Zimmerman (1993).

There are some small Etiopian taxa of broad-nosed weevils, e.g. Brachyceropsidinae, Cyclominae (=Hipporhininae), Somatodinae, and Ulomascinae, for which no immatures are described. Their adults have geniculate antennae and the derived type of male genitalia (Thompson, 1992). Information on larvae and pupae of these taxa would greatly contribute to recognition of natural groups and resolution of broad-nosed weevil relationships. For example, the sister group of Entiminae, here constituted by Aterpinae, Rhytirrhininae, and Gonipterinae, may also include Cyclominae as suspected from adult features. When immatures of Cyclominae become known, they will probably give stronger evidence to this proposal. Then, this sister group may be regarded as a single subfamily, which should be called Cyclominae.

Monophyly and Classification of Entiminae

The results of the cladistic analysis (Fig. 41) support the monophyly of Entiminae *sensu* Thompson (1992). The larvae with only four ventral setae on the maxillary mala (a character that needs careful observation), and with a particular shape of their antennal sensorium, provide good autapomorphies for the group.

The cladogram (Fig. 41) allows me to propose a natural classification of Entiminae, consisting of five monophyletic groups recognized here as tribes: Pachyrhynchini, Ectemnorhinini, Alophini, Sitonini, and Entimini.

According to the results, Pachyrhinchini are the closest relative of Ectemnorhinini. This hypothesis contrasts with two previous proposals that relate Ectemnorhinini with taxa from the New Zealand Subantarctic islands. May (1993) discussed a possible close relationship between *Canonopsis* (Ectemnorhinini) and *Gromilus* (Rhytirrhininae), based on some "similar" larval features; however, she admitted that *Gromilus* pupae lack the setae on the mandibular theca which are present in *Canonopsis* and other Entiminae pupae. This hypothesis is further weakened by evidence resulting from the cladistic analysis: *Gromilus* larvae are true Rhytirrhininae, having the lateral labral seta vestigial, the postdorsal seta 5 in abdominal segment VIII absent, and the spiracle of abdominal segment VIII laterodorsal or dorsal; while *Cananopsis* and other Ectemnorhinini are undoubtedly placed in Entiminae because their larvae have a cushion-like antennal sensorium and the maxillary mala with four ventral setae. Furthermore, the adults in *Christensenia* present deciduous mandibular processes (Chown, in litt.). One the other hand, I think that the fact that *Canonopsis* differs from other Ectemnorhinini in having the abdominal spiracular airtubes directed dorsoposteriorly instead of dorsally (May, 1970, 1993) should be considered with caution, as May's (1970) description was based on immature larvae and it is not uncommon among Entiminae that mature larvae have a quite different orientation of the airtubes than in earlier instars (Marvaldi, 1995). The other proposal is that of Kuschel and Chown (1995), who consider *Ectemnorhinus* and its allies to be most closely related to *Heterexis* and *Oclandius* (Entimini). May (1970) discussed this latter hypothesis, reaching the conclusion that the larvae of the two groups are not closely related, and I agree with her. According to the results of the cladistic analysis (Fig. 41), *Heterexis* and *Oclandius* have several apomorphic larval characters (e.g. the posterior extension of premental sclerite parallel-sided and truncate at apex, the antennal sensorium elliptical in apical view, and the mandibles lacking accessory teeth, among others) that certainly place them in Entimini and not among Ectemnorhinini which lack such apomorphies.

Results of the cladistic analysis (Fig. 41) support Alophini and Sitonini as true Entiminae *sensu* Thompson (1992), despite the doubts that previous authors may have had (e.g. Emden, 1952: 666; Crowson, 1967: 165; and others cited in Thompson, 1992: 885).

The huge tribe Entimini comprises the bulk of Entiminae, including the subfamilies of authors Entiminae (Leptopiinae), Brachyderinae (excluding Pachyrhynchini and Sitonini), Otiorhynchinae, Tanyrhynchinae, and Eremninae. This tribe certainly needs to be classified naturally into subtribes and the larval characters may prove helpful in this.

On the Position and Relationships of the Remaining Subfamilies of Curculionidae

The Sister Relationship of Rhynchophorinae—Platypodinae

The close relationship of Rhynchophorinae and Platypodinae is clearly supported by characters from the immature stages (Fig. 41), but is not so obvious in the adult stage and previously has never been proposed. Rhynchophorinae and Platypodinae have, in addition, important adult morphological differences from other Curculionidae and between themselves, both being very distinct subfamilies, and this is the reason why some specialists consider them as independent families (e.g. Morimoto, 1962; Thompson, 1992; Zimmerman, 1993). Their larvae, however, share a feature not found among any other Curculionoidea: the abdominal pleura subdivided into two or more superimposed lobes. Several other larval synapomorphies support the monophyly of these two subfamilies, such as the head bearing a posterior lamina with two attachment points, or apodemes, and the maxillae and epipharynx with some setae branched; the relationship is also supported by the larval parallelism of the spiracular airtubes dorsally directed on abdominal segments

