

Phylogenetic systematics of weevils (Coleoptera: Curculionoidea): A reappraisal based on larval and adult morphology

A. E. MARVALDI and J. J. MORRONE

Insect Syst. Evol. Marvaldi, A. E. & Morrone, J. J.: Phylogenetic systematics of weevils (Coleoptera: Curculionoidea): A reappraisal based on larval and adult morphology. *Insect Syst. Evol.* 31: 43-58. Copenhagen, April 2000. ISSN 0013-8711.



A cladistic analysis of Curculionoidea based on 100 morphological characters (28 from larvae and 72 from adults) is presented. The 13 terminal taxa correspond to 7 extant families of Curculionoidea of which the largest, Curculionidae, is represented by 7 smaller units. The terminal units are defined by morphological autapomorphies taken from published information on larvae and adults. The chrysoloid Palophaginae was used as outgroup. The cladogram shows that there is a basal dichotomy in the superfamily, Nemonychidae-Anthribidae being the monophyletic sister taxon to the remaining families, which follow the sequence Belidae, Attelabidae, Caridae, Brentidae, and Curculionidae. The units of Curculionidae are related as follows: Ithycerinae, Microcerinae, Brachycerinae, Ocladiinae, Dryophthorinae, Erihinae, and 'Curculionidae s.str.'. Important areas where further work should be directed are: the sister group relationship of Nemonychidae and Anthribidae, and the recognition of monophyletic subfamilies within the Curculionidae s.str. as well as the placement of Platypodinae.

A. E. Marvaldi, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), CRI-CYT, C. C. 507, 5500 Mendoza, Argentina. *Present address:* Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA. E-mail: amarvaldi@oeb.harvard.edu

J. J. Morrone, Museo de Zoología, Facultad de Ciencias, UNAM, Apdo. Postal 70-399, 04510 México D. F., México. E-mail: jjm@hp.fciencias.unam.mx

Introduction

The superfamily Curculionoidea, with about 57,000 species and 6,000 genera described (Thompson 1992), is one of the largest and most diverse beetle groups. It constitutes, together with its sister group Chrysomeloidea, the largest radiation of phytophagous insects (Anderson 1995; Farrell 1998). The superfamily Curculionoidea is a monophyletic group, supported by both morphological and molecular data (Crowson 1955; Kuschel 1995; Farrell 1998). Among the most important apomorphy of the group is the 'head prolonged into a rostrum' (Morimoto 1962a; Kuschel & May 1990). This rostrum is extremely variable in shape and length and, despite several taxa with shortened rostra, a fairly well-developed rostrum is deemed to be ancestral in weevils (Crowson 1955). Other features present in weevils, such as the clubbed antennae of the adults and the hypopharyngeal bracon of the larvae, are plesiomorphic

(Kuschel & May 1990) but useful to distinguish weevils from members of the sister group Chrysomeloidea (Crowson 1955).

The higher systematics of Curculionoidea has received much attention during the last years (Thompson 1992; Zimmerman 1993, 1994a, b; Kuschel 1995; Marvaldi 1997) and is changing greatly on the basis of phylogenetic principles and the availability of new data sets, like those coming from immature stages or DNA sequences.

We review herein the larval and adult morphological information currently available and use it to define the families of Curculionoidea and smaller units within Curculionidae s.lat., and to undertake their cladistic analysis. The main aims of this study are: (1) to propose a new hypothesis of higher relationships of Curculionoidea; (2) to test the monophyly of the Curculionidae; and (3) to justify a revised higher classification. We discuss the mentioned clades and highlight areas where fur-

ther research might be done, with the hope that this work will provide a basis for further phylogenetic studies.

Historical account of weevil higher systematics

The first comprehensive classification of the Curculionoidea was made by Schoenherr (1823, 1826, 1833-1845, 1847), who divided the 'Curculionides' into Orthoceri (weevils with straight antennae) and Gonatoceri (weevils with geniculate antennae), the latter including legions Brachyrhynchi (broad-nosed weevils) and Mecorhynchi (long-nosed weevils). Within Curculionides, Schoenherr also included Bruchidae and excluded Scolytidae and Platypodidae. Lacordaire (1863, 1866) recognised five families of weevils: Curculionides, Scolytides, Brentides, Anthribides, and Bruchides. He classified Curculionides into Adelognatha (weevils with prementum covering maxillae) with six tribes, and Phanerognatha (weevils with prementum leaving maxillae exposed) with 76 tribes. Pascoe (1870) gave Lacordaire's 82 curculionid tribes subfamily status, becoming the framework for weevil classification for decades (Gemminger & Harold 1871a-c; Sharp 1889-1911; Champion 1902-1911; Junk & Schenkling's *Coleopterorum Catalogus* 1909-1953; Blackwelder 1947).

Among modern authors, Crowson (1955) had a major influence on weevil classification. He transferred Bruchidae (except Urodontinae) to Chrysomeloidea, treated several subfamilies of Curculionidae as distinct families (Oxycorynidae, Belidae, Apionidae, and Attelabidae), and demoted Scolytinae and Platypodinae to subfamilies of Curculionidae. Crowson (1955) recognised nine families of Curculionoidea: Nemonychidae, Anthribidae, Belidae, Oxycorynidae, Aglycyderidae, Attelabidae, Brentidae, Apionidae, and Curculionidae. Later, Crowson promoted Urodontidae (1984) and Cimberididae (1986) to a separate family status.

Morimoto (1962a, b, 1976, 1978, 1981) discussed the phylogenetic value of several characters in a series of detailed comparative studies of Japanese Curculionoidea, and reinstated Scolytidae and Platypodidae as families distinct from Curculionidae. Morimoto (1962a) provided a cladogram depicting the following sequence among the studied families of Curculionoidea: Anthribidae, Attelabidae, Platypodidae plus Scolytidae, Rhyncho-

phoridae (= Dryophthoridae), Brentidae, and Curculionidae. Morimoto (1962a, b) merged Apionidae and Brentidae in a single family. In 1976, he promoted Ithyceridae to family status from Curculionidae. Based on the analysis of the mouth parts, Morimoto (1981) arranged weevil subfamilies into four groups: Anthribidae, Attelabidae, Scolytidae-Platypodidae, and Apionidae-Brentidae-Curculionidae-Dryophthoridae.

Other important contributions were made during 1970-1990. Muñiz (1970) outlined a phylogenetic arrangement of Curculionoidea, based mainly on the rostrum length, type of oviposition, and taxonomy of the host plants. Sanborne (1981) estimated the cladistic relationships of some families of 'higher weevils', suggesting that the placement of Ithyceridae is close to Brentidae-Apionidae-Curculionidae, and promoting Antliarhinidae to family status. Wood (1986, 1993) reviewed the characters, status and position of Scolytidae and Platypodidae, concluding that they are very closely related and that both should be treated as valid families, placed among the 'primitive' families of Curculionoidea. Burrini et al. (1988) analysed the sperm structure of several representatives of the Curculionoidea, finding diagnostic characters for several taxa, and concluded that the group was monophyletic, with Rhynchitidae being the sister taxon to Apionidae plus Curculionidae. Calder (1989, 1990) undertook comparative morphological studies of the alimentary canal and the nervous and reproductive systems of several weevil taxa, finding a basic distinction between 'primitive' weevils (Nemonychidae, Anthribidae, Belidae, and Attelabidae) and the 'higher' weevils (Ithyceridae, Brentidae, Apionidae, Platypodidae, and Curculionidae). Calder's (1990) morphological study on male and female reproductive systems supported the placement of Scolytinae within Curculionidae, whereas Platypodidae were considered as a distinct family.

Thompson (1992) gave a major impetus for the classification of Curculionoidea, based on detailed and clearly illustrated morphological studies, particularly of the abdomen, deciduous mandibular processes, tibiae, and male genitalia. Several changes proposed by Thompson involve weevil taxa of familial or subfamilial rank, e.g., Brachyceridae, Erihynidae, Cryptolar yngidae, and Raymondionymidae are promoted to family status from Curculionidae; Antliarhinidae are treated as a subfamily of Brentidae; Allocoryninae are treated

as a subfamily of Oxycorynidae; and the subfamily Carinae is erected as new and assigned to the Belidae. Thompson re-defined the Curculionidae in a more strict sense, as including 'entirely and exclusively' those weevils with the derived (gonatoceros) type of male genitalia. The 16 families recognised by Thompson (1992) are Aglycyderidae, Anthribidae, Attelabidae, Belidae, Brachyceridae, Brentidae, Cryptolaryngidae, Curculionidae, Dryophthoridae, Erihrinidae, Ithyceridae, Nemonychidae, Oxycorynidae, Platypodidae, Raymondionymidae, and Urodontidae.

Zimmerman (1993, 1994a, b) provided some modifications to the classification of the Curculionoidea, proposing the Heteromorphi, a 'division of convenience' between the traditional Orthoceri and Gonatoceri. Zimmerman's Orthoceri are the families Aglycyderidae, Allocorynidae, Anthribidae, Antliarhinidae, Apionidae, Attelabidae, Belidae, Brentidae, Caridae, Eurhynchidae, Ithyceridae, Nemonychidae, Oxycorynidae, Pterocolidae, and Rhynchitidae; the Heteromorphi are Erihrinidae, Nanophyidae, and Dryophthoridae; and Gonatoceri are Curculionidae and Platypodidae.

May (1993, 1994) provided two major works on the immature stages of weevils. Her detailed descriptions and illustrations of larval characters allowed recognition and definition of several major groups of Curculionoidea. May's contributions on immature weevils provided valuable evidence, incorporated in Kuschel's (1995) cladistic analysis, that helped to clarify the relationships of several higher taxa, particularly of the 'orthoceros' groups.

Kuschel (1995) presented the first formal cladistic analysis of the Curculionoidea to families and subfamilies. Within Curculionoidea, Kuschel recognised (in phylogenetic sequence) the families Nemonychidae, Anthribidae (incl. Urodontinae), Belidae (incl. Oxycoryninae and Aglycyderinae), Attelabidae (incl. Rhynchitinae), Brentidae (incl. Apioninae, Carinae, and Cyladinae), and Curculionidae. The latter comprises only six subfamilies: Brachycerinae, Curculioninae, Rhynchophorinae (= Dryophthorinae), Cossoninae, Scolytinae, and Platypodinae.