I–VII, and by the pupal synapomorphy related to the last pair of legs not covered by pterothecae. To the evidence mentioned above I would add some other features suggesting that Rhynchophorinae and Platypodinae present similar development patterns: larva I of Platypodinae (according to Browne, 1972 and Milligan, 1979) presents only the thoracic and last abdominal (VIII) spiracles, while larvae of successive instars have the complete complement of nine spiracles; similarly, in certain Rhynchophorinae, as *Dryophthorus* spp (W. H. Anderson, 1948; pers. obs.), *Polytus* spp, and other species described by May (1994), the larva presents non-functional abdominal spiracles I–VII (as in larva I of *Platypus* and its allies). Furthermore, larvae of several Rhynchophorinae (W. H. Anderson, 1948; May, 1994) have unisegmented labial palps, a condition extremely frequent in Platypodinae. The two latter features may probably be a case of "underlying synapomorphies" (*sensu* Saether, 1983, 1986) which, although not useful as evidence of grouping (Forey et al., 1992), may be caused by apomorphic tendencies of the Rhynchophorinae—Platypodinae ancestor.

None of the immature characters mentioned above, as shared by Rhynchophorinae and Platypodinae, have been observed in any of the numerous larvae and pupae of Cossoninae and Scolytinae. Cossoninae, however, have been classified close to Rhynchophorinae for a long time (see Zimmerman, 1993; Kuschel, 1995). On the other hand, Scolytinae and Platypodinae have been frequently considered as separate families and separated from Curculionidae (see Lawrence and Newton, 1982). Crowson (1967) considers these taxa as subfamilies within Curculionidae.

Evidence supporting a closer relationship of Cossoninae with Scolytinae, instead of with Rhynchophorinae, is given later in this paper. The close relationship between Rhynchophorinae and Platypodinae, proposed here on a cladistic basis, may not be so evident from the adult external morphology. Instead, from the adult aspect a relationship between Scolytinae and Platypodinae may be justified, because their similar lignicole habits are reflected in superficially similar adult morphologies. For instance, a cylindrical body form, legs with denticulate tibiae, and a truncate head are typical of wood-boring beetles, and are thus also present, for example, in Anobiidae and Bostrychidae (Morimoto, 1962; Richards and Davies, 1984). In addition to the evidence presented here for a sister relationship between Rhynchophorinae and Platypodinae (Fig. 41), recent detailed morphological studies on adults (Thompson, 1992; Lyal, 1995) do not support the hypothesis of Scolytinae—Platypodinae monophyly. Lyal (1995) refutes Wood's (1986, 1993) proposal of Scolytinae—Platypodinae monophyly, based on characters from the ventral structure of the adult head, by showing that it is a case of misinterpreted homologies. Thompson's morphological studies (1992) also do not support a Scolytinae—Platypodinae monophyly. The latter author restricts the concept of Curculionidae for the weevils that have male genitalia of the gonatocerous type, and consequently retains Scolytinae within Curculionidae *sensu stricto* and separates the Platypodinae at the family rank on the basis of unique features from male and female genitalia and the total loss of the rostrum. Thompson affirms that even the less differentiated or "primitive" taxa of Platypodidae show no clear relationship to any Scolytinae. Since the Playtpodinae present such reduced and simplified male genitalia, it is difficult to determine whether they are of the orthocerous or gonatocerous type (they are therefore coded as "?" in the data matrix of Table 2). Evidence from Morimoto (1962) and Thompson (1992) suggests that they may be the orthocerous type, a condition that is supported by the cladogram (Fig. 41).

Although the recent proposal of Zherikhin and Gratshev (1995), uniting Rhynchophorinae with Brachycerinae because of their distinctive claw segments, is not supported by the present study, it is important to note that both groups occupy a relatively close and basal phylogenetic position.

The phylogenetic position of Playtpodinae is another controversial problem in weevil systematics. Some authors consider them as relatively "primitive" weevils, suggesting that they would have separated from the ancestral stem before the Curculionidae (e.g. Morimoto, 1962; Wood, 1986), although part of the evidenced for this proposal is erroneous (Lawrence and Newton, 1982). In contrast, Kuschel (1995) considers them to be the most "advanced" subfamily of Curculionidae. According to my phylogenetic hypothesis resulting from the cladistic analysis (Fig. 41), Rhynchophorinae and Platypodinae are sister groups and, although both are highly divergent, their

ancestor separated relatively early in the evolutionary history of Curculionidae.

Position of Erirhininae

Species of Erirhininae have the orthocerous or primitive type of male genitalia, but the antennae are typically geniculate and the larvae and pupae present their characters at the apomorphic states as present in the Curculionidae *sensu stricto* or with the derived type of male genitalia. Accordingly, Erirhininae have an intermediate phylogenetic placement, before the Curculionidae *sensu stricto* (Fig. 41).

A different placement of Erirhininae is suggested by the cladogram based only on characters from immatures (Fig. 40). According to this tree, Erirhininae are placed together with some broad-nosed weevils. This is mainly due to the shared possession of the dorsoepicranial seta 3 in the frontal line or on the frons. On the other hand, several erirhinine characters were coded as missing (?) as they are heterogeneous because of larval modifications associated with aquatic habits, leading to a character interpretation in agreement with that placement.

The placement of Erirhininae depicted in Fig. 41 is accepted because the result of the first analysis (Fig. 40) would imply that this taxon has a reversal to the ancestral type of male genitalia; I consider this latter hypothesis to be less probable than the independent acquisition by the larva of a similar location of dorsoepicranial seta 3.

The present cladistic analysis does not support the inclusion of Erirhininae within Curculioninae, as in none of the obtained cladograms (Figs 40, 41) do Erirhininae form a monophyletic group with Curculioninae.

The Raymondionyminae is another interesting taxon for which immatures are unknown. They are a group of hypogean weevils with the orthocerous type of male genitalia, considered by Kuschel (1995) as hypogean derivatives of the Erirhininae *sensu* Kuschel (1971). Thompson (1992) gives them family rank because of unique tarsal features and orthocerous male genitalia, but does not comment on their probable relationships with other weevils. Characters given by Thompson (1992) in his key and the similar shape of male sternite 8 shown in his figures 50–52 lead me to suspect that Raymondionyminae might belong to or be phylogenetically close to Erirhininae or Cryptolarynginae, and the discovery of their larvae would be very important to resolve this problem.

On the Monophyly of Curculioninae

This enormous subfamily cannot be defined as a monophyletic group on the basis of characters from the immature stages used in the present analysis, as it has no autapomorphies (Fig. 41). It is suggestive that Kuschel (1995) also recorded no adult autapomorphy. Curculioninae may be regarded as a "metataxon" (Archibald, 1994: 28), as it is a previously named taxon for which positive evidence of monophyly or paraphyly is lacking or ambiguous. Whether this subfamily forms a monophyletic or paraphyletic group is a problem that needs further investigation, such as subdividing this taxon into smaller units and performing other cladistic analyses with more evidence. Difficulties in diagnosis of Curculioninae also arise from several polymorphic characters (coded "?") because the larvae known for this species of this large group show different modifications, associated with a variety of habitats, affecting quetotaxia and position of spiracles and airtubes. However, a particular combination of adult and immature characters allows a definition of Curculioninae: the larvae have the dorsoepicranial seta 3 on the epicranium and well-developed postoccipital condyles; the adults have geniculate antennae and male genitalia of the gonatocerous type. Furthermore, adults have a well-developed rostrum, used by females to prepare oviposition sites; larvae are almost always endophytic, feeding inside plant tissues (except for some taxa with ectophytic larvae, such as *Cionus* or *Hypera* and their allies) and adults and larvae (R. S. Anderson, 1993) usually have a restricted range of host plants, being oligophagous or monophagous.

The Close Relationship of Cossoninae—Scolytinae

According to the result of the cladistic analysis (Fig. 41), Cossoninae and Scolytinae are sister groups; this relationship is supported by the larval synapomorphy

regarding the inconspicuous postoccipital condyles represented by a thickened ridge. To this may be added a feature of the alimentary canal described by May (1993, 1994), the rectal bracon as a sclerotized loop, not included in this analysis because, although it is present in all Cossoninae, it is lacking in about half of the Scolytinae. This latter character has also been observed in zylophagous larvae of other taxa (May, 1994), all within Curculioninae, and may indicate that Cossoninae—Scolytinae share with the former subfamily a capacity to develop a sclerotized loop when it is selectively advantageous to the taxon.

The immature stages do not provide autapomorphies to clearly distinguish Cossoninae from Scolytinae clearly, but their typical forms are rather distinct at the adult stage due to their different biologies. To this difficulty is added the existence of the tribe Araucariini of Cossoninae, whose members present the typical biology of Scolytinae and larval and adult characters of both subfamilies (Kuschel, 1966; May, 1993). Eventually, Thompson (1992) found that the male sternite 8 in the less-modified members of Scolytinae showed "a clear relationship" to that of Cossoninae.

There are some Scolytinae ("bark beetles") that culture fungi, similar to the Platypodinae or true "ambrosia beetles". They possess mycetangia to carry the spores and this capacity would have evolved independently several times in Scolytinae (different genera have distinct types of mycetangia in different body parts) and in the ancestral line of Paltypodinae (Hinton, 1981). In addition, in Scolytinae generally it is the female that constructs the gallery and the male that carries the spores, while in Platypodinae the reverse is the case. See above for more evidence against the relationship Scolytinae—Platypodinae.

According to the cladistic analysis and the information discussed here, I do not discard the possibility that the Scolytinae represent a more advanced group within the Cossoninae.

CONCLUSIONS

The use of characters from immature stages, as well as their combination with adult ones in the final analysis, leads to the conclusion that the broad-nosed weevils do not constitute a single monophyletic group. Their shared mode of oviposition without rostrum participation appeared more than once in the evolutionary history of weevils, and it is associated with the subterranean life of the immature stages, together with other homoplastic characters such as adults with adelognathous mouthparts and mandibular processes, and pupae with setae in the mandibular theca.

The proposed phylogenetic hypothesis shows Ithycerinae, Microcerinae, and Brachycerinae *sensu stricto* as the most basal Curculionidae, forming a grade or paraphyletic group. The remaining broad-nosed weevils included in the analysis form a clade ("Entiminae and allied subfamilies") phylogenetically closer to other weevil subfamilies than to any of the basal ones mentioned above, on the basis of larval, pupal, and adult characters. This latter clade has Thecesterninae at the base, followed by Amycterinae which are the sister taxon of the clade involving two main natural groups; one comprises Aterpinae, Rhytirrhininae, and Gonipterinae in that sequence, and the other comprises Entiminae. The monophyly of Entiminae is well supported by larval autapomorphies, as is their classification into tribes herein proposed. The sister group of Entiminae may become a single subfamily, with the proposed name Cyclominae (=Hipporhininae) if immatures of the latter, when they become known, support their position in this sister group.