Zherikhin & Gratshev (1995) reclassified the Curculionoidea on the basis of a comparative study of the hind wing venation. They recognized the following families: Nemonychidae, Urodontidae, Anthribidae, Belidae, Ithyceridae, Oxycorinidae, Allocorynidae, Aglycyderidae, Brentidae, At-

telabidae, Brachyceridae, Barididae and Curculionidae.

Lawrence & Newton (1995) presented an annotated classification of Curculionoidea, and summarized and discussed most recent changes in composition of the higher groups. They follow Kuschel's (1995) scheme to families and subfamilies, except for the recognition of Ithyceridae and Caridae as distinct families.

Lyal & King (1996) made a comparative morphological study of the elytro-tergal stridulation in Curculionoidea, illustrated with scanning electron micrographs representing the taxonomic variation. They found that the elytro-tergal stridulation in Curculionoidea is restricted to some members of Curculionidae (only in some phanerognath subfamilies), Scolytidae and Platypodidae. Evidence from the stridulatory system supported the placement of Scolytinae within Curculionidae, whereas Platypodidae were kept as a distinct family, because the quite different structure of the platypodid elytral file and tergal plectrum provided equivocal evidence of homology with curculionids.

Marvaldi (1997) undertook a higher-taxon cladistic analysis of the Curculionidae s.lat., based mainly on larval characters. It dealt with relationships of the 'higher weevils' which were less understood than those of the 'primitive' ones. Results of her study show the non-monophyletic nature of Kuschel's (1995) subfamily Brachycerinae, this being an assemblage of different groups of broad-nosed weevils: Ithycerinae, Microcerinae, Brachycerinae s.str. (these forming a basal grade of 'orthoceros' weevils), while several others, namely Thecesterninae, Amycterinae, Aterpinae, Gonipterinae, Rhytirrhininae and Entiminae, are within the 'more advanced' Curculionidae s.str. In Marvaldi's (1997) study the immature characters support a close relationship between Dryophthorinae and Platypodinae.

Farrell (1998) undertook a quantitative phylogenetic analysis of the Phytophaga Chrysomeloidea plus Curculionoidea, based on DNA sequences (from the 18S ribosomal subunit gene), and complemented by a morphological matrix (data on weevils compiled from Kuschel's (1995) paper). The weevil families represented in Farrell's study are, in phylogenetic sequence: Nemonychidae, Belidae, Attelabidae, Brentidae, Rhynchophoridae and Curculionidae.

Morrone (1998a) presented an annotated classification of Curculionoidea, discussing previous

changes in composition of the higher groups. He basically followed Kuschel's (1995) scheme to families and subfamilies, except for the recognition of Caridae, Brachyceridae (incl. Cryptolarynginae and Desmidophorinae), Ithyceridae, Eirrhinidae, Dryophthoridae, and Platypodidae as distinct families.

Ingroup taxa

The terminal taxa of our study partially conform to current classifications of Curculionoidea (Thompson 1992; Zimmerman 1993, 1994a, b; Kuschel 1995; Lawrence & Newton 1995; Morrone 1998a). In the present analysis the concept of Brentidae is less inclusive than in Kuschel (1995) by treating Caridae as a distinct family, because it appears to be more distantly related to Brentidae (May 1994; Kuschel et al. 1994). The family Curculionidae s.lat. is herein represented by smaller units that are not equivalent to Kuschel's (1995) six subfamilies, reflecting our personal perspective based mainly on evidence provided by Thompson (1992), Zimmerman (1993, 1994a,b), and Marvaldi (1997).

The 13 terminal units represent extant taxa. To these might be added the extinct Mesozoic families Obrieniidae and Eobelidae. The Obrieniidae, described for fossils from the Triassic of Asia, represent the oldest curculionoids known so far (Zherikhin & Gratshev 1993), whereas the Eobelidae, described by Arnoldi (1977) for several taxa found in late Jurassic beds from Karatau (Kazakhstan), has been usually considered to be closely related to Belidae (Arnoldi et al. 1977; Zimmerman 1994a: 243; Zherikhin & Gratshev 1995). Kuschel (1983, 1995), however, assigned them to Nemonychidae. We decided not to include fossils in the present analysis, as too many characters would have to be coded as missing.

A brief discussion of the circumscription of the taxa analysed and the possible autapomorphies justifying their monophyly is given.

Nemonychidae

The family Nemonychidae is small and with a highly relictual distribution (Kuschel 1983, 1995; Morrone 1996). According to Kuschel (1995), the Nemonychidae comprise three extant subfamilies: Nemonychinae, Rhinorhynchinae, and Doydirhynchinae.

Monophyly of the Nemonychidae is supported by autapomorphies of the larvae: frons produced forward forming a pseudoclypeus, and mandibles with a diagonal masticatory ridge (May 1993), and of the adults: male tergite 9 desclerotized to a narrow, wellpigmented, sharply defined band arching over sternite 9 (Kuschel 1995). The indistinct frontoclypeal suture found in all known nemonychid larvae, however, is not exclusive to them, because it has been also described for some representatives of the three anthribid subfamilies (May 1993, 1994), which could suggest a common ancestor relationship of these taxa, rather than a case of convergence. Furthermore, such an indistinct suture also occurs in larvae of the chrysomeloid family Megalopodidae (Monrós 1955; Kuschel & May 1990, 1996), where their convergence was proposed based on the similar pollen feeding habits of these beetles (Kuschel & May 1990).

Anthribidae

Commonly known as 'fungus weevils', they are predominantly distributed in tropical and subtropical areas (Holloway 1982). Many adult Anthribidae browse on fungi and lichens, others are pollen feeders, whereas larvae develop in fungi, lichens, seeds, stems, bark, or wood. The Urodontinae were given family rank by Crowson (1984), and restored as a subfamily of Anthribidae by Kuschel (1995). The Anthribinae may end to be paraphyletic with respect to Choraginae, because no autapomorphy was found to support its monophyly (Kuschel 1995), and this was also suggested by Zherikhin & Gratshev (1995) based on characters of the hind wing. Until Anthribinae monophyly is tested, which is out of the scope of the present paper, we follow Kuschel (1995) in that the family Anthribidae comprises three subfamilies: Urodontinae, Anthribinae, and Choraginae.

Monophyly of Anthribidae is supported by the larval possession of more than five setae on the frons (excessive number of setae also found in areas of thorax and abdomen). Nemonychid larvae have also been reported to have more than five frontal setae (e.g. May 1993), but in this case it appears that it is just because the setae of the clypeus (added to the frons) have also been counted. An adult autapomorphy is the notosternal suture represented by a weak and transverse line extended vertically to the notum (Zimmerman 1994a; Kuschel 1995).

Belidae

The family Belidae is a relictual group, with 24 genera and 295 species, basically ranged in the Holotropical and Austral regions (Kuschel 1959; Vanin 1976; Thompson 1992; Morrone 1996). Species of Belidae are associated with conifers, e.g., Araucariaceae, Cupressaceae, and Podocarpaceae; Pteridophyta, e.g., Blechnaceae, Cyathaceae, and Polypodiaceae (Kuschel 1959; Vanin 1976); association with angiosperms is shown by most Australian species of Belini and by some Oxycoryninae and Aglycyderinae (Kuschel 1995). Kuschel (1995) assigned Aglycyderinae and Oxycoryninae, previously treated as separate families, to the Belidae.

The monophyly of this 'enlarged' concept of Belidae is supported by larval and adult autapomorphies: larvae with head deeply and permanently retracted, attached to prothoracic shield by heavy musculature (May 1993, 1994); adults have the fore tibiae with a broad apical groove or impression clothed in fine, dense vestiture on the inner face opposite the tarsal articulation; and the spermatheca is strongly atrophied (small, membranous and sickle-shaped) to absent (Kuschel 1995).

Attelabidae

This family includes the 'leaf-rolling weevils', and comprises about 2000 species, predominantly ranged in the Northern Hemisphere, which are mostly associated with dicotyledonous angiosperms. The oldest known fossils attributable to Attelabidae are from Middle or Upper Cretaceous (Kuschel 1995). Zimmerman (1994a) gave separate familial status to Rhynchitinae and Pterocolinae. The former were regarded as a subfamily of Attelabidae (Thompson 1992; Kuschel 1995), and the latter as a subfamily of Attelabidae (Thompson 1992) or as a synonym of Rhynchitinae (Kuschel 1995).

Attelabidae comprise two subfamilies: Attelabinae and Rhynchitinae (Kuschel 1995), joined by synapomorphies from the larvae: with the epicranium bearing a hyaline posterior extension (May 1993), and from the adults: males with the 8th sternite fused or articulated to 9th sternite on each side beyond the arms (Kuschel 1995). In addition, the attelabids share an 'advanced' nervous cord, with the abdominal ganglia fused to one conglomerate (Calder 1989).

Caridae

Species of this family develop on strobili of coniferous Cupressaceae, comprising five extant genera: *Car* and *Carodes* from Australia and Tasmania, *Chilecar* from southern Chile, *Caenomiturus* from southern Argentina, and an unnamed genus from New Guinea (Zimmerman 1994; Morrone 1996). Fossils attributable to Caridae have been described from the Jurassic (Zherikhin & Gratshev 1995) and also from the Lower Cretaceous (Kuschel 1983; Zimmerman 1994). Different authors have included *Car* and related taxa in different families, e.g., Attelabidae (Crowson 1955), Apionidae (Wibmer & O'Brien 1986), Belidae (Thompson 1992; Zherikhin & Gratshev 1995), Curculionidae (Kuschel et al. 1994), and Brentidae (Kuschel 1995).