The immature characters were particularly significant in supporting the monophyly of Rhynchophorinae—Platypodinae, a sister relationship not suggested by previous studies focused on adults. Erirhininae was the only taxon that showed a different placement depending on the data set analysed: the taxon is among some broad-nosed weevils (Aterpinae, Rhytirrhininae, and Gonipterinae) when only immature characters are used, but according to the combined immature and adult data it has an intermediate position, as a sister taxon of the "Curculionidae *sensu stricto*" (i.e. Curculioninae, Cossoninae—Scolytinae, and "Entiminae and allied subfamilies") and the latter hypothesis seems to be better justified. There is a need for additional data to test the monophyly or paraphyly of the Curculioninae, and to resolve the trichotomy involving the three main branches of Curculionidae *sensu stricto* mentioned above.

It is notable that the rank of the groups studied here depends on which concept of the family Curculionidae

is accepted: the more inclusive concept of Kuschel (1995), which is based on that of Crowson (1967) but including *Ithycerus*, or the restricted concept of Thompson (1992), also applied by Zimmerman (1993). The former represents the ingroup chosen for the present study; the latter comprises only and exclusively the weevils sharing the gonatocerous type of male genitalia. It is important to remember that the rank of a taxon does not affect its status in the phylogenetic system, and both concepts of Curculionidae refer to monophyletic groups. Kuschel's (1995) work has the merit of being the first major attempt to classify the Curculionoidea to families and subfamilies via a rigorous, phylogenetic methodology. My findings, however, suggest an alternative hypothesis regarding the monophyletic groups and relationships within Curculionidae. The results presented here are in agreement with Thompson's (1992) views regarding the primary grouping of weevils on the basis of the two basic forms of male genitalia, the derived type (48.1) supporting the monophyly of the Curculionidae *sensu stricto*. If the name "Curculionidae" is used in this restricted sense, then the remaining clades depicted in my cladogram should be treated with family rank as in Thompson (1992). Microcerinae should perhaps also be treated as such because evidence presented here, though incomplete, does not support their inclusion in Thompson's Brachyceridae. There are some odd and problematical taxa, with the primitive type of male genitalia, for which no immatures are available, i.e. Desmidophorinae, Cryptolarynginae, and Raymondionyminae. Further knowledge of their larvae and pupae may help in testing some of the phylogenetic hypotheses considered in the Discussion, elucidating whether they belong to other family groups (e.g. Brachyceridae or Erirhinidae) or are independent families.

According to this study, both immature and adult characters define higher groups in Curculionidae, though not always at the same level. It seems that larval differentiation preceded adult differentiation in the evolutionary history of weevils. For example, the larval novelties "frontal lines incomplete", "legs absent", and "abdominal segments with 3-4 dorsal folds" preceded the adult novelty "geniculate antennae"; similarly, larvae with "postoccipital condyles" appeared before adults with the "derived type of male genitalia". The paper shows that immature stages represent a valuable source of evidence for the recognition of natural groups and relationships of such a large and phylogenetically confusing group as Curculionidae. Several further steps are needed to ensure the stability of weevil higher relationships and classification. These include discovery and detailed study of the still unknown immature stages of some weevil taxa and a broader survey of new adult features. I would also emphasize the potential value, as source of new data, of DNA sequencing on Curculionoidea. I feel confident that an enlarged data base made available for cladistic analyses will ultimately lead to a better understanding of weevil phylogeny and more stable natural classifications. I hope my findings represent a valuable step towards this goal.

ACKNOWLEDGEMENTS

I express my appreciation to all the specialists and curators of the institutions that provided material for this study. I am very grateful to M. M. Cigliano, A. A. Lanteri, and J. J. Morrone for comments and criticisms on earlier versions of this manuscript. I am much indebted to C. H. C. Lyal for his assistance and encouragement to conduct this project, and also to R. T. Thompson for all his help and valuable comments. I am very grateful to The British Council and "Fundación Antorchas" that awarded me with a term visit to study weevil larvae at the Natural History Museum, London. I also appreciate the help of S. Roig-Juñent to obtain further financial assistance for facilities, coming from a grant of "Fundación Antorchas". Finally, I express my thanks to the "Consejo Nacional de Investigaciones Cientificas y Técnicas", Argentina, for its continuing support.

REFERENCES

Anderson, D. M. (1991). Curculionidae (broad sense) (Curculionoidea). *In* "Immature Insects" (F. W. Stehr, Ed.), Vol. 2, pp. 594-612. Kendall / Hunt Publishing Company.

Anderson, R. S. (1991). Larva and pupa of *Cleonidius erysimi* (Fall) with a discussion of the phylogenetic position of Lixini (*sensu* Kuschel) (Coleoptera: Curculioniodea). *Proc. Entomol. Soc. Wash.* **93(2)**, 288–297.

Anderson, R. S. (1993). Weevils and plants: Phylogenetic versus ecological mediation of evolution of host plant associations in Curculioninae (Coleoptera: Curculionidae). *Mem. Ent. Soc. Can.* **165**, 197–232.

Anderson, R. S. (1995). An evolutionary perspective on diversity in Curculionidae. *Mem. Entomol. Soc. Wash.* **14**, 103–114.

Anderson, W. H. (1948). Larvae of some genera of Calendrinae (=Rhynchophorinae) and Stromboscerinae (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* **41**, 413–437.

Archibald, J. D. (1994). Metataxon concepts and assessing possible ancestry using phylogenetic systematics. *Syst. Biol.* **43(1)**, 27–40.

Böving, A. G., and Craighead, F. C. (1931). An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomol. Amer.* **11(1)**, 351.

Browne, F. G. (1972). Larvae of the principal old world genera of the Platypodinae (Coleoptera: Platypodinae). *Trans. R. Entomol. Soc. Lond.* **124**, 167–190.

Chippindale, P. T., and Wiens, J. J. (1994). Weighting, partitioning, and combining characters in phylogenetic analysis. *Syst. Biol.* **43(2)**, 278–287.

Chown, S. L., and Scholtz, C. H. (1989). Immature stages of Curculionidae (Coleoptera) from the sub-Antarctic Prince Edward Islands. *J. Ent. Soc. Sth. Afr.* **52(2)**, 253–275.

Chown, S. L., and Scholtz, C. H. (1990). Description of the larva of *Christensenia antarctica* Brinck with implications for the phylogeny of Ectemnorhinini (Coleoptera: Curculionidae). *Coleopt. Bull.* **44(3)**, 255–264.

Costa, C., Vanin, S. A., and Casari-Chem, S. A. (1988). "Larvas de Coleoptera do Brasil". Museu de Zoologia, Univ. de São Paulo, São Paulo.

Crowson, R. A. (1967). (Reprinted from 1955 edition). "The Natural Classification of the Families of Coleoptera". Classey Ltd., Middlesex.

van Emden, F. I. (1938). On the taxonomy of Rhynchophora larvae (Coleoptera). *Trans. R. Entomol. Soc. Lond.* **87**, 1–37.

van Emden, F. I. (1952). On the taxonomy of Rhynchophora larvae: Adelognatha and Alophinae (Insecta: Coleoptera). *Proc. Zool. Soc. Lond.* **122(3)**, 651–795.

Farris, J. S. (1988). Hennig86, Version 1.5. Published by the author, Port Jefferson, New York.

Farris, J. S. (1989). The retention index and the rescaled consistency index. *Cladistics* **5**, 417–419.

Forey, P. L., Humphries, C. J., Kitching, I. J., Scotland, R. W., Siebert, D. J., and Williams, D. M. (1992). "Cladistics. A Practical Course in Systematics". Clarendon Press, Oxford.

Gardner, J. C. M. (1932). Immature stages of Indian Coleoptera (11) (Platypodidae). *Indian Forest Records (Entomol. Ser.)* **17(3)**, 1–12.

Gardner, J. C. M. (1934a). Immature stages of Indian Coleoptera (14) (Curculionidae). *Indian Forest Records (Entomol. Ser.)* **20(2)**, 1–48.

Gardner, J. C. M. (1934b). Immature stages of Indian Coleoptera (15) (Scolytidae). *Indian Forest Records (Entomol. Ser.)* **20(8)**, 1–17.

Gardner, J. C. M. (1938). Immature stages of Indian Coleoptera (24 Curculionidae Contd.). *Indian Forest Records (Entomol. Ser.)* **3(12)**, 227–261.

Hinton, H. E. (1981). "Biology of Insect Eggs". Vols. I–III. Pergamon Press, Oxford.

Howden, A. T. (1995). Structures related to oviposition in Curculionoidea. *Mem. Entomol. Soc. Wash.* **14**, 53–100.

Kissinger, D. G. (1964). "Curculionidae of America North of Mexico. A Key to the Genera". Taxonomic Publications, South Lancaster, MA.

Kluge, A. G., and Farris, J. S. (1969). Quantitative phyletics and the evolution of anurans. *Syst. Zool.* **18**, 1–32.

Kuschel, G. (1943). Un "gorgojo acuático del arroz" Argentino. "*Lissorhoptrus bosqi*" n. sp. (Col. Curculionidae). *Notas Mus. La Plata 8 Zool.* **71**, 305–315.

Kuschel, G. (1966). A cossonine genus with bark-beetle habits, with remarks on relationships and biogeography (Coleoptera: Curculionidae). *N. Z. Jl. Sci.* **9**, 3–29.

Kuschel, G. (1971). Entomology of the Aucklands and other islands south of New Zealand: Coleoptera: Curculionidae. *Pacif. Ins. Monogr.* **27**, 225–259.

Kuschel, G. (1985). A new scheme of families and subfamilies for Curculionoidea. Entomology Division, DSIR, Auckland, New Zealand. Manuscript distributed by the author.

Kuschel, G. (1987). Erirhininae Erirhinini (male genitalia of the orthoceri-group). Key to the genera of the world. Manuscript distributed by the author.

Kuschel, G. (1988). Families and subfamilies of Curculionoidea. Auckland, New Zealand. Manuscript distributed by the author.

Kuschel, G. (1990). "Beetles in a Suburban Environment: A New Zealand Case Study". DISR Plant Protection Report No. 3, Auckland.