Monophyly of Caridae is supported by the adults having only five pairs of abdominal spiracles, those of 6th and 7th segments being absent (Kuschel 1992, 1995), and also probably by their club-like spermathecal gland (Calder 1990). A possible larval autapomorphy is the presence of claws in the segmented legs, a feature not found so far in any other curculionoid with the exception of *Nemonyx* (May 1994).

Brentidae

The original concept of Brentidae was widened by several authors (Morimoto 1976; Kuschel 1990, 1995; Thompson 1992) to include Eurhynchinae, Antliarhininae, Cyladinae, Apioninae, and Nanophyinae (and also Carinae in Kuschel 1995). Based on the dubious position of the Caridae, we preferred to keep them as a separate family, in order to determine their proper placement, but kept the remainder taxa in the family Brentidae.

The monophyly of Brentidae is supported by the adult ventrites 1-2 more convex and protruding than the 3rd, and by the labial palpi with a reduced number of 2 to 1 segments (Kuschel 1995).

Curculionidae

There have been considerable changes in the suprageneric taxa included in this family, specially in the last decades, and several taxa have been promoted to separate families: Dryophthoridae (Morimoto 1962a, b, 1978), Ithyceridae (Morimoto 1976; Sanborne 1981; Lawrence & Newton 1995), Erihinae (Thompson 1992; Zimmerman 1993), Brachyceridae, Cryptolaryngidae, Raymondiony-

midiae, and Platypodidae (Thompson 1992). Kuschel (1995) demoted dryophthorids and platypodids to subfamilies of Curculionidae, and merged most traditional subfamilies in his subfamilies Brachycerinae and Curculioninae. Kuschel (1995) recognised only six subfamilies: Brachycerinae (for the former Adelognatha and some subfamilies of Phanerognatha), Curculioninae (including most traditional phanerognathan subfamilies, Rhynchophorinae (= Dryophthorinae), Cossoninae, Scolytinae, and Platypodinae. This classification goes against other phylogenetic arguments presented by Thompson (1992) and Zimmerman (1993), and is not supported by further phylogenetic studies (Marvaldi 1997). In the present paper we consider the more inclusive concept of the family Curculionidae (Kuschel 1995), the Curculionidae s.lat., represented by smaller units in the analysis (see below). If the name 'Curculionidae' is used in a more restricted sense, then these units would require being treated with family rank, as in other classifications (e.g. Thompson 1992; Zimmerman 1993; Morrone 1998a).

Ithycerinae

The subfamily Ithycerinae comprises the single monotypic genus *Ithycerus*, from eastern USA and Canada (Sanborne 1981). Although Ithycerinae were originally described as a subfamily of Curculionidae, Morimoto (1976) promoted them to family status, which was further supported by Sanborne (1981), Thompson (1992), Lawrence & Newton (1995), and Morrone (1998a). Kuschel (1995) placed *Ithycerus* within Curculionidae Brachycerinae, but Marvaldi (1997) showed that the other taxa placed in Brachycerinae are more closely related to other weevils than to Ithycerinae.

The larva of *Ithycerus* shares with those of other curculionids the apomorphic incomplete frontal lines (May 1993). The Ithycerinae have a reduced number of Malpighian tubules in larvae and adults, like in Brentidae (May 1993; Calder 1989), and the adults have unique derived characters in male genitalia (Sanborne 1981; R. Thompson, pers. comm.) and in the hind wings (Zherikhin & Gratshev 1994).

Microcerinae, Brachycerinae, and Ocladiinae

These three taxa have been considered as belonging to Curculionidae Brachycerinae (Kuschel 1995) or as subfamilies of Brachyceridae (Thompson 1992; Morrone 1998a). We have not found any

clear synapomorphy to join these taxa. Based on data currently available, it is more convenient to treat them separately.

The Microcerinae constitute a morphologically distinct group (Louw 1986), and the labial palpi set in pits or grooves is considered a good adult apomorphy for this taxon (Thompson 1992: 881). Several microcerine larval characters, described by Louw (1995), suggest a basal placement of the taxon with respect to Brachycerinae s.str. and the Curculionidae s.str. (Louw 1995; Marvaldi 1997).

The Brachycerinae have an apomorphic condition at the larval stage: a completely flat, not protruding, antennal sensorium (Marvaldi 1997). The deciduous mandibular processes found in most adult brachycerines are not unique for this taxon (Thompson 1992), and thus can not be presented as autapomorphic.

With respect to Ocladiinae (= Desmidophorinae), we agree that *Ocladius* and its allies are closely related to *Desmidophorus* (Thompson 1992). In the absence of counter-evidence, we consider as representative of the subfamily the larval characters of *O. dianthi* (Marvaldi, in press a), the only species for which larvae are known. Although larval characters remain unknown for the problematical orthocerous Cryptolarynginae, we propose to assign them tentatively to Ocladiinae. *Cryptolarynx* and its allies share with the latter similar male and female genital characters (illustrated by Thompson 1992), and externally they also resemble the Ocladiinae because of their globose body and the rostrum in repose being retractable in a prosternal furrow. The distinct lacinia and galea of *Cryptolarynx* is almost certainly an apomorphic reversal, and does not denote the primitiveness of the group, whose other characters place it closer to Curculionidae.

Dryophthorinae

Formerly known by their junior synonym Rhynchophorinae, they have been either considered as a distinct family (Morimoto 1962a, b, 1978; Thompson 1992; Zimmerman 1993; Morrone 1998a) or as a subfamily of Curculionidae (Kuschel 1995). The Dryophthorinae include the following tribes (Kuschel 1995): Cryptodermatini, Dryophthorini, Orthognathini, Rhinostomini, Rhynchophorini, Siophilini, Sphenophorini, and Stromboscerini.

The Dryophthorinae are easily recognised at the

adult stage by the autapomorphic antennal club, which is shiny and spongiform at the apex, the funicle always having less than seven segments. Thompson (1992: 876) proposed that the club is in fact the enlarged funicular article 7, into which the 'true' club has been compressed. Monophyly of this taxon is supported by several other adult features: prementum not visible in ventral view, inflexed over postmentum (Thompson 1992, Kuschel 1995); presence of dorsal and ventral dermal lobes separating tarsal claws (Zimmerman 1993); aedeagal pedon (male genitalia) with a lateral line or groove (Morimoto 1962a); tegminal dorsal plate absent and replaced by the membranes of 9th segment (Thompson 1992). Many apomorphic larval features defining the Dryophthorinae, such as the head bearing a posterior lamina with apodemes, some setae of the epipharynx or maxillae branched, and the abdominal pleura subdivided into two or more superimposed lobes, are also found in the Platypodinae (Marvaldi 1997), at least in the known larvae of Platypodini (sensu Wood 1993).

Eriirhininae

Most members of the Eriirhininae are aquatic or semiaquatic, with larvae host-specific to water plants, horsetails, and mosses, and represent the most successful aquatic group of weevils (Kuschel 1971). Both Thompson (1992) and Zimmerman (1993) gave familial status to this taxon, whereas Kuschel (1995) demoted them to a tribe of his enlarged concept of Curculioninae. Independently of the rank assigned, authors accept the concept of Eriirhininae restricted by Kuschel (1971, 1987a) to include only those species with male genitalia of the orthocerous type. According to Zimmerman (1993: 135) they also include the Australian Tadiinae, and Kuschel (1995) proposed that Raymondionyminae (Osella 1977) are hypogean relatives of the eriirhinines. Unfortunately, larvae of these taxa remain unknown to test this assignments.

The Eriirhininae are externally very similar to members of the more 'advanced' Curculionidae s.str. (Thompson 1992). They have retained the plesiomorphic (orthocerous type) male genitalia, but possible apomorphic conditions are that the tectum of the aedeagus, although present, is represented by a narrow strip or is membranous; and the rostrum in lateral view is strongly deflexed ventrad from its base, a feature paralleled in some Dryoph-

thorinae and some Curculionidae s.str. (Thompson 1992). The hind wing of most 'true' eriirhinines studied by Zherikhin & Gratshev (1995: 771) share the proximal radial sclerite reduced and fused to the stigmal patch.

Curculionidae s.str.

This terminal unit is the largest group of weevils and is in agreement with the restricted concept of Curculionidae of Thompson (1992) and Zimmerman (1993, 1994a,b), including those weevils with the derived (gonatocerous) type of male genitalia. It is worth noting that the Platypodinae have been considered by several authors (Calder 1990; Thompson 1992; Zimmerman 1993; Morrone 1998a) as a distinct family. New analyses (Farrell 1998), however, indicate that Platypodinae are best included in the Curculionidae s.str., as proposed by Crowson (1955) and Kuschel (1995). Because the male genitalia of the Platypodinae are so reduced and simplified, the synapomorphic genital features defining the Curculionidae (see below) are not easily recognised in this taxon.

The recognition of monophyletic subfamilies within the Curculionidae s.str. remains unsatisfactory. Different subfamily arrangements are found in recent major works on the classification of weevils (Thompson 1992; Zimmerman 1992, 1994a; Kuschel 1995). Because elucidation of the monophyly and relationships of the subfamilies within this unit is out of the scope of this paper, we simply list the principal subfamilies in current use: Baridinae, Brachyceropsidinae, Cossoninae, Curculioninae (sensu Zimmerman 1994a, an arrangement, rather coincident with Thompson's [1992: 874] informal group 'Curculiones longirostres', of several traditional subfamilies demoted to tribes, mainly: Anthonomini, Camarotini, Ceutorhynchini, Cionini, Curculionini, Derelomini, Eugnomini, Gymnetrini, Otidocephalini, Rhamphini [= Rhynchaenini], Smicronychini, Storeini, Tachygonini, and Tychiini), Cryptorhynchinae, Cyclominae (sensu Morrone 1997b, 1998b, including: Amycterini, Aterpini, Cyclomini [= Hipporhinini], Diabathrariini, Gonipterini, Haplopodini, Rhytirrhini, and Somatodini; although their monophyly is not sufficiently tested yet, see also Marvaldi 1997), Entiminae (Thompson 1992; Marvaldi 1997, 1998), Lixinae (= Cleoninae), Magdalinae, Molytinae (sensu Kuschel 1987b, see also Thompson 1992), Phytominae (= Hyperinae),

Platypodinae, Scolytinae, Thecesterninae, Ulo-mascinae, and Zygotinae.

The monophyly of Curculionidae s.str. is supported by the autapomorphic male genitalia (Mormoto 1962a; Thompson 1992; Zimmerman 1993): the tectum or dorsal plate of the aedeagus is lacking; the dorsal plate (parameral sector) of the tegmen is reduced to a pair of weak asetose lobes or absent; the apodemal bridge of the aedeagus is absent; and the manubrium (apodeme of tegmen) is smaller than the spiculum gastrale (apodeme of 9th sternite).

Outgroup

The Palophaginae, one of the most basal taxa of the Chrysomeloidea (Kuschel & May 1990, 1996; Reid 1995; Farrell 1998) was used as outgroup.

Characters

The characters were assembled from published information on both larvae and adults. The data matrix is given in Table 1.

The lists of morphological characters of Kuschel (1995) and Marvaldi (1997) provided us a framework to look for informative characters, and on that basis we construct a revised and enlarged list. As the present paper deals with families of Curculionoidea, a great proportion of the characters used by Kuschel (1995) are incorporated into our analysis, though not always with the same coding strategies. These characters are indicated between square brackets in our list, with the number as in Kuschel's list preceded by a 'K'. In addition, we have now been able to incorporate new characters, like those for the larvae of Caridae (May 1994) and of Ocladiinae (Marvaldi, in press a) that were unavailable when Kuschel (1995: 19)

Table 1. Data matrix used in the cladistic analysis of Curculionoidea. Characters are listed under the heading 'Characters'.

	Characters 1-50				
Palophaginae	00000000?0	0100000001	0000000000	0000000000	0000000000
Nemonychidae	0001010000	0110000100	0000?00010	0000010100	0000000000
Anthribidae	0001021000	0?0000?000	0000100010	0000000100	0000000000
Belidae	1000000010	0000001011	0002101010	0000000101	1010100000
Attelabidae	0100000010	000100101?	0002100010	01000?0101	1010100100
Caridae	0011010?10	0001001011	1000001010	0100000101	1011110100
Brentidae	0001030010	0001001011	11?0101010	01?0010101	1011110101
Ithycerinae	0011020010	0001001011	1100101010	0111000111	1011110100
Microcerinae	00110?0??? ?0?0???1???		1??110?010	0111000111	1011110110
Brachycerinae	0011130010	0001001011	1112111010	0111000111	1111110100
Ocladiinae	0011030110	0001001011	1112111011	0111100111	1?11110100
Dryophthorinae	001103011?	1001111011	1112110110	0111101111	1011111100
Erihinae	0011030111	0001101011	1112111010	1111100111	1011110100
Curculionidae s. str.	0011030111	0001101011	1112111010	0111100111	1011110100
	Characters 51-100				
Palophaginae	0000000000	0000000000	0000000000	0000000000	0000000000
Nemonychidae	0000000010	01?000?0??	0000000101	2000000000	00000?0011
Anthribidae	1??0100110	0110100011	0000101000	10000000?0	00000??1?1
Belidae	00?0000000	0??0?1000?	0000000?00	10000000?0	01100?1001
Attelabidae	0?10100100	000?000?0	0100001011	1000000011	1010001121
Caridae	0101110200	0110000001	0000010000	1010010001	1010001111
Brentidae	0111111200	0110?0000?	0111000100	10100100?1	1011011111
Ithycerinae	0111111200	0111101?00	0101001100	1010010001	1021011111
Microcerinae	011111????	?111101?00	0101000000	101001??11	1021??11?1
Brachycerinae	011111????	?111101?00	0101000100	101001??11	1021?011?1
Ocladiinae	0111111201	0111101?00	0101000?00	101001?0?1	10210?11?1
Dryophthorinae	0111111201	1111101100	1101?01001	1011130011	1021101111
Erihinae	0111111201	1111101100	0101000100	1020011011	1021101111
Curculionidae s. str.	0111111201	111?1011?0	0101000101	1130021111	1021101111

and Marvaldi (1997: 304) undertook their respective analyses. Information on the larvae and adults of the outgroup Palophaginae was taken from Kuschel & May (1990, 1996), with the exception of characters 94, 98-100 that were inferred according to the states found in other Chrysomeloidea (Calder 1989, 1990; Reid 1995).

We are aware that many characters, particularly those of the internal adult morphology and from the larvae, are known from a relatively small sample of species per family or subfamily. In the absence of counter-evidence we extrapolate these character states to the whole taxon. Similarly, we use characters that weevil workers have indicated as diagnostic for a given higher-taxon.

We found various characters that are variable within some families. When possible, we determined the groundplan condition based on previous phylogenetic studies (Kuschel 1995; Marvaldi 1997). Also, since most of these characters from larvae (e.g. number of antennal segments, stemmata, labral setae, and leg segments) and from adults (e.g. number of labial palpi, wing veins, Malpighian tubules) obviously involve loss or reduction, we scored the most complete state found in the taxon.

Larvae (characters 1-28)

The larval characters have been compiled from recent contributions by May (1993, 1994) particularly for the families Nemonychidae, Anthribidae, Belidae, Attelabidae, Caridae, and Brentidae, and by Marvaldi (1997, in press a) mainly for Ithycerinae, Microcerinae, Brachycerinae, Ocladiinae, Dryophthorinae, Eirrhinae, and Curculionidae s.str. General information and illustrations on larval morphology can be found in Lawrence (1991) for Coleoptera, and in Anderson (1991), May (1994), and Marvaldi (in press b) for weevils.

Head

1. Head: (0) extrusible; (1) permanently retracted. [K20].
2. Epicranium: (0) without posterior extension; (1) with hyaline posterior extension. [K31].
3. Frontal lines: (0) complete, extending to mandibles; (1) incomplete, not extending to mandibles. [K39].
4. Antennae: (0) 3-2-segmented; (1) 1-segmented. [K87].
5. Antennal sensorium: (0) convex, protruding; (1) flat, not protruding at all.
6. Number of stemmata or eye spots on each side of head capsule: (0) 6; (1) 4; (2) 3; (3) 2 or less. [K78]. The maximum number of stemmata found within each family (according to May 1993, 1994) was

scored, as the most plesiomorphic state in this loss sequence. When there are 6 stemmata, 3 of them are anterior near antenna, and in subsequent apomorphic states there is one primary stemma close to antenna.

7. Frons: (0) with 5 or fewer setae; (1) with more than 5 setae. [K12].
 8. Sensillum next to dorsoepicranial seta 2: (0) present; (1) absent.
 9. Hypopharyngeal bracon: (0) with sclerome; (1) without sclerome. [K13]. The bracon is absent in Chrysomeloidea, thus this character was coded following Anderson (1991: 161).
 10. Head: (0) without postoccipital condyles; (1) with postoccipital condyles. [K40]. Curculionidae s.str. = 1 (the condyles are obsolete or totally lost in wood-boring weevils like Cossoninae, Scolytinae, and Platypodinae).
 11. Head: (0) lacking postoccipital lamina with apodemes; (1) with such lamina. Curculionidae = 0 (Platypodini = 1).
 12. Frontoclypeal suture: (0) distinct; (1) effaced. Anthribidae = ? (several species = 0, several others = 1).
 13. Pseudoclypeus formed by the frons produced forward: (0) absent; (1) present.
 14. Labral scleromes: (0) lateral or tormae; (1) submedian or labral rods. [K21]. [Anderson 1991].
 15. Labrum: (0) with 4 pairs of setae; (1) with 3 or less pairs of setae. [K32]. Brentidae = 0 (reduction in the number of labral setae is frequent within Brentidae, e.g. Cyladinae or Apioninae, but because the maximum number of 4 setae is found in this family, it is deemed as the ancestral state; furthermore, a transitional condition, with the 4th pair of setae very small, is presented by some species, e.g. *Lasiorhynchus* sp. [A. Marvaldi, pers. observ.]).
 16. Setae on epipharynx and/or maxillae: (0) simple; (1) some branched or tufted. Dryophthorinae = 1 (Sitophilini = 0); Curculionidae s.str. = 0 (Platypodini = 1, but is 0 in relatively 'basal' Platypodinae: *Diapus* sp. [Gardner 1932: fig. 23]).
 17. Mandibles: (0) with mola; (1) lacking mola.
 18. Mandibles: (0) lacking diagonal masticatory ridge; (1) with such ridge. [K3].
 19. Maxillary articulatory lobes: (0) distinct; (1) absent. [K14].
 20. Maxilla: (0) with lacinial lobe or spine; (1) without lacinial lobe or spine.
 21. Maxillary palp: (0) 3-segmented; (1) 2-segmented. [K88]. Anthribidae, Belidae, and Attelabidae = 0 (some species = 1), being the most plesiomorphic state scored for these families.
 22. Maxillary palp: (0) with seta on last segment; (1) lacking seta on last segment. [K33].
- #### Thorax
23. Thoracic spiracle: (0) on mesothorax or intersegmental; (1) on prothorax. [K95].
 24. Legs: (0) present and segmented; (1) vestigial with faint segmentation; (2) absent.

Nemonychidae, Anthribidae, and Brentidae = 0 (several species in these taxa = 1 or 2, but irreversibility in this loss sequence is assumed, so the most plesiomorphic state was scored for each of these families [see also Marvaldi 1997: 303]).

25. Legs: (0) with claws; (1) without claws. [K48].

Abdomen

26. Abdominal segments: (0) with 2 folds; (1) with 3-4 folds. [81].
Brentidae = 0 (Brentinae = 1).
27. Spiracular airtubes of abdominal segments I-VII: (0) dorsally directed; (1) posterior or dorsoposteriorly directed.
Eirrhiniinae = 1 (species with spiracles adapted to plant piercing = 0).
28. Abdominal pleura: (0) entire; (1) subdivided in two or more superimposed lobes.
Curculionidae s.str. = 0 (Platypodinae = 1).