Kuschel, G. (1995). A phylogenetic classification of Curculionoidea to families and subfamilies. *Mem. Entomol. Soc. Wash.* **14**, 5–33.

Kuschel, G., and Chown, S. L. (1995). Phylogeny and systematics of the *Ectemnorhinus*—group of genera (Insecta: Coleoptera). *Invert. Taxon.* **9**, 841–863.

Lacordaire, [J.] T. (1863). "Histoire Naturelle des Insectes. Genera des Coléoptères". Vol. 6. Roret, Paris.

Lacordaire, [J.] T. (1866). "Histoire Naturelle des Insectes. Genera des Coléoptères". Vol. 7. Roret, Paris.

Lawrence, J. F., and Newton, A. F. (1982). Evolution and classification of beetles. *Ann. Rev. Ecol. Syst.* **13**, 261–290.

Louw, S. (1990). The life history and immature stages of *Brachycerus ornatus* Drury (Coleoptera: Curculionidae). *J. Ent. Soc. Sth. Afr.* **53(1)**, 27–40.

Louw, S. (1995). Systematics and biogeography of the subfamily Microcerinae (Coleoptera: Curculionidae): A re-evaluation based on larval morphology. *Mem. Entomol. Soc. Wash.* **14**, 169–174.

Lyal, C. H. C. (1995). The ventral structures of the weevil head (Coleoptera: Curculionoidea). *Mem. Entomol. Soc. Wash.* **14**, 35–51.

Maddison, W. P., Donoghue, M. J., and Maddison, D. R. (1984). Outgroup analysis and parsimony. *Syst. Zool.* **33**, 83–103.

Marvaldi, A. E. (1995). "Morfologia biologia e importancia filogenética de los estados inmaduros de la subfamilia Brachycerinae (Coleoptera: Curculionidae)". Ph.D. thesis. Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata. No. **639**.

Marvaldi, A. E. (in press). Larvae of South American Rhytirrhininae (Coleoptera: Curculionidae). *Coleopt. Bull.*

Marvaldi, A. E., and Loiácono, M. S. (1994). First instar larvae in the tribe Naupactini (Coleoptera: Curculionidae). *Revta bras. Ent.* **38(2)**, 453–466.

May, B. M. (1970). Immature stages of Curculionidae of Heard Island. *Pacif. Insects Monogr.* **23**, 261–270.

May, B. M. (1978). Immature stages of Curculionidae (Coleoptera): Some species in the genus *Pantorhytes* Faust (Pachyrhynchini) from the papuan region and phylogenetic implications of certain characters. *J. Aust. Ent. Soc.* **17**, 351–360.

May, B. M. (1993). Larvae of Curculionoidea (Insecta: Coleoptera): A systematic overview. *Fauna N.Z.* **28**, 1–225.

May, B. M. (1994). An introduction to the immature stages of Australian Curculionoidea. *In* "Australian Weevils" (E. C. Zimmerman), Vol. II, pp. 365-755. Melbourne, CSIRO.

McClay, A. S., and Anderson, D. M. (1985). Biology and immature stages of *Thecesternus hirsutus* Pierce (Coleoptera: Curculionidae) in north-eastern Mexico. *Proc. Entomol. Soc. Wash.* **87(1)**, 207–215.

Milligan, R. H. (1979). In May, 1993.

Morimoto, K. (1962). Comparative morphology and phylogeny of the superfamily Curculionoidea of Japan. (Comparative

morphology, phylogeny and systematics of the superfamily Curculionoidea of Japan. I). *J. Fac. Agric. Kyushu Univ.* **11(4)**, 331–373.
Nixon, K. C., and Carpenter, J. M. (1993). On outgroups. *Cladistics* **9**, 413–426.
Platnick, N. I. (1989). An empirical comparison of microcomputer parsimony programs. II. *Cladistics* **5**, 145–161.
Richards, O. W., and Davies, R. G. (1984). "Tratado de Entomologia Imms". Vol. 2. Omega, Barcelona.
Saether, O. A. (1983). The canalized evolutionary potential: Inconsistencies in phylogenetic reasoning. *Syst. Zool.* **32**, 343–359.
Saether, O. A. (1986). The myth of objectivity—post-Hennigian deviations. *Cladistics* **2**, 1–13.
Sanborne, M. (1981). Biology of *Ithycerus noveboracensis* (Forster) (Coleoptera) and weevil phylogeny. *Evol. Monog.* **4**, 1–80.
Scherf, H. (1964). Die entwicklungsstadien der mitteleuropäischen Curculioniden (Morphologie, Bionomie, Ökologie). *Abh. Senckenberg. Naturf. Ges.* **506**, 1–355.
Schoenherr, C. J. (1826). "Curculionidum Dispositio Methodicus cum Generum Characteribus Descriptionibus atque Observationibus variis, seu Prodromus ad Synonymiae Insectorum". Fleischer, Lipsiae.
Thompson, R. T. (1992). Observations on the morphology and classification of weevils (Coleoptera, Curculionidae) with a key to major groups. *J. Nat. Hist.* **26**, 835–891.
Watrous, L. E., and Wheeler, Q. D. (1981). The out-group comparison method of character analysis. *Syst. Zool.* **30**, 1–11.
Wood, S. L. (1986). A reclassification of the genera of Scolytidae (Coleoptera). *Great Basin Nat. Mem.* **10**, 1–126.
Wood, S. L. (1993). Revision of the genera of Platypodinae (Coleoptera). *Great Basin Nat.* **53(3)**, 259–281.
Zherikhin, V. V., and Gratshev, V. G. (1995). A comparative study of the hind wing venation of the superfamily Curculionoidea, with phylogenetic implications. *In* "Biology, Phylogeny and Classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson" (J. Pakaluk, and S. A. Slipinski, Eds). Vol. 2, pp. 633-777. Museum i Instytut Zoologii PAN, Warszawa, Poland.
Zimmerman, E. C. (1993). "Australian Weevils". Vol. II. Melbourne, CSIRO.
Zimmerman, E. C. (1994). "Australian Weevils". Vol. III. Melbourne, CSIRO.
Zwölfer, H. (1980). Weevil and its environment, an ecological chapter. Translation from German (by Al-Ahram Center for Scientific Translations, for USDA and NSF, Wash. D.C.): Rüsselkäfer and ihre Umwelt—ein Kapited Ökologie. *Stuttgarter Beiträge zur Naturkunde.* **3**, 19–31, 1975.