Adults (characters 29-100)

The characters of the adult external and internal morphology have been compiled from several studies or reviews by different authors (most of them cited in the historical account section of this paper). Particularly important publications here followed to character interpretation, other than Kuschel's (1995), are given under each character.

Head

29. Rostrum: (0) absent; (1) present. [Crowson 1955; Kuschel & May 1990; Reid 1995].
30. Rostrum in repose: (0) not retractable; (1) retractable in prosternal furrow. [Thompson 1992: 873, 881].
Eirrhiniinae = 0 (Tadiinae = 1 [Zimmerman 1993: 135]); and Curculionidae s.str. = 0 (Cryptorhynchinae and some others = 1).
31. Rostrum in lateral view: (0) not or weakly deflexed ventrad from its base; (1) strongly deflexed ventrad from its base.
Dryophthorinae = 0 (some species = 1); and Curculionidae s.str. = 0 (some species, e.g. Tychiini = 1). [Thompson 1992: 883].
32. Gular suture: (0) double; (1) simple. [K16]. [Lyal 1995].
33. Scrobe shape: (0) foveiform; (1) sulciform. [K100].
34. Scrobe depth: (0) shallow; (1) deep. [K116].
Brentidae = 0 (Cyladinae and Apioninae = 1).
35. Type of antennae: (0) orthocerous or straight; (1) geniculate. [K34].
Brentidae = 0 (Nanophyinae = 1).
36. Scape: (0) long, passing front margin of eyes; (1) short, not passing front margin of eyes. [K117].
37. Number of funicular segments: (0) 7 or less because of fusion of segments; (1) 6 or less, with the 7th added to the club. [K118]. [Thompson 1992: 876].
38. Antennal club: (0) indistinct; (1) distinct. [K72].
Belidae = 1 (Belinae = 0); Brentidae = 1 (Brentinae = 0).
39. Antennal club (segments 9-11): (0) first 2 or all 3

segments loosely articulated; (1) all segments tightly articulated or compact. [K35].

40. Clypeolabral suture: (0) distinct; (1) indistinct. [K4].
41. Mandibular mola: (0) present; (1) absent. [K6].
42. Deciduous processes on mandibles: (0) absent; (1) present. [Thompson 1992].
Curculionidae s.str. = 0 (most Entiminae = 1); Ocladiinae = ? (some = 1, *Ocladius* = 0).
43. Teeth on mandibular incissor area: (0) absent; (1) present. [K5].
44. Maxillary galea and lacinia: (0) distinct; (1) indistinct. [K27].
45. Maxillary palpi: (0) elongate, projecting antero-antero-lad; (1) short, not projecting.
46. Number of segments of maxillary palpi: (0) 4; (1) 3 or 2. [K28].
47. Prementum in ventral view: (0) visible; (1) not visible, inflexed over postmentum. [K82].
48. Labial palpi: (0) near base or middle of prementum; (1) near apex. [K17].
49. Labial palpi: (0) free; (1) set in pits or grooves. [Thompson 1992: 872, 881].
50. Number of segments of labial palpi: (0) 3; (1) 2 or 1. [K36]. [Zimmerman 1994a].
Attelabidae = 0 (the condition is rather indistinct in Attelabinae because the palps are atrophied); Caridae = 0 (except *Caenominurus* = 1, which appear to be an apomorphic taxon [Kuschel 1992], and since *Car* and *Carodes* both bear the plesiomorphic condition of 3 labial palpi, the groundplan for Caridae = 0).

Thorax, elytra, and hind wings

51. Notosternal suture: (0) at first transverse, then horizontally cephalad; (1) only transverse, vertically to the notum. [K8]. [Zimmerman 1994a: 6].
52. Elytral punctae: (0) irregularly punctata; (1) aligned to striae. [K49].
Nemonychidae = 0 (Rhinorhynchinae = 1).
53. Elytral erect sensory hairs: (0) present; (1) absent. [K73].
54. Scutellar striae: (0) present (unless elytra lacking striae); (1) absent on striate elytra. [K22].
55. Inferolateral flange of elytron: (0) absent; (1) present. [K18].
56. Inferolateral line or carina apicad from flange of elytron: (0) absent; (1) present. [K23].
57. Radial cross vein (R-m) in hind wings: (0) present; (1) vestigial or absent. [K75]. [Zimmerman 1994a: fig. 340; several examples figured in Zherikhin & Gratshev 1995].
58. Number of anal veins in hind wings: (0) 5; (1) 4; (2) 3 or fewer. [K24].
It is assumed irreversibility in this loss sequence, thus Nemonychidae = 0 (Rhinorhynchinae = 0, others = 1), and Belidae = 0 (Belinae = 0, others = 2).
59. Connection between vein CuA1 and cubito-anal cell(s): (0) present; (1) absent. [Reid 1995, after Kukulová-Peck and Lawrence 1993; several examples in figures of Zherikhin & Gratshev 1995].
60. Radial sclerite in hind wing: (0) single; (1) paired, two sclerites. [Zherikhin & Gratshev 1995: 768].
61. Point of origin of vein Rr in hind wings: (0) at the radial cell; (1) shifted so that it is placed at the ante-

rior portion of r-m. [Zherikhin & Gratshev 1995, their figure 89 shows condition in Dryophthorinae = 1].

Legs

62. Fore coxal cavity: (0) partially open laterally; (1) completely closed laterally. [K25].
63. Mid coxal cavity: (0) open laterally to pleurites; (1) closed laterally by meso- and metasternal lobes. [K26].
64. Tibial apex: (0) lacking mucro or uncus (at least in females); (1) mucronate and/or uncinata (at least on fore and middle tibiae) in both sexes. [K92]. [Thompson 1992].
65. Tibial spurs: (0) present; (1) absent or very rudimentary. [K91].
Rudimentary spurs exist in some Erihriniinae and in some Curculionidae s.str. (e.g. Entiminae).
66. Groove on fore tibiae on face opposite tarsal articulation: (0) absent; (1) present. [K15].
67. Tarsal segment 2: (0) projecting at apical angles; (1) rounded at apical angles. [K45]. Belidae = 0 (Aglycyderinae = 1)
68. Tarsal groove on dorsal edge of hind tibiae: (0) absent; (1) present. [K93].
69. Tarsal claws: (0) simple; (1) appendiculate with laminate expansion on small tooth near base. [K46].
Brentidae = 0 (Apioninae = 1).
70. Tarsal claws: (0) divergent; (1) divaricate. [K114].
71. Dorsal and ventral dermal lobes separating tarsal claws: (0) absent; (1) present. [Zimmerman 1993: 43].

Abdomen

72. Ventrites: (0) all free, with sutural areas membranous and extendible; (1) last 2 or 3 free, the others fused with sutural areas well pigmented and rigid. [K9].
The Anthribidae Urodontinae have free ventrites, as illustrated by Thompson (1992: fig. 6), but the condition in Anthribinae and Choraginae is quite different because the ventrites (except the last one, usually free) are 'braced' or partially fused, with pale non-extendible sutures (Kuschel 1995: 9, 29).
73. Relative position of ventrites 1-3: (0) ventrites 1-2 at same level with 3; (1) ventrites 1-2 more convex, more protruding than 3 in lateral view. [K97].
74. Relative length of ventrites 2 and 3: (0) similar; (1) 3 shorter than 2. [K96].
75. Shape of tergites 6 and 7: (0) medially not grooved; (1) medially grooved (one or both of them). [K10].
76. Number of abdominal spiracles: (0) 6-7 pairs; (1) 5 pairs. [K98].

Male abdomen

77. Male pygidium: (0) absent; (1) present. [Thompson 1992: 839, 840].
78. Male tergite 8: (0) concealed under tergite 7; (1) exposed beyond tergite 7. [K76]. [Thompson 1992: 840, 872].
Curculionidae s.str. = 1 (some taxa = 0, see Thompson's 1992 key).
79. Male sternite 8: (0) completely free; (1) fused or articulated to sternite 9 on each side beyond arms. [K29].

80. Plate of male sternite 8: (0) undivided; (1) divided to form paired hemisternites. [Thompson 1992].
81. Male tergite 9: (0) completely sclerotized; (1) only laterally sclerotized to completely membranous; (2) desclerotized to a narrow band over sternite 9. [K1].
Anthribidae = 1 according to El Sayed (1940) and Kuschel's (1995) data matrix, but tergite 9 is absent in males of Anthribidae of the Australian Region (Kuschel 1994: 568), and the male genitalia of anthribids of other regions remain almost unknown (Zimmerman 1994: 40).
82. Male genitalia: manubrium (apodeme of tegmen): (0) larger than spiculum gastrale (apodeme of sternite 9); (1) smaller than spiculum gastrale. [Thompson 1992; Zimmerman 1994a: 3].
83. Aedeagal dorsal plate or tectum: (0) large, of similar size than aedeagal pedon; (1) well developed but distinctly shorter than the pedon; (2) a narrow strip; (3) obsolete or absent. [Morimoto 1962a; Thompson 1992].
When the tectum is present (states 0, 1, 2), the male genitalia is referred as being of the 'orthocerous type', and when the tectum is absent (state 3) it is of the 'gonatocerous type'.
84. Lateral line or groove on aedeagal pedon: (0) absent; (1) present. [K130]. [Morimoto 1962a].
85. Tegminal ring, ventrally: (0) slender; (1) strong.
86. Tegminal dorsal plate (= cap piece or parameral sector of tegmen): (0) large, not bilobed, triangular or trapezoidal, anterior margin setose; (1) large, bilobed, often articulated to the basal piece, apical part hirsute or setose; (2) vestigial, reduced to a pair of delicate asetose lobes, or absent; (3) absent but replaced by the membranes of segment 9. [Morimoto 1962: 360, 361; Thompson 1992].
87. Insertion and relative position of aedeagal apodeme in lateral view: (0) dorsal, on line with aedeagal body axis; (1) lateral or ventral, deflexed from aedeagal body axis. [K131]. [See figures by Morimoto to 1962a].
88. Apodemal bridge of aedeagus: (0) present; (1) absent. [K55]. [Morimoto 1962a; Zimmerman 1993].

Female abdomen

89. Spiculum ventrale or apodeme of female sternite 8: (0) present; (1) vestigial or absent. [K63]. [Thompson 1992: 842].
90. Female tergite 9: (0) sclerotized, at least at margins; (1) completely membranous. [53]. [Kuschel 1994: 567, 568; Howden 1995: 57, 60, 61, 95].
Belidae = 0 (Aglycyderinae = 1); Anthribidae = 0.
91. Proximal hemisternites of ovipositor: (0) separated from distal hemisternites; (1) fused to distal hemisternites to one body. [K70]. [Several examples in Howden (1995)].
92. Spermatheca: (0) falciform, well pigmented; (1) not falciform, very reduced to absent. [K19]. [Calder 1990].
93. Spermathecal duct and gland: (0) on common atrium outside spermathecal body; (1) contiguous or subcontiguous on spermathecal body; (2) well apart on spermathecal body. [K11]. [Calder 1990].
94. Number of ovarioles per ovary: (0) 4 or more; (1) 2. [K30]. [Calder 1990].

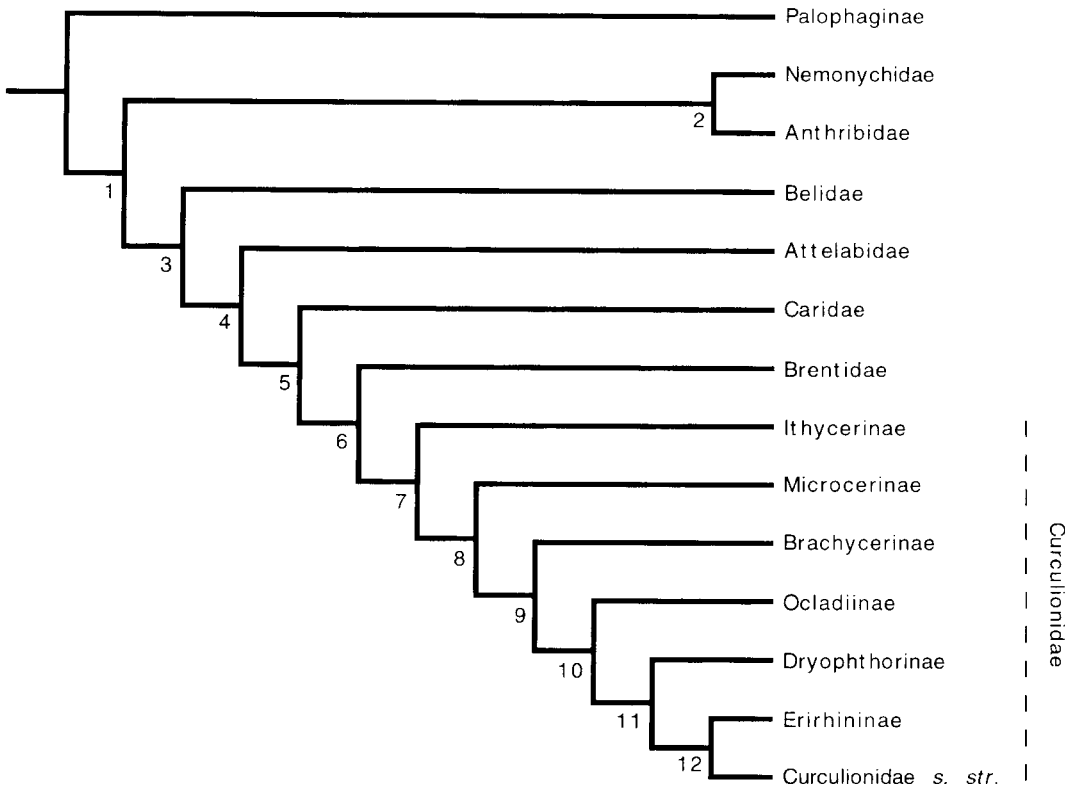


Fig. 1. Cladogram of Curculionoidea. See the text for characters diagnosing the nodes and terminal taxa.

Alimentary canal

95. Proventricular blades: (0) not developed; (1) well-developed. [K85]. [Calder 1989].
 96. Number of Malpighian tubules: (0) 6; (1) 4. [Examples of adults in Calder (1989), see also May (1993, 1994) for larvae].
 97. Rectal plates on hind gut: (0) present; (1) absent. [K67]. [Calder 1989].

Nervous system

98. Meso- and metathoracic ganglia of nervous cord: (0) separate; (1) fused. [Calder 1989].
 99. Ganglia in abdominal sector of nervous cord: (0) 3 or more free ganglia; (1) 2 to 1 free ganglia; (2) all ganglia fused in one conglomerate with thoracic ones. [K68]. [Calder 1989].
 Anthribidae = ? (three states present in the family, Choraginae = 0, others = 1 or 2); Brentidae = 1 (Apioninae and Nanophyinae = 2); Curculionidae = 1 (several taxa = 2). The groundplan is scored 1 for Brentidae and Curculionidae s.str., as this is the most plesiomorphic state of this fusion sequence found in these groups.
 100. Last abdominal ganglia of nervous cord: (0) 7-8 or 6-8 fused; (1) 5-8 fused. [Calder 1989; Reid 1995].

Cladistic analysis

The data (Table 1) were analysed using Hennig86 Version 1.5 (Farris 1988), applying the implicit enumeration option 'ie*'. The consistency index (CI) was calculated excluding uninformative characters (synapomorphies of the ingroup and autapomorphies of the terminal taxa). Multistate characters 81 and 86 were treated as non-additive ('cc-' option in Hennig86). The program Clados Version 1.1 (Nixon 1992) was used to examine character distributions.

As result of the analysis of the complete data matrix, one most parsimonious cladogram was obtained (145 steps, CI = 0.76 [or = 0.70 excluding uninformative characters], and RI = 0.84). The cladogram (Fig. 1) represent the following hypothesis of relationships to the weevil families: the clade Nemonychidae-Anthribidae is followed by the phylogenetic sequence: Belidae, Attelabidae, Cari-

dae, Brentidae, Ithycerinae, Microcerinae, Brachycerinae, Ocladiinae, Dryophthorinae, Eirrhiniinae, and Curculionidae s.str.

The nodes (labelled 1-12 in Fig. 1) and terminal taxa are diagnosed by the following characters (asterisks indicate parallelisms):

- Node 1: 25(1), 29(1), 38(1), 81(1), 100(1).
 Node 2: 4(1)*, 6(1)*, 20(0), 59(1), 62(1)*, 63(1)*, 99(1)*.
 Node 3: 9(1), 12(0), 17(1), 19(1), 41(1), 43(1), 45(1), 93(1), 97(1).
 Node 4: 14(1), 32(1), 48(1), 53(1), 55(1)*, 58(1)*, 90(1), 91(1), 98(1)*, 99(1)*.
 Node 5: 4(1)*, 6(1)*, 21(1), 27(1)*, 46(1), 54(1), 56(1), 58(2), 62(1)*, 63(1)*, 83(1), 86(1).
 Node 6: 6(2)*, 22(1), 57(1), 72(1)*, 74(1), 78(1)*, 94(1).
 Node 7: 3(1)*, 33(1), 34(1), 39(1), 64(1), 65(1)*, 67(1), 93(2).
 Node 8: 6(3)*, 24(1), 68(1), 89(1)*.
 Node 9: 23(1), 24(2)*, 26(1).
 Node 10: 8(1), 35(1).
 Node 11: 15(1), 61(1), 95(1).
 Node 12: 10(1), 83(2), 87(1).

Nemonychidae: 13(1), 18(1), 36(1)*, 78(1)*, 80(1)*, 81(2).

Anthribidae: 6(2)*, 7(1), 51(1), 55(1)*, 58(1)*, 65(1)*, 69(1), 70(1)*, 75(1), 77(1)*, 98(1)*.

Belidae: 1(1), 24(2)*, 27(1)*, 66(1), 92(1).

Attelabidae: 2(1), 24(2)*, 72(1)*, 77(1)*, 79(1), 80(1)*, 89(1)*, 99(2).

Caridae: 3(1)*, 25(0), 53(0), 70(1)*, 76(1).

Brentidae: 6(3)*, 36(1)*, 50(1), 73(1), 96(1)*.

Ithycerinae: 77(1)*, 96(1)*.

Microcerinae: 49(1), 78(0).

Brachycerinae: 5(1), 42(1).

Ocladiinae: 30(1).

Dryophthorinae: 11(1), 16(1), 27(0), 28(1), 37(1), 47(1), 71(1), 77(1)*, 78(0), 80(1)*, 84(1), 85(1), 86(3).

Eirrhiniinae: 31(1).

Curculionidae s.str.: 80(1)*, 82(1), 83(3), 86(2), 88(1).

Discussion

Results of the present analysis are in some respect similar to those of Kuschel (1995). The main differences are:

1. The sister group relationship of Nemonychidae and Anthribidae.
2. The Caridae as a distinct family and sister of the clade Brentidae - Curculionidae.
3. Although results of this study support the monophyly of Curculionidae sensu Kuschel, herein called Curculionidae s.lat., the present hypothesis is different with regard to the monophyletic groups and relationships within this clade, as already proposed by Marvaldi (1997) based mainly on larval characters.

Sister group relationship of Nemonychidae and Anthribidae

According to the cladogram (Fig. 1) the Anthribidae are hypothesised to be the sister taxon of Nemonychidae, as was suggested by Zherikhin & Gratshev (1995) based on evidence from the hind wing venation. Anderson (1947: 516) preferred to retain *Cimberis* (Nemonychidae: Doydirhynchinae) as part of the Anthribidae based on larval features. The sister relationship here proposed is not without doubt. The close relationship of Anthribidae with Nemonychidae is justified by their larvae with one-segmented antennae, and by a reduced number of stemmata, features paralleled in some Belidae (Oxycoryninae) and in the clade Caridae - Brentidae - Curculionidae, and by their larval maxillae with lacinial spine. Among adult characters, Nemonychidae and Anthribidae share an apomorphic feature of the hind wings. Several other characters that are common to both Nemonychidae and Anthribidae, e.g., distinct labrum at the apex of rostrum or the projecting and elongate maxillary palpi, although useful in keys to separate these taxa from other weevils (Thompson 1992; Kuschel 1995), are in fact symplesiomorphies, and thus uninformative about their close relationship.