APPENDIX I

List of Species Studied

The material studied was borrowed from the following institutions: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina [MACN]; Museo de La Plata, La Plata, Argentina [MLP]; National Museum of Natural History, Washington D.C., USA [NMNH]; New Zealand Arthropod Collection, Auckland, New Zealand [NZAC]; The Natural History Museum, London, England [NHM]. The following specialists also lent or donated specimens for this study: Roy A. Crowson, Glasgow University, Glasgow, Scotland [RAC]; Anne T. Howden, Carleton University, Ontario, Canada [ATH]; Brenda M. May, Landcare Research, Auckland, New Zealand [BMM]; Germano H. Rosado-Neto, Universidade Federal do Paraná, Curitiba, Brasil [GHR]; and Michael Sanborne, McGill University, Quebec, Canada [MS]. Specimens obtained by my collectings and rearings from various parts of Argentina during 1991–1995 are indicated by [AEM].

Ingroup

Ithycerinae. *Ithycerus noveboracensis* (Forster) [MS; NHM].

Microcerinae. Material of this taxon was not available for this study, but information on larval characters is found in Louw (1995).

Brachycerinae sensu stricto. *Brachycerus albidentatus* Gyllenhal [NMNH]; Brachycerini gen. sp. indet. [NHM].

Rhynochophorinae. *Cosmopolites sordidus* (Germar) [NHM]; *Diocalandra frumenti* (Fabricius) [NHM]; *Dryophthorus corticalis* (Paykull) [NHM]; *Sipalinus hypocrita* (Boheman) [NHM]; *Sphenophorus incurrens* Gyllenhal [NHM].

Platypodinae. *Platypus cylindrus* (Fabricius) [NHM]; *Platypus* sp. [NHM].

Erirhininae. *Erirhinus nereis* (Paykull) [NHM]; *Notaris acridulus* (L.) [NHM]; *Tanysphyrus lemnae* (Paykull) [NHM].

Curculioninae sensu lato. (Curculionini)—*Curculio glandium* Marsham [NHM], *C. nasicus* (Say) [NHM]; (Molytini)—*Hylobius abietis* (L.) [NHM], *Conotrachelus quadrinotatus* (Fabricius) [NHM]; (Cryptorhynchini)—*Cyrptorhynchus lapathi* (L.) [NHM]; (Lixini)—*Cleonis pigra* (Scopoli) [NHM], *C. brevirostris* Gyllenhal [NHM];. *Lixus paraplecticus* (L.) [NHM]; *L. algirus* (L.) [NHM]; (Cionini)—*Cionus fraxini* (De Geer) [NHM]; (Hyperini)—*Hypera arator* (L.) [NHM]; *Phelypera griseofasciata* Capiomont [NHM]; *Cepurus torridus* (Olivier) [NHM].

Cossoninae. *Cossonus binodosus* Marshall [NHM]; *C. parallelepipedus* (Herbst) [NHM].

Scolytinae. *Scolytus scolytus* (Fabricius) [NHM].

Thecesterninae. Material of this taxon was not available for this study, but information on immature stages is found in McClay and Anderson (1985).

Amycterinae. *Cubicorhynchus crenicollis* (Waterhouse) [BMM; NZAC]; *Sosytelus pubescens* (Lea) [BMM; NZAC].

Aterpinae. *Aegorhinus phaleratus* Erichson [NHM]; *Anagotus helmsi* Sharp [BMM; NZAC]; *Anagotus occonori* Broun [BMM; NZAC]; *Chrysolopus spectabilis* (Fabricius) [ATH]; *Rhadinosomus acuminatus* (Fabricius) [BMM; NZAC].

Rhytirrhininae. *Antarctobius falklandicus* (enderlein) [NHM]; *Gromilus exiguus* (Brookes) [BMM; NZAC]; *G. thoracicus* (Broun) [BMM; NZAC]; *Listeroderes abditus* Enderlein [NHM]; *L. bruchi* Hustache [AEM]; *L. costirostris* Schoenherr [AEM; MACN]; *Listronotus bonariensis* (Kuschel) [MLP; NHM]; *Rhigopsidius piercei* Heller [MLP]; *Tristanodes* sp. [RAC].