An alternative placement for these families is provided by Kuschel (1995): Anthribidae follows Nemonychidae in the phylogenetic sequence, and is the sister group of the remaining weevil families, by sharing the male tergite 9 desclerotized to the sides (only laterally pigmented to completely membranous) (Kuschel 1995: 12). This hypothesis is not supported by our current data set and resulting cladogram (Fig. 1). The male tergite 9 (character 81) is autapomorphic in the nemonychids (depigmented to a narrow transverse band or arc) but, interestingly, their female tergite 9 (character 90) is sclerotized or desclerotized to the sides, suggesting a more conservative nature of females.

The phylogenetic placement of Anthribidae have not been tested yet using DNA sequences (Farrell 1998), but further molecular studies might clarify this problem. The fossil evidence currently available shows that both Nemonychidae and Belidae were present in Jurassic times (Zherikhin & Gratshev 1995), whereas fossils attributable to anthribids are unknown from the Mesozoic. This allows a possible origin of Anthribidae from a nemonychid-like ancestor, later than the divergence leading to Belidae-remaining families. The Beli-

dae together with the Nemonychidae are the only weevils that have retained the plesiomorphic condition of 'separate meso- and metathoracic ganglia of nervous cord'. In addition, at least the Belinae have also retained the plesiomorphic condition of 'three discrete abdominal ganglia of nervous cord', and together with Rhinorhynchinae, deemed as the most basal Nemonychidae (Kuschel 1995) have the ancestral number of five anal veins on the hind wings.

Caridae and Brentidae

The phylogenetic position of *Car* and its allies has remained enigmatic for a long time. May (1994) described for the first time the larval characters of *Car*, that were included herein in the cladistic analysis, and certainly helped to elucidate the phylogenetic placement of Caridae. In the present study Caridae are postulated to be a distinct family, as was also proposed by Zimmerman (1994a), but according to our analysis this family is phylogenetically placed as the sister taxon of the clade Brentidae plus Curculionidae s.lat. Brentidae sensu Kuschel (1995) are thus rendered monophyletic by excluding Caridae.

Larvae of *Car* have the apomorphic incomplete frontal lines, as found in the Curculionidae s.lat. According to the cladogram (Fig. 1), two equally parsimonious hypotheses can be proposed for the distribution of this character: that the incomplete frontal lines evolved independently in Caridae and in Curculionidae or that they have appeared once in the ancestor of the clade Caridae-Brentidae-Curculionidae and reverted to be complete in the Brentidae, while remaining incomplete in the Curculionidae.

Curculionidae s.lat. and Curculionidae s.str.

The sister clade of Brentidae is equivalent to the family Curculionidae sensu Kuschel (1995), referred herein as Curculionidae s.lat. Kuschel's resolution of the Curculionidae into six subfamilies implies that the gonatoceros type of male genitalia developed independently several times. The present cladistic analysis, in contrast, proposes that several taxa with the orthoceros male genitalia form a paraphyletic grade and that the gonatoceros male genitalia evolved only once and are synapomorphies supporting, and defining, the terminal Curculionidae s.str.

Acknowledgements

We especially thank Richard Thompson and Christopher Lyal for the critical reading of an earlier version of the manuscript. We also appreciate the help of Sergio Roig with literature and the assistance of Andrea Sequeira in the cladogram illustration. Support from the 'Consejo Nacional de Investigaciones Científicas y Técnicas' (Argentina) to A. Marvaldi is gratefully acknowledged.

References

- Anderson, R. S. (1995) An evolutionary perspective of diversity in Curculionoidea. *Mem. ent. Soc. Wash.* 14: 103-114.
- Anderson, W. H. (1947) Larvae of some genera of Anthribidae (Coleoptera). *Ann. ent. Soc. Am.* 40: 25-35.
- Arnoldi, L. V. (1977) Family Eobelidae L. Arnoldi fam. nov. In Arnoldi et al. (Ed.), *Mesoz. zhest.* 161: 144-176, Nauka, Moscow.
- Blackwelder, R. E. (1947) Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 5. *Bull. U.S. natn. Mus.* 185: 765-925.
- Burrini, A. G., Magnano, L., Magnano, A. R., Scala, C. & Baccetti, B. (1988) Spermatozoa and phylogeny of Curculionoidea (Coleoptera). *Int. J. Insect Morph. Embryol.* 17: 1-50.
- Calder, A. A. (1989) The alimentary canal and nervous system of Curculionoidea (Coleoptera): Gross morphology and systematic significance. *J. Nat. Hist.* 23: 1205-1265.
- Calder, A. A. (1990) Gross morphology of the soft parts of the male and female reproductive systems of Curculionoidea (Coleoptera). *J. Nat. Hist.* 24: 453-505.
- Champion, G. C. (1902-1906) Insecta. Coleoptera. Rhynchophora. Curculionidae. Curculioninae (part). *Biologia cent.-am.* 4 (4): 1-144 (1902); 145-312 (1903); 313-440 (1904); 441-600 (1905); 601-750 (1906).
- Champion, G. C. (1906-1908) Insecta. Coleoptera. Rhynchophora. Curculionidae. Curculioninae (part). *Biologia cent.-am.* 4(5): 1-136 (1906); 137-240 (1907); 241-400 (1908).
- Champion, G. C. (1909-1910) Insecta. Coleoptera. Rhynchophora. Curculionidae. Curculioninae and Callandrinae. *Biologia cent.-am.* 4 (7): 1-78 (1909); 79-212 (1910).
- Champion, G. C. (1911) Insecta. Coleoptera. Rhynchophora. Curculionidae. Otiorhynchinae. *Biologia cent.-am.* 4 (3): 178-354.
- Crowson, R. A. (1955) *The natural classification of the families of Coleoptera.* Lloyd and Co., London [reprinted 1967, Classey Ltd. Middlessex].
- Crowson, R. A. (1984) On the systematic position of *Bruchela* Dejean (*Urodon* auctt.) (Coleoptera). *Coleopt. Bull.* 38: 91-93.
- Crowson, R. A. (1986) The systematic position of *Nemonyx* Redtenbacher. *Entomologist's mon. Mag.* 121: 144.
- El Sayed, M. T. (1940) The morphology, anatomy and biology of *Araecerus fasciculatus* De Geer (Coleoptera: Anthribidae). *Bull. Soc. ent. Egypte* 24: 82-151.

- Farrell, B. D. (1998) 'Inordinate fondness' explained: Why are there so many beetles? *Science* 281: 555-559.
- Farris, J. S. (1988) *Hennig86, version 1.5*. Published by the author, Port Jefferson, New York.
- Gardner, J. C. M. (1932) Immature stages of Indian Coleoptera (11) (Platypodidae). *Indian Forest Rec.* (Ent. Ser.) 17 (3): 1-12.
- Gemminger, M. & Harold, E. von. (1871a) *Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus*. Vol. 8, Curculionidae, pp. 2181-2668. Gummi, Monachii.
- Gemminger, M. & Harold, E. von. (1871b) Berichtigungen und Zusätze zum Catalogus Coleopterorum synonymicus et systematicus. *Coleopt. Hefte* 7: 113-119.
- Gemminger, M. & Harold, E. von. (1871c) Berichtigungen und Zusätze zum Catalogus Coleopterorum synonymicus et systematicus. *Coleopt. Hefte* 8: 117-123.
- Holloway, B. A. (1982) Anthribidae (Insecta: Coleoptera). *Fauna N. Z.* 3: 1-264.
- Junk, W. & Schenkling, S. (Ed.) (1909/1953) *Coleopterorum Catalogus*. W. Junk; Berlin & 's-Gravenhage.
- Kukalová-Peck, J. & Lawrence, J. F. (1993) Evolution of the hind wing in Coleoptera. *Can. Ent.* 125: 181-258.
- Kuschel, G. (1959) Nemonychidae, Belidae y Oxycorynidae de la fauna chilena, con algunas consideraciones biogeográficas (Coleoptera Curculionoidea, aporte 28). *Invest. Zool. Chil.* 5: 229-271.
- Kuschel, G. (1971) Entomology of the Aucklands and other islands south of New Zealand: Coleoptera: Curculionidae. *Pacif. Ins. Monogr.* 27: 225-259.
- Kuschel, G. (1983) Past and present of the relict family Nemonychidae (Coleoptera, Curculionoidea). *Geographical J.* 499-504.
- Kuschel, G. (1987a) *Erirhininae Erirhinini (male genitalia of the orthoceri-group)*. Key to the genera of the world. Manuscript distributed by the author.
- Kuschel, G. (1987b) The subfamily Molytinae (Coleoptera: Curculionidae): General notes and descriptions of new taxa from New Zealand and Chile. *N. Z. Ent.* 9: 11-29.
- Kuschel, G. (1990) *Beetles in a suburban environment: A New Zealand case study*. DSIR Plant Protection Report 3: 1-118. New Zealand Department of Scientific and Industrial Research, Auckland.
- Kuschel, G. (1992) Reappraisal of the Baltic amber Curculionoidea described by E. Voss. *Mitt. geol.-paläont. Inst. Univ. Hamburg* 73: 191-215.
- Kuschel, G. (1994) Nemonychidae of Australia, New Guinea and New Caledonia. In Zimmerman's: *Australian weevils*, Vol. 1: 563-637. Melbourne, CSIRO.
- Kuschel, G. (1995) A phylogenetic classification of Curculionoidea to families and subfamilies. *Mem. ent. Soc. Wash.* 14: 5-33.
- Kuschel, G. & May, B. M. (1990) Palophaginae, a new subfamily for leaf-beetles, feeding as adult and larva on *Araucaria* pollen in Australia (Coleoptera: Megalopodidae). *Invertebr. Taxon.* 3: 697-719.
- Kuschel, G. & May, B. M. (1996) Discovery of Palophaginae (Coleoptera: Megalopodidae) on *Araucaria araucana* in Chile and Argentina. *N. Z. Ent.* 19: 1-13.
- Kuschel G., Oberprieler, R. G. & Rayner, J. (1994) Cretaceous weevils from southern Africa, with description of a new genus and species and phylogenetic and zoogeographical comments (Coleoptera: Curculionoidea). *Ent. scand.* 25: 137-149.
- Lacordaire, J. T. (1863) *Histoire naturelle des insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes*. Vol. 6: 1-608, 615-637. Paris.
- Lacordaire, J. T. (1866) *Histoire naturelle des insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes*. Vol. 7: 1-620. Paris.
- Lawrence, J. F. (1991) Order Coleoptera. In Stehr (Ed.): *Immature insects*, Vol. 2: 144-298. Kendall/Hunt Publishing Company, Dubuque, Iowa.
- Lawrence, J. F. & Newton, A. F. (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In Pakaluk & Slipinski (Ed.): *Biology, phylogeny, and classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson*, Vol. 2: 778-1006. Muzeum i Instytut Zoologii PAN, Warszawa, Poland.
- Louw, S. (1986) Revision of the Microcerinae (Coleoptera: Curculionidae) with an analysis of their phylogeny and zoogeography. *Mem. natn. Mus. Bloemfontein* 21: 1-331.
- Louw, S. (1995) Systematics and biogeography of the subfamily Microcerinae (Coleoptera: Curculionidae): A re-evaluation based on larval morphology. *Mem. ent. Soc. Wash.* 14: 169-174.
- Lyal, C. H. C. (1995) The ventral structures of the weevil head (Coleoptera: Curculionoidea). *Mem. ent. Soc. Wash.* 14: 169-174.
- Lyal, C. H. C. & King, T. (1996) Elytro-tergal stridulation in weevils (Insecta: Coleoptera: Curculionoidea). *J. Nat. Hist.* 30: 703-773.
- Marvaldi, A. E. (1997) Higher level phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. *Cladistics* 13: 285-312.
- Marvaldi, A. E. (1998) Larvae of Entiminae (Coleoptera: Curculionidae): Tribal diagnoses and phylogenetic key, with a proposal about natural groups within Entimini. *Ent. scand.* 29: 89-98.
- Marvaldi, A. E. (In press a) Morphologic characters of the immature stages of *Ocladius dianthi* Marshall (Coleoptera: Curculionidae: Ocladiinae), with phylogenetic implications. *Coleopt. Bull.* 54.
- Marvaldi, A. E. (In press b) Morfología larval en Curculionidae. *Acta zool. lilloana* 45.
- May, B. M. (1993) Larvae of Curculionoidea (Insecta: Coleoptera): A systematic overview. *Fauna N. Z.* 28: 1-221.
- May, B. M. (1994) An introduction to the immature stages of Australian Curculionoidea. In Zimmerman's: *Australian weevils*, Vol. 2: 365-755. Melbourne, CSIRO.
- Monrós, F. (1955) *Megalopus jacobyi*, nueva plaga de solanáceas en el noroeste argentino, con notas sobre biología y taxonomía de Megalopodinae (Col., Chrysomelidae). *Revta agron. NE Argent.* 1: 167-179.
- Morimoto, K. (1962a) Comparative morphology, phylogeny and systematics of the superfamily Curculionoidea of Japan I. *J. Fac. Agric. Kyushu Univ.* 11: 331-373.
- Morimoto, K. (1962b) Key to families, subfamilies, tribes and genera of the superfamily Curculionoidea of Japan excluding Scolytidae, Platypodidae and Cos-

- soninae. *J. Fac. Agric. Kyushu Univ.* 12: 21-66.
- Morimoto, K. (1976) Notes on the family characters of Apionidae and Brentidae (Coleoptera), with key to the related families. *Kontyû* 44: 469-476.
- Morimoto, K. (1978) Checklist of the family Rhynchophoridae (Coleoptera) of Japan, with descriptions of a new genus and five new species. *Esakia* 12: 103-118.
- Morimoto, K. (1981) Functional morphology and phylogeny of the superfamily Curculionoidea (Coleoptera). Part 1. The mouth parts. *Akitu* (N.S.) 34: 1-10.
- Morrone, J. J. (1996) Austral biogeography and relict weevil taxa (Coleoptera: Nemonychidae, Belidae, Brentidae, and Caridae). *J. comp. Biol.* 1: 123-127.
- Morrone, J. J. (1997a) Argentinean weevils (Coleoptera: Curculionoidea): Preliminary overview, with nomenclatural and distributional notes. *Physis B. Aires* (C) 53: 1-17.
- Morrone, J. J. (1997b) Nomenclatural notes on the subfamily Cyclominae (Coleoptera: Curculionidae). *Acta ent. chil.* 21: 101-102.
- Morrone, J. J. (1998a) The impact of cladistics on weevil classification, with a new scheme of families and subfamilies (Coleoptera: Curculionoidea). *Trends Ent.* 1 (1997): 129-136.
- Morrone, J. J. (1998b) Sinopsis genérica de las Cyclominae argentinas (Coleoptera: Curculionidae). *Neotropica* 44: 13-22.
- Muñiz, R. (1970) Relación entre taxonomía y tipos de vida en Curculionidae. *An. Esc. nac. Cienc. biol. Méx.* 17: 169-187.
- Nixon, K. C. (1992) *Clados, version 1.2. Program and documentation*. Trumansburg, New York.
- Osella, G. (1977) Revisione della sottofamiglia Raymondionyminae. *Memorie Mus. civ. Stor. nat. Verona* (11) 1: 1-162.
- Pascoe, F. P. (1870) Contributions towards a knowledge of the Curculionidae. *J. Linn. Soc. (Zool.)* 10: 434-493.
- Reid, C. A. M. (1995). A cladistic analysis of subfamilial relationships in the Chrysomelidae s.lat. (Chrysomeloidea). In Pakaluk & Slipinski (Ed.): *Biology, phylogeny and classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson*, Vol. 2: 559-631. Muzeum i Instytut Zoologii PAN, Warszawa, Poland.
- Sanborne, M. (1981) Biology of *Ithycerus noveboracensis* (Forster) (Coleoptera) and weevil phylogeny. *Evolut. Mon.* 4: 1-80.
- Sharp, D. (1889-1911) Insecta. Coleoptera. Rhynchophora. Curculionidae. Attelabinae, Pterocolinae, Allocoryninae, Apioninae, Thecesterninae, Otiorynchinae. *Biologia cent.-am.* 4 (3): 1-40 (1889); 41-80 (1890a); 81-168 (1891a); 169-178 (1911).
- Schoenherr, C. J. (1823) Tabula synoptica familiae curculionidum. *Isis, Jena* 7: 1132-1146.
- Schoenherr, C. J. (1826) *Curculionidum dispositio methodica cum generum characteribus, descriptionibus atque observationibus variis, seu prodrromus ad synonymiae insectorum*. Pt. 4. Fleischer, Lipsiae.
- Schoenherr, C. J. (1833-1845) *Genera et species curculionidum, cum synonymia hujus familiae*. Vol. 1-8. Paris.
- Schoenherr, C. J. (1847) *Mantissa secunda familiae curculionidum. Seu descriptiones novorum quorundam generum curculionidum*. 86 pp. Holmiae.
- Thompson, R. T. (1992) Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. *J. Nat. Hist.* 26: 835-891.
- Vanin, S. A. (1976) Taxonomic revision of the South American Belidae (Coleoptera). *Archos Zool. S. Paulo* 28: 1-75.
- Voss, E. (1932) Monographie der Rhynchitinen-Tribus Rhinomacerini und Rhynorhynchini. *Ent. Bl. Biol. Syst. Käfer* 18: 153-189.
- Wibmer, G. J. & O'Brien, C. W. (1986) Annotated checklist of the weevils (Curculionidae s.lat.) of South America (Coleoptera: Curculionoidea). *Mem. Am. ent. Inst.* 39: 1-563.
- Wood, S. L. (1986) A reclassification of the genera of Scolytidae (Coleoptera). *Gt Basin Nat. Mem.* 10: 1-126.
- Wood, S. L. (1993) Revision of the genera of Platypodiidae (Coleoptera). *Gt Basin Nat.* 53: 259-281.
- Zherikhin, V. V. & Gratshev, V. G. (1993) Obrieniidae, fam. nov., the oldest Mesozoic weevils (Coleoptera, Curculionoidea). *Paleont. Zh.* 27: 50-69.
- Zherikhin, V. V. & Gratshev, V. G. (1995) A comparative study of the hind wing venation of the superfamily Curculionoidea, with phylogenetic implications. In Pakaluk & Slipinski (Ed.): *Biology, phylogeny and classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson*, Vol. 2: 633-777. Muzeum i Instytut Zoologii PAN, Warszawa, Poland.
- Zimmerman, E. C. (1992) *Australian weevils*. Vol. 6. Colour plates 305-632. Melbourne, CSIRO.
- Zimmerman, E. C. (1993) *Australian weevils*. Vol. 3. Nanophyidae, Rhynchophoridae, Erihniidae, Curculionidae: Amycterinae, literature consulted. Melbourne, CSIRO.
- Zimmerman, E. C. (1994a) *Australian weevils*. Vol. 1. Orthoceri: Anthribidae to Attelabidae. Melbourne, CSIRO.
- Zimmerman, E. C. (1994b) *Australian weevils*. Vol. 2. Brentidae, Eurhynchidae, Apionidae and a chapter on immature stages by Brenda May. Melbourne, CSIRO.
- Zimmerman, E. C. & Perrault, G. (1989) Aglycyderidae of the Society Islands (Coleoptera: Curculionoidea). *Occ. Pap. Bernice P. Bishop Mus.* 29: 151-173.