Gonipterinae. *Gonipterus gibberus* Boisduval [GHR; NHM]; *G. scutellatus* Gyllenhal [GHR; NHM].

Entiminae: Pachyrhynchini. *Pantorhytes biplagiatus* (Guérin) [NHM]; *P. plutus* (Oberthür) [NHM]; *P. proximus* (Faust); *P. szentivanyi* Marshall (BMM; NHM; NZAC].

Entiminae: Ectemnorhinini. Material of this taxon was not available for this study (larvae and pupae sent by S. L. Chown were lost in transit) but information on immature stages is found in van Emden (1952), May (1970), and Chown and Scholtz (1989, 1990).

Entiminae: Alophini. *Alophus triguttatus* (Fabricius) [NHM]; *Trichalophus didymus* (LeConte) [NHM]; *Triglyphulus ater* LeConte [NMNH].

Entiminae: Sitonini. *Sitona cylindricollis* (Fåhraeus) [NHM]; *S. crinitus* (Herbst) [NHM]; *S. flavescens* (Marsham) [NHM]; *S. gressorius* (Fabricius) [NHM]; *S. griseus* (Fabricius) [NHM]; *S. puncticollis* Stephens [NHM]; *S. lineatus* (L.) [NHM]; *S. regensteinensis* (Herbst) [NHM]; *S. tibialis* (Herbst) [NHM].

Entiminae: Entimini. *Agasphaerops nigra* Horn [NMNH]; *Amblyrhinus poricollis* Boheman; *Asynonychus cervinus* (Boheman) [AEM; NMNH]; *Atrichonotus taeniatulus* (Berg) [AEM; NMNH]; *Barynotus obscrurs* (Fabricius) [NHM]; *Barypeithes mollicomus* Ahrens [NHM]; *Callirhopalus bifasciatus* (Roelofs) [NHM]; *Colomycterus* sp. [NHM]; *Chlorophanus viridis* (L.) [NHM]; *C.* sp. [NHM]; *Cylydrorhinus farinosus* (Burmeister) [AEM]; *Cyrtepistomus juncundus* (Redtenbacher) [NHM]; *Diaprepes abbreviatus* (L.) [NHM]; *D. boxi* Marshall [NHM]; *Epicaerus cognatus* Sharp [NMNH]; *Eurymetopus oblongus* (Hustache) [AEM]; *Geoderces* sp. [NMNH]; *Hormorus undulatus* (Uhler) [NMNH]; *Leptomias mundali* Marshall [NHM]; *Malvinius compressiventris* (Enderlein) [NHM]; *Mesagroicus* sp. [NMNH; NHM]; *Naupactus leucoloma* Boheman [AEM; MLP; NMNH]; *N. peregrinus* (Buchanan) [NMNH]; *N. rugosus* Hustache [AEM]; *N. ruizi* (Brèthes) [AEM]; *N. sulphurifer* Pascoe [AEM]; *N tucumanensis* Hustache [AEM]; *N. verecundus* Hustache [AEM]; *N. xanthographus* (Germar) [AEM; MLP]; *Neliocarus faber* (Herbst) [NHM]; *Oclandius cinereus* (Blanchard) [BMM; NZAC]; *Otiorhynchus meridionalis* Gyllenhal [NHM]; *O. sulcatus* (Fabricius) [ATH]; *Scythropus mustela* (Herbst) [NHM]; *Pachnaeus litus* (Germar) [NMNH] *P.* sp. [NMNH]; *Pachynotus globulicollis* Redtenbacher [NHM]; *Peritelinus variegatus* Casey [NMNH]; *Philopedon plagiatum* (Schaller) [NHM]; *Phyllobius calcaratus* (Fabricius) [NHM]; *P. pomaceus* Gyllenhal [NHM]; *Platyaspistes argentinensis* Kuschel [AEM]; *Polydrusus cervinus* (L.) [NHM]; *P. mollis* (Stroem) [NHM]; *Pororhynchus* sp. [AEM]; *Premnotrypes* sp. [NHM]; *Psalidium maxillosum* (Fabricius) [NHM]; *Rhyncogonus extraneus* Perkins [NMNH]; *R. griseus* Van Dyke [NMNH]; *Sciaphilus asperatus* (Bonsdorff) [NHM]; *Strophosoma capitatum* (Marsham); *Tanymecus confusus* Say [NMNH]; *Thylacites incanus* (L.); *Trachyphloeus bifoveolatus* (Beck) [NHM; NMNH]; *T. scabriculus* (L.) [NHM]; *Trigonoscuta pilosa* Motschulsky [NHM].

Outgroup

(Brentinae)—*Anisognathus csikii* Bolkay [NHM]; *Arrhenodes minuta* (Drury) [NHM]; *Lasiorhynchus barbicornis* (Fabricius) [RAC]; *Mygaleicus vittipennis* (Fåhraeus) [NHM]; (Cyladinae) *Cylas formicarius* (Fabricius) [NHM]; (Apioninae)—*Apion* spp. [NHM]; *Nanophyes robustus* Pic [NHM]; *N. terminalia* Marshall [NHM].